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Habitat selection of seabirds in a highly dynamic coastal sea: temporal variation and influence of hydrographic features

Dissertation

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Summary

In the German Bight (south-eastern North Sea), recent high efforts of at-sea studies have led to an increasing knowledge of key hotspots and general distribution patterns of the most common seabird species. Distribution patterns were shown to undergo temporal variation, in particular at the order of seasons. So far, less attention was paid to variability of distribution patterns at smaller time scales. Variability of seabird distribution complicates conservation and management efforts as it constrains the ecological evaluation of specific areas, the calculation of total numbers, and the assessment of population trends or shifts in distribution. The next step on our way to a thorough picture of the life of seabirds at sea has thus to be the understanding of factors and processes driving the observed patterns. This thesis consequently focused on habitat choice of seabirds in the German Bight and on temporal variability of seabird distribution patterns. Study objectives were addressed by analysing dedicated seabirds at sea surveys and long-term survey data.

Small scale temporal variability of seabird distribution patterns was found to be substantial at the order of days. However, several factors and mechanisms influencing distribution patterns and their temporal variation at the order of seasons and days were identified. A significant influence was revealed for large scale hydrographic structures, i.e. water masses, small scale hydrographic structures such as fronts, tidal stage, wind speed and fishing activity. Most of these factors represent direct or indirect indicators of food availability for seabirds. The connecting link between hydrographic features and seabird distribution was addressed in one case study dealing with the diet of Black-legged Kittiwakes *Rissa tridactyla* in the study area. Their main prey was found to be juvenile Whiting *Merlangius merlangus*. These fish concentrate in frontal areas of the North Sea. Accordingly, Kittiwakes showed a significant association with fronts in the German Bight in summer. Habitat choice is additionally influenced by the presence of other individuals. Results of this thesis implied a significant influence of intraspecific competition on seabird distribution. Seasonally differing distribution patterns of seabirds were paralleled by seasonal differences in habitat choice, comprising both differences in the quality and the strength of habitat bonds. No obvious contrasts in habitat preferences were found between winter and summer surveys but habitat bonds varied in strength. Seasonality of habitat choice was explained by seasonally varying food availability and by differing demands of birds. Analyses of seasonal differences in at-sea activity of seabirds e.g. implied significantly higher demands of birds during the breeding season.

The information derived in this thesis contributes to our understanding of seabird habitat choice at sea and provides the basis for the design of future monitoring programmes and conservation measures.

Zusammenfassung

In der Deutschen Bucht (südöstliche Nordsee) konnte in den letzten Jahren durch intensive Studien auf See eine verbesserte Kenntnis der Verbreitungsschwerpunkte und der generellen Verteilungsmuster für die häufigsten Seevogelarten gewonnen werden. Es konnte gezeigt werden, dass die Verteilungsmuster zeitlich variieren, insbesondere auf der Ebene der verschiedenen Jahreszeiten. Der Variabilität von Verteilungsmustern auf geringerer zeitlicher Ebene wurde bisher jedoch weniger Aufmerksamkeit geschenkt. Die Variabilität von Seevogelverteilungsmustern erschwert Naturschutz- und Managementmaßnahmen, da sie die ökologische Bewertung von Gebieten, die Bestandsberechnung und die Erfassung von Bestandstrends und Bestandsverlagerungen beeinträchtigt. Der nächste Schritt zu einem umfassenden Bild der Biologie von Seevögeln auf See muss deshalb das Verständnis der für die beobachteten Muster verantwortlichen Faktoren und Prozesse sein. Im Fokus dieser Doktorarbeit stand deshalb die Habitatwahl von Seevögeln in der Deutschen Bucht und die Variabilität von Seevogelverbreitungsmustern auf geringer zeitlicher Ebene. Um diese Ziele zu erreichen, wurden Seabirds at Sea Daten von Spezialreisen und Langzeituntersuchungen ausgewertet.

Insgesamt wurde ein erhebliches Ausmaß kleinskaliger zeitlicher Variabilität nachgewiesen. Es wurden jedoch verschiedene Faktoren und Prozesse identifiziert, die einen Einfluss auf die Verteilungsmuster und deren zeitliche Variabilität auf der Ebene von Jahreszeiten und Tagen haben. Ein signifikanter Einfluss wurde für großskalige hydrographische Strukturen (Wassermassen), kleinskalige hydrographische Strukturen (Fronten), den Gezeitenzyklus, die Windgeschwindigkeit und die Fischereiaktivität nachgewiesen. Die meisten dieser Faktoren stellen direkte oder indirekte Zeiger für die Nahrungsverfügbarkeit für Seevögel dar. Die Verbindung zwischen hydrographischen Strukturen und der Verbreitung von Seevögeln wurde in einer Fallstudie zur Nahrung der Dreizehenmöwen *Rissa tridactyla* im Untersuchungsgebiet untersucht. Die Hauptbeute, junge Wittlinge *Merlangius merlangus*, sammelt sich in Frontengebieten der Nordsee. In Übereinstimmung damit wurde eine signifikante Assoziation von Dreizehenmöwen mit Fronten der Deutschen Bucht im Sommer festgestellt. Zusätzlich wird die Habitatwahl von der Anwesenheit anderer Individuen der gleichen Art beeinflusst. Verschiedene Ergebnisse in dieser Doktorarbeit lassen auf einen signifikanten Einfluss von intraspezifischer Konkurrenz auf die Verteilung von Seevögeln schließen. Mit saisonal variierenden Verteilungsmustern von Seevögeln gehen Unterschiede in der Habitatwahl zwischen verschiedenen Jahreszeiten einher, die sowohl Unterschiede in der Qualität als auch der Stärke der Habitatbindungen umfassen. Offenkundige Gegensätze in Habitatpräferenzen wurden dabei nicht festgestellt, jedoch variierte die Stärke der Habitatbindungen. Die Saisonalität der

Habitatwahl wurde zum Einen durch jahreszeitliche Variationen in der Nahrungsvfügbarkeit und zum Anderen durch unterschiedliche Ansprüche der Vögel erklärt. Eine Analyse der jahreszeitlichen Unterschiede in der Aktivität von Seevögeln auf See ließ auf einen signifikant höheren Energiebedarf während der Brutzeit schließen.

Die im Rahmen dieser Doktorarbeit erworbenen Kenntnisse tragen zum Verständnis der Habitatwahl von Seevögeln auf See bei und bilden die Basis für die Entwicklung zukünftiger Monitoringprogramme und Naturschutzmaßnahmen.

1 General Introduction and Methods

1.1 Scientific background

In the south-eastern North Sea, the German Bight, recent high efforts of at-sea studies have led to increasing knowledge of key hotspots and general distribution patterns of the most common and characteristic seabird species (Garthe et al. 2003*b*, Garthe and Schwemmer 2005). Distribution patterns were shown to undergo temporal variation at various scales. Pronounced differences were in particular revealed at the order of seasons as depicted in the example of the Black-legged Kittiwake *Rissa tridactyla* (Fig. 1.3). So far, less attention was paid to variability of seabird distribution patterns at smaller temporal scales, e.g. at the order of weeks, days and hours. However, small and meso scale variability can be substantial, thus constraining explanatory power of mean distribution patterns. Variability of seabird distribution patterns consequently complicates conservation and management efforts as it constrains (a) the ecological evaluation of specific areas, (b) the calculation of total numbers, and (c) the assessment of population trends or shifts in distribution. The next step on our way to a thorough picture of the life of seabirds at sea has thus to be the understanding of processes driving the observed patterns (Hunt 1990, Shealer 2002). A comprehensive knowledge of the factors and mechanisms influencing seabird distributions will enable us (a) to evaluate results of past and future studies on seabird distribution patterns, e.g. by assessing the importance and stability of observed concentrations, (b) to predict distribution patterns of seabirds, (c) to design monitoring programmes focusing on changes in distribution and numbers, (d) to evaluate consequences of anthropogenic impacts and (e) to set up appropriate conservation measures.

This thesis consequently focused on the habitat choice of seabirds at sea in the German Bight in order to reveal the environmental characteristics that cause and drive distribution patterns and their variation in time and space. Special emphasis was laid on hydrography as this factor proved to be a key determinant of seabird distribution in many studies all over the world (for reviews see Brown 1980, Hunt and Schneider 1987, Haney and Solow 1992) as well as in the North Sea (e.g. Garthe 1997, Skov and Durinck 2000). Hydrography represents the major physical aspect of the marine habitat of seabirds. It forms the living conditions for prey organisms of seabirds and can thus be used as an indicator for prey availability. Thus, an association of a specific seabird species to a particular water mass can be explained by the occurrence of a preferred prey

organism that is linked to this water mass. In the German Bight, this link between hydrography and the distribution of seabirds was so far not studied in situ and assumptions based on literature only could be made regarding the underlying causes for the association of seabirds to different hydrographic structures (see e.g. Garthe 1996, chapter 5.4.2, page 83). Sampling of the abundance of seabird prey organisms such as fish and zooplankton however was not possible within the scope of this thesis. However, information on the link between hydrography and seabirds may also be derived by studying diet composition of seabirds. Knowledge of habitat choice of the prey organisms consumed can thus infer information on the foraging area of the bird.

Like the marine environment in general, hydrography is characterised by strong heterogeneity at different scales of space and time. Patterns of seabird distribution and abundance thus emerge at various scales reflecting the influence of different oceanographic features and processes affecting prey availability of seabirds (Hunt and Schneider 1987). An important property of oceanographic structures is a positive relation between space and time such that large structures remain relatively stable while a decreasing size generally is connected to a decreasing longevity (Stommel 1963, Haury et al. 1978). Thus, a link of seabird occurrence to smaller habitat features implies also temporal variation of seabird distribution patterns at smaller time scales.

In the German Bight, the distribution of several seabird species was shown to correlate significantly with the occurrence of the two main water masses (Garthe 1997) which represent large scale hydrographic structures within this area. Overall, an association of seabirds to small short-lived hydrographic structures has been seldom revealed and most seabird-hydrography associations refer to large stable structures such as water masses and shelf-break fronts. To my knowledge, the correlation of the distribution of Black-throated *Gavia arctica* and Red-throated Divers *G. stellata* with fronts in the river Elbe outflow region of the German Bight (Skov and Prins 2001) so far represents the only documentation world-wide that describes a significant influence of river plume fronts on seabird distribution. It is worthwhile to study the effect of small scale hydrographic structures in the German Bight as the hydrography in this area is characterised by very high variability both in time and space (Becker and Prahm-Rodewald 1980). Dominant hydrographic structures comprise two different water masses and different fronts which vary in extent, strength and longevity (see chapter 1.3.1, page 4). With the exception of the study mentioned above, an influence of these different types of fronts on the distribution of seabirds in the German Bight was so far not studied in detail.

Moreover, an extensive analysis of the relation between hydrography and seabird distribution in the German Bight comprising all common seabird species was only carried out for the influence of water masses during summer (Garthe 1997). The correlation of divers with estuarine fronts on the other hand was tested with a dataset comprising surveys from October to May (Skov and Prins 2001) and thus the main period of their presence in the study area. Except for these species, no information so far existed on habitat choice of seabirds outside the summer period. However, habitat choice of birds may vary substantially between seasons due to differing demands of birds and varying

habitat quality.

In general, the habitat of a species or individual is chosen to enhance survival and/or increase reproductive success (Salewski and Bruderer 2007). Proximate factors controlling habitat choice are the structure of the landscape, resources for foraging or reproduction and the presence of other individuals which represent e.g. competitors, predators or providers of information and resources (Bezzel and Prinzinger 1990). These factors however undergo temporal variation, e.g. in the form of vegetation growth in terrestrial habitats, depletion of resources, migration and reproduction of competitors, predators and prey organisms. In consequence, habitat quality is not stable over time and thus forces individuals to alter habitat choice in reaction to this variation.

Moreover, different life stages and seasons impose differing demands on individuals. A typical migrating bird species e.g. has to select for different habitats throughout the annual cycle. During the breeding season, birds choose their habitat e.g. according to the presence of suitable nesting sites, the level of competition and predation, and the availability of food resources enabling self-provisioning and chick-rearing. During migration, birds have to select for stop-over sites enabling fast refuelling, while wintering or staging areas have to be selected to increase survival. Thus, the same habitat can be expected to play a different role for a particular seabird species throughout the annual cycle. The German Bight is inhabited by several species which occur in relatively high numbers throughout the year (Garthe et al. 2007). Differing total numbers and differing distribution patterns imply a seasonally varying role of this region for these species. An analysis of habitat choice in the different seasons can be expected to contribute to our understanding of the observed differences.

1.2 Study objectives and Chapter outline

This thesis aimed at filling important gaps described above. In consequence, the following study objectives were derived:

- (1) Habitat choice was studied by identifying factors controlling and shaping seabird distribution patterns in the German Bight. Special emphasis was placed on hydrographical features, in particular the **influence of small scale structures such as fronts** (chapter 2, page 13).
- (2) Diet composition of a key study species, the Black-legged Kittiwake, was analysed to gain information on the **link between hydrography and seabird distribution** (chapter 3, page 27).
- (3) Several case studies were combined to assess the extent of **temporal variability of seabird distribution patterns at smaller scales** (weeks, days, hours) and to identify possible controlling environmental factors (chapter 4, page 49).
- (4) **Variability of habitat choice** was studied with respect to seasonally differing habitat preferences and strength of habitat-seabird relationships (chapter 5, page 71). Seasonality of habitat choice is driven by varying habitat quality and by varying demands of birds. In this context, I studied seasonality of seabird activity to infer information on the differing demands (chapter 6, page 89).

1.3 General Material and Methods

1.3.1 Study area

Hydrography

The German Bight is a shallow shelf sea region of the south-eastern North Sea and is defined here as the area between 53.35° and 55.2° N and 4.4° to 9.2° E (Fig. 1.1). Apart from the pelagic offshore region it includes extensive Wadden Sea areas and tidally influenced estuaries of several large rivers like Elbe and Weser, covering on the whole about 50,000 km². The hydrographic situation is characterised by tidal currents and substantial gradients in salinity that are formed by the encounter of different water bodies. Generally, two distinct water masses are known in the German Bight. The Continental Coast water mass is characterised by low salinity and low transparency whereas the Central North Sea water mass can be identified by high salinity, high transparency and a stratification in summer (Becker et al. 1983). Throughout the year, a haline stratification occurs in the area of the Elbe river plume, where fresh water forms a layer on the specifically heavier, highly saline North Sea water. On a horizontal scale, three different

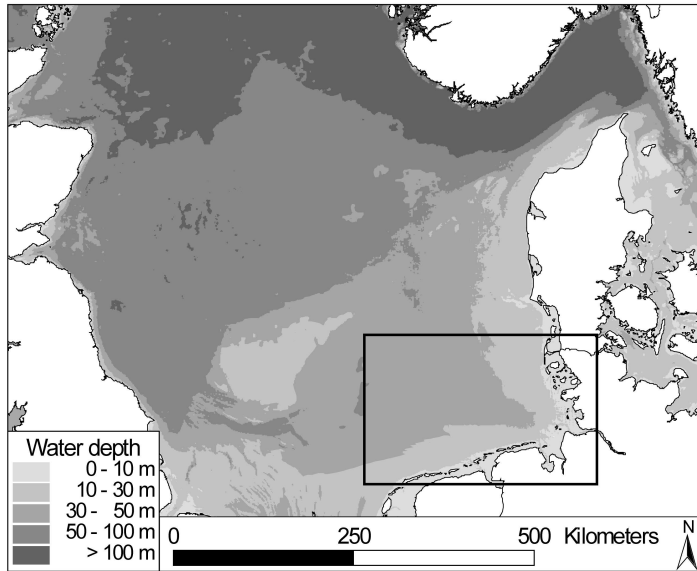


Figure 1.1: Location of the German Bight in the North Sea.

types of fronts can be identified in the German Bight (Krause et al. 1986): Firstly, a tidal mixing front forms the boundary between stratified and tidally mixed water along the southern part of the area during summer. Secondly, certain wind conditions can lead to an ephemeral upwelling of North Sea bottom water in the post-glacial Elbe valley that forms a distinct frontal boundary to the surrounding medium. Krause et al. (1986) who studied upwellings in the post-glacial Elbe valley found highest concentration of planktonic organisms at such fronts. Thirdly, in the eastern part of the area, strong salinity gradients and fronts are formed by the encounter of the Elbe river plume and adjacent North Sea waters. Fronts in the Elbe estuary are known to act as a barrier between different plankton communities (Gerdes 1985, Krause et al. 1986, Hesse et al. 1989a) and as a region of biomass accumulation (Hesse et al. 1989a,b). The concentration of prey attracts predators like fish larvae and fishes (Valenzuela et al. 1991) and thereby also larger predators such as planktivorous or piscivorous seabirds. These predictable prey aggregations are believed to be the cause for the strong correlation of Red- and Black-throated Divers with the estuarine frontal system of the Elbe river plume (Skov and Prins 2001).

Weather conditions and tides have a particular strong influence on the hydrography of the German Bight due to the low water depth, leading to high variability in time and space (Becker and Prahm-Rodewald 1980, Dippner 1993).

Seabird community

In the German Bight, few of the regularly occurring seabird species can be termed ‘true’ seabirds. Especially during the summer months, the avifauna of the German Bight is dominated by gulls and terns. Solely Northern Gannet *Sula bassana*, Northern Fulmar *Fulmarus glacialis*, Black-legged Kittiwake and Common Guillemot *Uria aalge* represent true offshore species in the study area (Garthe et al. 1995). Within the study area, these species occupy a single breeding colony on the rocky island of Helgoland (54°11’N, 7°53’E). Due to distances of several hundred kilometres to other breeding sites, these species presumably face comparatively low intraspecific and interspecific competition and virtually no overlap of foraging ranges and areas with that of other seabird colonies. The majority of seabird species in the south-eastern North Sea consists of surface feeders such as gulls (Laridae) and terns (Sternidae), pursuit divers as auks (Alcidae) and divers (*Gavia* spp.) or plunge divers like the Northern Gannet. Most seabird species of the German Bight are piscivorous (Camphuysen 1996) or omnivorous. Exceptions comprise the benthivorous diving ducks which feed predominantly on bivalves. Overall, diet composition of seabirds comprises mainly fish, crustaceans, polychaetes, molluscs and anthropogenic food sources such as fisheries discards.



Figure 1.2: The Black-legged Kittiwake *Rissa tridactyla*. Photo: N. Guse.

1.3.2 The Black-legged Kittiwake

This thesis aimed at assessing relevant aspects of habitat choice and of temporal variability in distribution patterns for *all* common seabird species of the German Bight. However, one species, the Black-legged Kittiwake (Fig. 1.2), qualified for the analysis of all these objectives and thus will be treated in more detail.

The Black-legged Kittiwake (hereafter ‘Kittiwake’) is the only common gull species which

is characterised by a truly pelagic mode of life. It is a small gull with a body size comparable to the Black-headed Gull *Larus ridibundus* and the Common Gull *L. canus*. The Kittiwake is a cliff-nesting species breeding circumpolar on islands and along coasts of the arctic to temperate zone of the northern hemisphere (Lloyd et al. 1991). In the German Bight, it breeds in a single colony of approximately 7,500 apparently occupied nests (AON) on Helgoland. This breeding site was re-colonised in 1938 after an absence of 100-150 years which was most probably due to an intensive human persecution (Drost 1938, Fleet 1984). Breeding numbers were regularly monitored since 1952 (Hüppop 1997). A detailed description of the population trend is given in chapter 3.2.1 on page 29. The re-colonisation of the breeding colony at Helgoland coincides with a general expansion of the distribution area to the South and the establishment of colonies e.g. in southern Sweden, Denmark, France, Spain and Portugal (Lloyd et al. 1991, BWPi 2004). Important breeding sites are located along the coasts of Scandinavia and the British Isles. These colonies however suffered substantial declines in breeding numbers over the last years, connected to a low breeding success apparently caused by low food availability (Frederiksen et al. 2004, see chapter 3.1, page 28).

Kittiwakes are mainly piscivorous, feeding to a substantially higher amount on fish than all other gull species of the German Bight (Prüter 1986). The Kittiwake is a surface-feeder and thus restricted to prey concentrations at the sea surface. Consequently, it is dependent on mechanisms aggregating prey at the surface, e.g. tidally induced currents (Irons 1998), or predators that drive prey up to the surface such as diving seabirds (Harrison et al. 1994, Camphuysen and Webb 1999). A strong association with certain hydrographic structures aggregating biomass at the sea surface can therefore be predicted for Kittiwakes.

Next to its dependence on prey aggregations at the sea surface, several other characteristics of this species contributed to its important role in this thesis. Kittiwakes are numerous in the German Bight throughout the year (Garthe et al. 2007). They are truly pelagic and feed exclusively at sea. In contrast, all other gull species of the German Bight forage at least partly in terrestrial habitats or on the mud flats of the Wadden Sea region. Kittiwakes are highly visible and observations concerning the foraging behaviour of this species can easily be made from ships due to its surface-feeding behaviour. On the other hand, little information can be gained on the foraging behaviour of diving species such as Common Guillemots during ship-based studies. Unlike Northern Gannets which travel up to several hundred kilometres within a single foraging trip (Hamer et al. 2001), Kittiwakes exhibit maximum foraging ranges of 80 km (Camphuysen 2005) during the breeding season and thus do not leave the study area within single foraging trips. The distribution pattern of Kittiwakes varies seasonally with a rather uniform distribution in winter and concentrations in the vicinity of the breeding colony and along the post-glacial river Elbe valley in summer (Fig. 1.3).

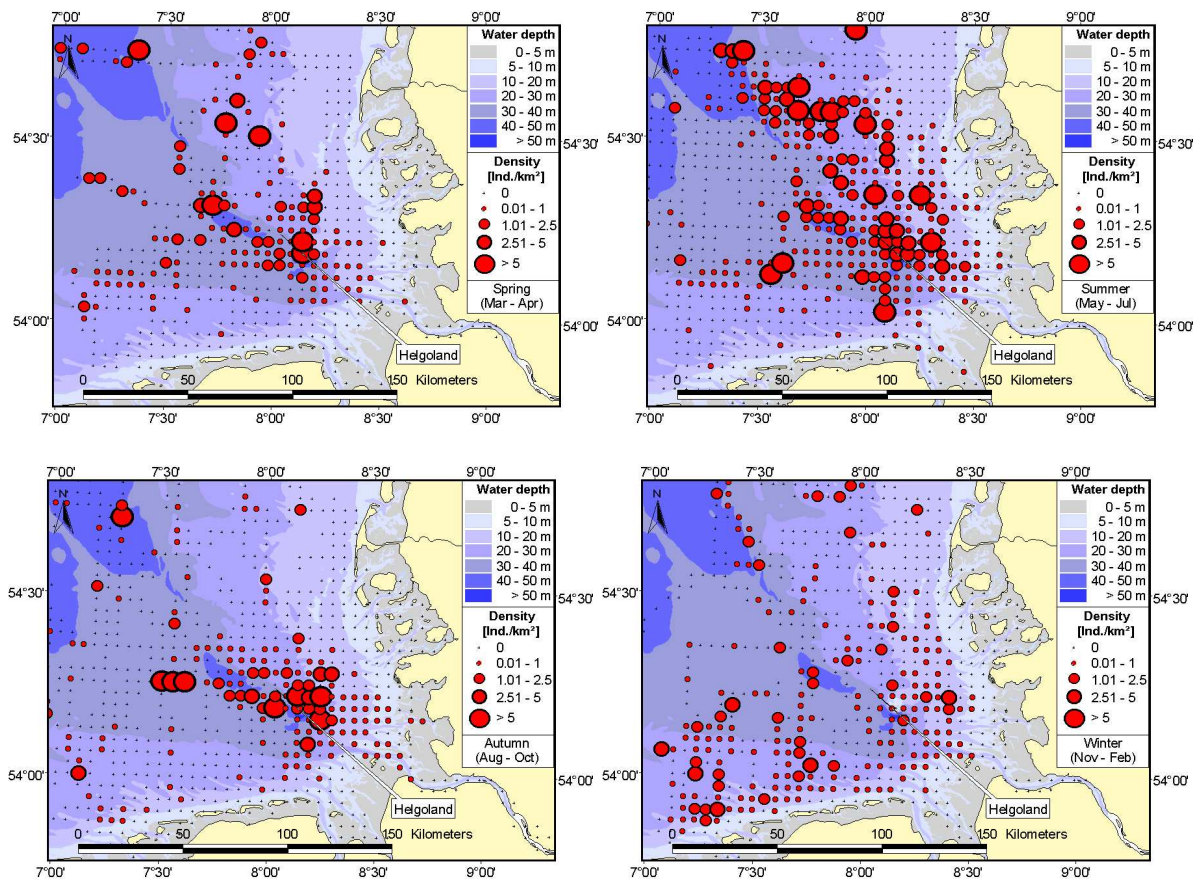


Figure 1.3: Seasonal variation in distribution patterns of Black-legged Kittiwakes in the German Bight as recorded during ship-based studies (1990-2006, German Seabirds at Sea database v5.07).

1.3.3 Methodology for studying seabirds at sea

An assessment of the influence of hydrographic structures on seabird distribution and an analysis of habitat choice of seabirds in general is constrained by the dynamics and the relative inaccessibility of their marine habitats. The majority of data on the biology of seabirds was collected in breeding colonies and thus in the short period the birds are bound to stay on land. However, most seabirds spend the majority of their life at sea (Ainley 1980) where they often cover distances of hundreds to thousands of kilometres in search for food (e.g. Weimerskirch et al. 1993). Thus, most seabirds are highly mobile while seabird researchers focusing on the at-sea aspects of the biology of seabirds are bound to use observation platforms like ships and aircrafts which cover limited parts of the sea area. Moreover, an application of both ships and airplanes is strongly constrained by weather conditions that influence both observation conditions and secure manoeuvrability of platforms. An alternative way to study habitat choice of seabirds at sea is by

using the birds themselves as sampling platforms. The development of telemetry and remote-sensing logger technology has enabled detailed studies of individual foraging behaviour, especially with respect to diving birds (e.g. Benvenuti et al. 2001, Garthe et al. 2003a, Ropert-Coudert et al. 2004). Fine scale analyses of seabird habitat use were recently made possible by the incorporation of Global Positioning Systems (GPS; Petersen et al. 2006, Weimerskirch 2007). Various sensor types moreover enable sampling of physiology and behaviour of birds and of environmental parameters, thus providing information on the oceanic habitat of the species studied (reviewed in Ropert-Coudert and Wilson 2005).

However, logger methodology is less suited for the topic of this thesis due to various reasons. Birds have to be captured for the attachment of devices and in addition mostly need to be recaptured to retrieve devices and download data. Consequently, most studies focus on chick-rearing birds which regularly return to the same site on land. So far, only few studies took place during the non-breeding season or concerned non-breeding birds (but see Croxall et al. 2005, Daunt et al. 2006). Moreover, handled birds carrying extra weight might not behave ‘normally’. Thus, logger studies are at risk to produce unrepresentative or biased results (e.g. Ropert-Coudert and Wilson 2004). Furthermore, data storage and energy supply has to be traded off against weight and size of devices. Thus, in particular long-term studies are restricted to larger species such as albatrosses, gannets and cormorants (e.g. Croxall et al. 2005, Daunt et al. 2006). Moreover, sample sizes are generally low.

In contrast, ship-based or aerial seabirds at sea-studies may comprise observations of a substantial part of the local population of all common seabird species, thus enabling also comparisons between species and inter-specific associations. Moreover, survey efforts may be equally applied to all different seasons although weather conditions admittedly impose higher restrictions during winter. Furthermore, survey data comprise presence as well as absence data of certain species while logger data produce presence data of single individuals only. Finally, seabirds at sea counts are highly suitable for the evaluation of specific areas and thus qualify over logger studies with respect to this study objective as logger birds can not be ‘programmed’ to use a specific region. Thus, the influence of specific hydrographic structures on seabird distribution can be studied well by conducting ship-based surveys covering the different hydrographic features. In conclusion, surveys conducted from observation platforms were regarded highly suitable for the study aims of this thesis, in particular as the German Bight is not too large for being covered by ship-based and aerial surveys.

Ship-based surveys

Seabird surveys followed the internationally standardised ‘Seabirds at Sea’ method as described by Tasker et al. (1984), Webb and Durinck (1992) and Garthe et al. (2002). The occurrence of birds was recorded within a 300 m wide transect running parallel to the keel line of the observation platform. Swimming birds were counted continuously

whereas flying individuals were recorded using the ‘snapshot’ method (Tasker et al. 1984) to correct for overestimation of particularly mobile species.

Densities of all species were obtained by correcting for undetected birds away from the centreline through use of the distance-sampling methodology developed by Buckland et al. (1993) and by applying functions available in the DISTANCE software package (Laake et al. 1993). This method implied the multiplication of numbers of swimming birds within the observation transect by species-specific correction factors adopted from Garthe et al (2007).

Ship-based studies are highly suitable to study habitat affinities of seabirds as environmental parameters such as hydrography can be sampled simultaneously along with seabird counts. While the influence of meso scale hydrographic structures can be assessed by use of satellite imagery (Brown 1988), the coupling of seabird distribution patterns with small scale short-lived structures can only be achieved by simultaneous in situ measurements. Furthermore, ship-based studies allow the assessment of detailed data on seabird behaviour (Camphuysen and Garthe 2004) which enable the identification of habitats representing a specific function, e.g. foraging areas and migration corridors (Schwemmer and Garthe 2006).

The German ‘Seabirds at Sea’ programme started in July 1990 carrying out ship-based studies in the German Bight (Garthe and Hüppop 1996, 2000) which were later complemented by studies in the German Baltic Sea (Garthe et al. 2002). Data are stored in the German Seabirds at Sea database coordinated by S. Garthe, FTZ Büsum. Analyses of this thesis based on data extracted from this database, e.g. dedicated cruises (see chapters 2 and 5, page 13 and 71, respectively) and data comprising surveys from 1990 to 2006 (e.g. chapter 4, page 49). The latter were also used to analyse long-term trends in seabird activity (chapter 6, page 89). Further data were assessed during dedicated cruises in the course of this thesis (e.g. chapter 4, page 49) which were incorporated in the German Seabirds at Sea database.

Aerial surveys

Aerial surveys followed standardised methods described by Kahlert et al. (2000) and Diederichs et al. (2002). Surveys were performed from a high winged twin-engine Partenavia P-68 provided with bubble windows at a flight altitude of 78 m (250 feet) and a cruising speed of circa 185 km/h (100 knots). The occurrence of birds was recorded within 397 m wide transects running parallel to the flight route of the observation platform. Under good observation conditions, both sides of the flight route could be covered by two trained observers, resulting in a survey transect of 794 m. All birds were recorded to the second giving details on species, number, and activity.

Aerial surveys enable the sampling of large areas within relatively short time periods and thus may depict a ‘snapshot’ of distribution patterns. The German part of the North Sea thus can be covered within 4-5 single survey days. As ships move at a speed approximately 10 times below that of survey planes, sampling time of the same area would be

substantially longer. Thus, the sampling speed of ships is of the same order as the relevant time scale of variation in seabird distributions. Consequently, temporal variation of large scale seabird distribution patterns at the order of single days can not be assessed in the course of ship-based surveys. However, aerial surveys are more restricted by weather conditions as good observation conditions in the offshore regions are only reached during wind speeds < 10 knots (≤ 3 Bft) and sea state < 3 . Whitecaps occurring at sea state 3 and above constrain the detectability especially of swimming birds substantially. Thus, even Northern Gannets which are generally very conspicuous due to their large size and predominantly white plumage may be missed during sea state 4 (pers. observation). Moreover, identification of species is difficult due to the high speed of the observation platform which does not allow the use of binoculars. Thus, observations are made with the naked eye and identification has to be achieved within the few seconds a bird is within the field of vision. Thus, similar species can be distinguished with a lower probability when compared to ship-based studies. Moreover, identification to species level is in particular constrained in case of large flocks, e.g. gulls, Gannets and Fulmars scavenging at fishing vessels or large aggregation of sea ducks (Garthe et al. 2004). Additionally, observations on age according to plumage differences and on behaviour of birds can only be made exceptionally. A comprehensive comparison of advantages and disadvantages and suitable applications of both methods, ship-based and aerial surveys, is given by Garthe et al. (2004).

In German waters, aerial surveys started in 2002. Data are stored in the German Seabirds at Sea database (see above). Within this thesis, aerial surveys were applied to assess small scale temporal variability of distribution patterns (chapter 4, page 49). Moreover, data from aerial surveys were chosen to analyse differences in seabird activity between different seasons due to the higher homogeneity of this dataset in comparison to the dataset of ship-based surveys (chapter 6, page 89).

2 Influence of ephemeral fronts on seabird distribution in the south-eastern North Sea

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Abstract

Most studies that found an influence of hydrographic fronts on seabird distributions referred to rather stable structures such as shelf break fronts and tidal mixing fronts. In contrast, an influence of ephemeral and dynamic frontal structures was seldom revealed. In the German Bight, we observed frontal areas associated with a river plume and an ephemeral upwelling event during dedicated summer cruises assessing the distribution of seabirds at sea. We tested whether the observed dynamic frontal structures had a significant influence on the distribution of seabirds in the German Bight. As hypothesised due to their ephemeral nature, frontal structures had a lower effect on seabird distribution patterns than water masses and a land-sea gradient. However, the distribution of primarily Black-legged Kittiwakes was strongly influenced by fronts. Fronts generally seem to play a major role for Kittiwakes in the German Bight as mean distribution patterns in summer exhibit strong concentrations in an area of frequent frontal activity. A strong link between seabird distribution and ephemeral or dynamic habitat structures is expected to cause high variation of seabird distribution patterns. In accordance, aerial surveys revealed distinct variation in at-sea distribution at the order of single days during the breeding season of 2006. Variation of seabird distribution in time and space complicates conservation efforts such as the identification and management of Important Birds Areas.

2.1 Introduction

Frontal structures may strongly influence food availability for seabirds because of high physical, chemical and biological activity in these zones. A concentration of biomass at frontal zones is due to passive aggregation of various organisms ranging from phyto- and zooplankton to fishes (Schneider et al. 1987, Franks 1992, Decker and Hunt 1996) as well as to an elevated productivity (Pingree et al. 1978, Floodgate et al. 1981, Munk et al. 1995). High densities of prey again enable seabirds and other predators to forage cost-efficiently (Brodie et al. 1978, Hunt 1997). Thus, a variety of studies throughout the world has detected a significant influence of fronts on the distribution of seabirds (for reviews see e.g. Brown 1980, Hunt and Schneider 1987, Haney and Solow 1992, Shealer 2002). In accordance with the finding that an influence of habitat characteristics is mostly found at larger scales (Briggs et al. 1987, Ainley et al. 2005), seabird distribution patterns were mostly related to larger frontal structures such as shelf break fronts and tidal mixing fronts that last at least several weeks or months. In contrast, an influence of ephemeral hydrographic structures was worldwide seldom revealed due to their small longevity (but see e.g. Vermeer et al. 1987). Moreover, a significant influence of highly dynamic frontal structures like estuarine or river plume fronts that vary with wind and current conditions in location and strength is rarely detected. Thus, several anecdotal descriptions refer to an association of seabirds with river plume fronts (Uspenski 1956, Briggs et al. 1987, Camphuysen 2001, Morgan et al. 2005). However, to our knowledge, the correlation of the distribution of wintering Black-throated and Red-throated Divers (*Gavia arctica* and *G. stellata*) with river plume fronts in the German Bight (Skov and Prins 2001) is so far the only study that revealed a significant influence of river plume fronts on the distribution of seabirds.

During dedicated summer cruises assessing the distribution of seabirds at sea in the German Bight, we detected frontal areas bordering a river plume and an ephemeral upwelling event. In the following analyses, we tested whether the observed dynamic frontal structures had a significant influence on the distribution of seabirds in the German Bight. Following the positive relation between space and time scales that was first described for oceanographic structures by Stommel (1963), smaller spatial patterns exhibit also smaller temporal patterns. In concordance, the hydrographic structures in our study were of short longevity, lasting only a few hours or days (according to local wind conditions and based on Krause et al. 1986) in the case of upwelling fronts. Due to their ephemeral nature, we expected fronts to have a lower influence on seabird distribution compared to larger and longer-lasting habitat characteristics like water masses. Nevertheless, in the case of an existing strong link between seabird occurrence and habitat structures, spatio-temporal shifts of habitat characteristics should be reflected in seabird distribution patterns. Thus, we hypothesize that a correlation of seabird distribution to ephemeral or dynamic structures implies a high variation of seabird distribution patterns.

2.2 Material and Methods

Data collection

To compare seabird distribution to hydrographic features, we carried out ship-based seabird counts (see chapter 1.3.3, page 8) simultaneously along with hydrographic measurements. For the present study, we analysed data collected during two summer cruises of the RV ‘Heincke’ (formerly Biologische Anstalt Helgoland, now Alfred-Wegener-Institut Bremerhaven): cruise ‘He 061’, surveying 643 km from 18 – 22 July 1994 and ‘He 122’, covering a survey transect of 1780 km during 27 July – 06 August 1999. In the following, the two cruises will be referred to as the 1994 and 1999 cruise, respectively.

Measurements of sea surface salinity and temperature were recorded simultaneously along with bird counts once per minute by a thermosalinograph at a depth of 4 m. Additionally, a total number of 115 and 192 hydrographic stations, respectively, was carried out during the 1994 and 1999 cruises. The distance between hydrographic stations averaged between 8 and 12 km. At these stations, water depth was recorded and vertical profiles of temperature and salinity were obtained from the sea surface to the sea bottom using CTD-casts. Additionally, water transparency was measured by use of a Secchi disk (Pickard and Emery 1990, Aarup 2002).

Data analysis

To obtain useful indicators for hydrographic structures such as stratification and frontal activities, we derived further hydrographic parameters in addition to the direct measurements. Horizontal temperature and salinity gradients were defined as the difference between the start and the end point of each counting interval. The average difference between consecutive sea surface hydrography measurements per minute served as an indicator for temperature and salinity fronts, respectively. To assess thermohaline stratification, we calculated differences in salinity and temperature between sea surface and seabed.

We carried out Principal Component Analyses to derive major habitat variables. Hydrographic parameters that did not meet the assumption of a normal distribution (checked by visual inspection) were transformed to reach normal distribution. The results of corresponding standard measures and tests justified the application of Principal Component Analyses for both cruises (1994 cruise: Kaiser-Meyer-Olkin measure of sampling adequacy: 0.684, Bartlett’s test of sphericity: $\chi^2=855$, $df=36$, $p<0.001$; 1999 cruise: Kaiser-Meyer-Olkin measure of sampling adequacy: 0.714, Bartlett’s test of sphericity: $\chi^2=1041$, $df=36$, $p<0.001$; McGregor 1992).

Only principal components with eigenvalues >1.0 were considered in subsequent analyses. Axes were rotated orthogonally using the VARIMAX option (Backhaus et al. 1996)

to facilitate interpretation and to allow for independent results of the subsequent computations of correlations between the derived principal components and the abundance of seabirds. An otherwise existing dependency between principal components would complicate the interpretation of correlation coefficients between each of these factors and seabird occurrence.

Three principal components with an eigenvalue >1.0 explained 81.5% and 76.2%, respectively, of parameter variance for the summer cruises of 1994 (Table 2.1a) and 1999 (Table 2.1b). Areas of frontal activity resulting from different mechanisms represented important hydrographic structures during both cruises. Regarding the 1994 cruise, the first principal component combines high positive loadings of all indicators for temperature and salinity gradients and fronts with high negative loading of water transparency according to Secchi disk measurements (Table 2.1a). Low loadings of sea surface salinity and water depth indicate that this component is not influenced by distance to land. The mapping of water transparency values (see Fig. 2.1a,b) and sea surface temperature (Fig. 2.1c) during the 1994 cruise reveals two larger cells in the central German Bight that were characterised by low sea surface temperature and low transparency. Being oriented along the post-glacial Elbe valley, these structures presumably resulted from wind-driven upwelling of colder bottom water. During the respective days, moderate to strong easterly winds prevailed which are known to cause upwelling events in the described region (Krause et al. 1986). In conclusion, the first component of the 1994 cruise most likely represents the described upwelling region with its adjacent fronts, but could also be an indicator for the Elbe river plume. The latter is well described by the second principal component derived in the analysis of the 1999 cruise, combining temperature and salinity fronts with haline stratification. No interpretation could be derived for component 3 of the 1999 cruise which combines high positive loading of horizontal salinity gradients with a high negative loading of horizontal temperature gradients (Table 2.1b).

Furthermore, all Principal Component Analyses stressed the existence of different water masses in the German Bight. The Continental Coast water mass that prevails nearshore in shallow depths is characterised by low values of salinity and transparency. In contrast, the Central North Sea water mass which dominates towards the deeper north-western part of the German Bight shows high salinity, high transparency and additionally thermal stratification during the summer months (Becker et al. 1983). Thus, the second principal component of the 1994 cruise and the first component of the 1999 cruise act as indicators for distance to coast as well as for the two different water masses. Positive values of these components indicate greater distance from land and presence of the stratified Central North Sea water mass whereas negative values stand for vicinity of the coast and presence of the Continental Coast water mass. While thermal stratification (high values of vertical temperature gradient) is incorporated in the water mass gradient (PC 1) in the 1999 cruise (Table 2.1b), it acts as a separate component, cleared for effects of water mass and distance from land, in the results of the 1994 cruise (PC 3 in Table 2.1a).

Table 2.1: Results of Principal Component Analyses for the cruises in 1994 (a) and 1999 (b). The loadings of the nine hydrographic parameters used for analysis on the first three principal components, derived from the correlation matrix and subsequent rotation, are shown. Rotation method: Varimax with Kaiser normalisation (Backhaus et al. 1996). Eigenvalues and percentages of variation are given for the three principal components. Bold faced values of loadings were used for interpreting and characterising the components; italicised values were considered additionally. SSS = sea surface salinity in psu; Depth = water depth in m; Secchi = water transparency in m according to Secchi disk measurements; vert. T-gradient = vertical temperature gradient in K; vert. S-gradient = vertical salinity gradient in psu; horiz. T-gradient = horizontal temperature gradient in K; horiz. S-gradient = horizontal salinity gradient in psu; T-fronts = indicator of temperature fronts; S-fronts = indicator of salinity fronts. Parameters marked with an asterisk were transformed to reach a normal distribution. See Methods for details of parameter calculation.

(a)	PC 1	PC 2	PC 3	
Eigenvalue	3.98	2.19	1.17	
% of Variance	44.2	24.3	13	\sum 81.5%
SSS	-0.23	0.93	-0.18	
Depth	-0.02	0.93	0.28	
Secchi	-0.62	<i>0.60</i>	-0.21	
vert. T-gradient	-0.05	0.56	0.79	
vert. S-gradient*	0.24	-0.18	0.91	
horiz. T-gradient*	0.85	0.00	-0.13	
horiz. S-gradient*	0.69	-0.02	0.08	
T-fronts*	0.82	-0.21	0.17	
S-fronts*	0.83	-0.26	0.25	

(b)	PC 1	PC 2	PC 3	
Eigenvalue	3.62	1.78	1.46	
% of Variance	40.3	19.7	16.2	\sum 76.2%
SSS	0.91	-0.23	-0.04	
Depth	0.96	-0.03	-0.01	
Secchi	0.90	-0.15	0.03	
vert. T-gradient*	0.87	0.15	0.13	
vert. S-gradient*	0.23	0.63	-0.09	
horiz. T-gradient	-0.09	-0.04	-0.88	
horiz. S-gradient	-0.01	0.00	0.89	
T-fronts*	-0.17	0.73	0.23	
S-fronts*	-0.3	0.83	-0.04	

For the correlation of seabird occurrence with habitat characteristics, the sampled transect area was divided into separate counting intervals corresponding to the single hydrographic stations. Each counting interval consisted of one transect segment prefacing the corresponding hydrographic station and one segment following it. In the case of short sampling distances between single hydrographic stations, the extension of each segment corresponded to half of the distance between the hydrographic stations. Otherwise, segments were confined to a maximum of 16 min sampling time following or prefacing the hydrographic station to achieve that counting intervals were representative of the seabird occurrence at the hydrographic station. Segments were excluded if they were temporarily not attached to the hydrographic station. Thus, bird density was calculated for counting intervals covering an area from 1.6 to 6.6 km² (average: 4.7 km²) around (i.e. prefacing and following) the corresponding hydrographic station.

Samples of seabird abundance exhibited two major characteristics: they comprised many zero density values violating the assumption of normality, and, furthermore, data points were characterised by strong autocorrelation. However, autocorrelation could not be quantified accurately due to the large number of zero values that complicated interpreting the results of autocorrelation analyses.

To account for non-independent data and distributions containing many zero values, we used a permutation procedure. To keep the major characteristics constant, the original data set was split up into alternating blocks of cases (= counting intervals) comprising consecutive zero values and blocks of cases with a consecutive occurrence of birds. During permutation the position of each single block was randomised while the alternating occurrence of 'zero value' - blocks and blocks containing seabird density values higher than 0 was kept constant. The sequence of cases containing seabird density values was not altered within each block. Following this method, all data sets (i.e. the original data set and all of the permuted data sets) contained the same number of blocks, the same seabird density values and within blocks of seabird occurrence the same sequence of density values.

Data were treated separately for the two cruises to allow for the detection of single hydrographic events possibly occurring in only one of the two cruises. Correlation between each data set (i.e. the original data set and all of the permuted data sets) and each principal component derived from the PCA of the hydrographic parameters was thus tested separately for the two cruises using Spearman's Rank Correlation analyses. The proportion of absolute correlation coefficients greater than or equal to the absolute correlation coefficient of the original data then corresponded to the p-value. The number of permutations was set to 1000 but was elevated to 10,000 (or 100,000 respectively) in cases of p-values lying near 0.05 after the first computations. To correct for multiple testing we applied Fisher's Omnibus-Test separately for each principal component and its associated analyses of correlation. This test combines a number of p-values into a single χ^2 -distributed variable with its degrees of freedom equalling twice the number of p-values (Haccou and Meelis 1994).

A test using log-transformed seabird density values revealed no major differences in results compared to results of analysing non-transformed density values. Due to identification difficulties during counts, Common *Sterna hirundo* and Arctic Terns *S. arctica* were grouped as "Commic Terns" for the 1999 cruise.

2.3 Results

2.3.1 Influence of fronts on seabird distribution

Small scale hydrographic structures had a clear influence on the occurrence of two species during the analysed cruises. The distribution of Black-legged Kittiwakes *Rissa tridactyla* correlated significantly positively with areas of strong frontal activities such as the Elbe river plume and upwelling regions during both summer cruises. During the 1994 cruise, the majority of Black-legged Kittiwakes was concentrated in the centre of the German Bight in an area where water bodies of low transparency and low temperature met adjacent warmer waters of high transparency (Fig. 2.1a,c). Most Great Black-backed Gulls *Larus marinus* were also observed in this region that was oriented along the post-glacial Elbe valley (Fig. 2.1b). In concordance, both species showed a positive correlation with areas of frontal activity (component 1 in Table 2.1a; see Table 2.2). Observations also confirmed an attraction of these fronts to Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus*. Likewise, the occurrence of Kittiwakes correlated positively with component 2 from the 1999 cruise which was also characterised by frontal zones (Tables 2.1b & 2.3). Accordingly, mapping of temperature fronts during the 1999 cruise revealed that Black-legged Kittiwakes were distributed closely along these structures that occur along the Elbe river plume (Fig. 2.1d).

2.3.2 Influence of large scale habitat characteristics (water masses) on seabird distribution

A higher number of species exhibited a significant influence of large scale habitat characteristics such as the occurrence of specific water masses on at-sea distribution. Thus, several seabird species of the German Bight showed a significant preference for one of the two prevailing water masses. The nearshore dominating Continental Coast water mass of low salinity and high turbidity was the preferred habitat of Common Gulls *Larus canus*, Common and Sandwich Terns *Sterna hirundo* and *S. sandvicensis*. On the other hand, Northern Fulmars *Fulmarus glacialis*, Northern Gannets *Sula bassana* and Common Guillemots *Uria aalge* were significantly associated with the high saline Central North Sea water mass of high transparency, which becomes dominant in the deeper north-western part of the study area (Tables 2.2 & 2.3).

Table 2.2: Spearman's Rank Correlations between the distribution of all common seabird species and the three principal components derived from Principal Component Analyses (see Table 2.1a) for the cruise in July 1994. To account for non-independent data and distributions containing many zero values we used a permutation procedure to calculate adequate p-values for all correlation coefficients (see Methods for more details). nPerm = number of Permutations. Bold values show significant correlations; trends are indicated by italicised values. To correct for multiple testing we applied Fisher's Omnibus-Test separately for each principal component. Commic Terns = Common *Sterna hirundo* and Arctic Terns *S. paradisica*.

	Component 1 <i>Elbe river plume / Upwelling</i>			Component 2 <i>Indicator of Central North Sea water mass and distance to land</i>			Component 3 <i>Stratification</i>		
	r_s	p	nPerm	r_s	p	nPerm	r_s	p	nPerm
Northern Fulmar	-0.331	<i>0.052</i>	100000	0.495	0.004	1000	-0.074	0.88	1000
Black-headed Gull	0.023	0.833	1000	-0.114	0.224	1000	-0.072	0.443	1000
Common Gull	0.276	0.139	1000	-0.387	0.011	1000	-0.172	0.374	1000
Lesser Black-backed Gull	0.145	0.236	1000	0.021	0.885	1000	-0.071	0.577	1000
Herring Gull	0.081	0.514	1000	-0.266	<i>0.074</i>	10000	-0.173	0.246	1000
Great Black-backed Gull	0.26	0.037	1000	-0.09	0.589	1000	-0.195	0.153	1000
Black-legged Kittiwake	0.256	0.039	10000	0.132	0.424	1000	0.027	0.833	1000
Commic Terns	0.138	0.269	1000	-0.321	0.035	10000	-0.188	0.159	1000
Common Guillemot	-0.055	0.633	1000	0.261	0.036	1000	-0.026	0.844	1000
Fisher's Omnibustest		0.03			0.0005			0.6	

Table 2.3: Spearman’s Rank Correlations between the distribution of all common seabird species and the three principal components derived from Principal Component Analyses (see Table 2.1b) for the cruise in July/August 1999. To account for non-independent data and distributions containing many zero values we used a permutation procedure to calculate adequate p-values for all correlation coefficients (see Methods for more details). nPerm = number of Permutations. Bold values show significant correlations. To correct for multiple testing we applied Fisher’s Omnibus-Test separately for each principal component.

	Component 1			Component 2			Component 3		
	<i>Indicator of Central North Sea water mass</i>			<i>Elbe river plume and adjacent fronts and distance to land</i>			<i>Salinity fronts in an area of stable temperatures</i>		
	r_s	p	nPerm	r_s	p	nPerm	r_s	p	nPerm
Northern Fulmar	0.551	0.001	1000	-0.184	0.104	1000	-0.003	0.981	1000
Northern Gannet	0.205	0.008	1000	-0.036	0.624	1000	-0.033	0.654	1000
Black-headed Gull	-0.11	0.118	1000	-0.046	0.539	1000	0.083	0.241	1000
Common Gull	-0.314	0.007	1000	-0.011	0.918	1000	-0.055	0.536	1000
Lesser Black-backed Gull	0.052	0.574	1000	-0.027	0.771	1000	-0.042	0.564	1000
Herring Gull	-0.135	0.187	1000	-0.06	0.544	1000	-0.059	0.406	1000
Great Black-backed Gull	0.051	0.548	1000	0.011	0.893	1000	-0.039	0.587	1000
Black-legged Kittiwake	-0.086	0.503	1000	0.296	0.006	1000	0.188	0.043	10000
Sandwich Tern	-0.277	0.002	1000	-0.064	0.472	1000	-0.034	0.667	1000
Common Tern	-0.24	0.005	1000	-0.03	0.727	1000	0.061	0.429	1000
Arctic Tern	-0.059	0.477	1000	-0.001	0.996	1000	0.096	0.175	1000
Common Guillemot	0.423	0.001	1000	-0.093	0.383	1000	-0.014	0.847	1000
Fisher’s Omnibustest		<0.0001			0.51			0.60	

2.4 Discussion

2.4.1 General discussion

Frontal structures did not have an equally strong effect on distribution patterns of the different seabird species as did the land-sea and water mass gradients. Nevertheless, the occurrence of above all Black-legged Kittiwakes was strongly influenced by frontal activity during the analysed summer cruises. These results seem to represent the general pattern well, as the distribution of Kittiwakes in the German Bight coincides with areas of high frontal activity during summer. Concentrations of Kittiwakes occur along the post-glacial river Elbe valley that forms the most distinctive bathymetrical feature in the rather shallow German Bight (Fig. 2.2). Currents interacting with the bottom topography lead to a frequent occurrence of fronts in this area.

Kittiwakes and other gulls are highly mobile and thus are able to sample wide-ranging sea areas in a relatively short amount of time. Consequently, they should experience a higher probability of encountering ephemeral prey patches than species that are less mobile. Moreover, Kittiwakes are breeding in the German Bight in a single colony on the small offshore island Helgoland. According to central place foraging theory, it can be expected that breeding Kittiwakes gain information on the location of valuable foraging grounds by observing individuals returning to the breeding colony. Furthermore, the breeding colony on Helgoland is conveniently located in the vicinity of the post-glacial river Elbe valley and other areas of high frontal activity. In comparison with other breeding birds on Helgoland, Kittiwakes are dependent on prey aggregations at the sea surface due to their surface-feeding foraging behaviour, and thus are more restricted in choice of prey patches than diving species such as Common Guillemots or plunge-diving species such as Northern Gannets. At a highly speculative level, it can be assumed that in accordance with their pronounced pelagic lifestyle, Kittiwakes potentially possess particular physiological abilities to detect ephemeral prey patches.

Most earlier studies that found an influence of frontal systems on seabird distributions related to rather stable structures such as shelf break fronts and tidal mixing fronts that last at least several weeks or months (for the North Sea see e.g. Leopold 1993, Skov and Durinck 1998). Although a tidal mixing front does exist in the German Bight during the summer months, there were no signs that it attracts seabirds to an important extent (unpublished data). An influence of ephemeral hydrographic structures was worldwide seldom revealed due to their short longevity (but see Vermeer et al. 1987). Our results imply that this shortage was not caused by the low ability of birds to locate such short-lived, temporally less predictable frontal systems as proposed by Hoefler (2000), but rather by inappropriate or low sampling effort of the human observers.

Though the estuarine front of the German Bight is a permanent feature existing throughout the year (Krause et al. 1986), its location, spatial extent and strength vary depending on physical forcing of wind and tides, interacting with bottom topography (Dippner

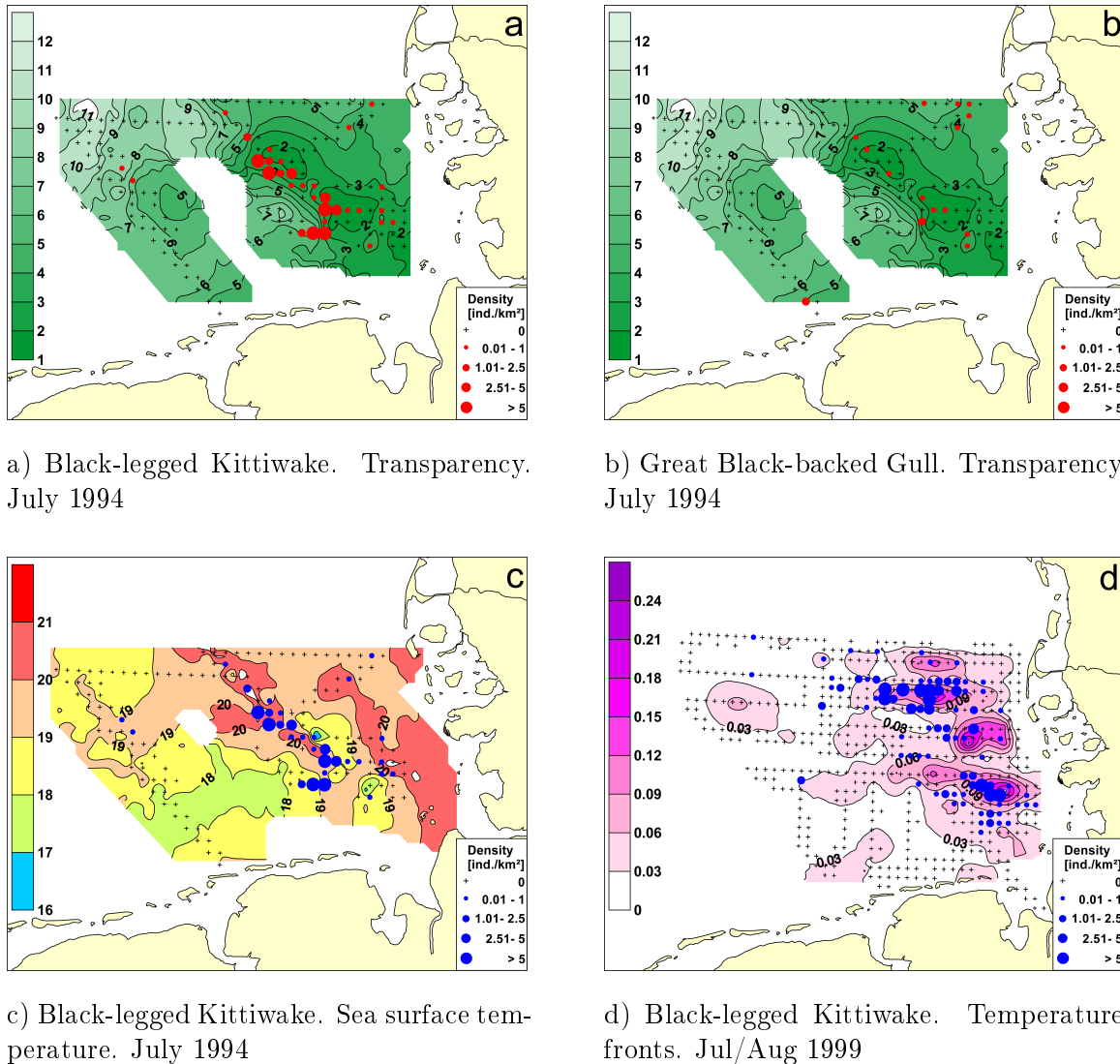


Figure 2.1: Influence of frontal structures on the distribution of Black-legged Kittiwakes and Great Black-backed Gulls as shown by synoptic bird – hydrography maps. Seabird distribution maps were created by calculating densities (sum of individuals / sum of surveyed area) for 3' latitude x 6' longitude grids. Hydrography was mapped by interpolating measurements in Surfer 8.01 using a kriging method (Anonymous 2002, A. Schulz pers. comm.). Transparency (water transparency according to Secchi disk measurements) is given in m, sea surface temperature (SST) in °C and temperature fronts (average sea surface temperature difference between single minute measurements) in K. See Methods for more details.

1993). Thus, distribution patterns of seabird species like Black-legged Kittiwakes and divers that concentrate along the described river plume fronts undergo spatiotemporal variation, following variation of the frontal system. In accordance, consecutive aerial surveys during the breeding season 2006 recorded short-term variation of at-sea distribution of Black-legged Kittiwakes in the inner German Bight (Fig. 4.4, page 58).

On 12 July, a concentration area of Kittiwakes was observed to the north of Helgoland along the 20 m depth contour (Fig. 4.4, top left). A survey on the following day recorded no individuals in the same area (Fig. 4.4, top right). Thus, this spot apparently hosted a short-lived occurrence of prey that was present only on the first of the two survey days. So far, no information has been gained on the respective hydrographic situations for the two days. However, it is possible that currents interacting with the bottom topography caused the presumable ephemeral prey patch in this situation, too.

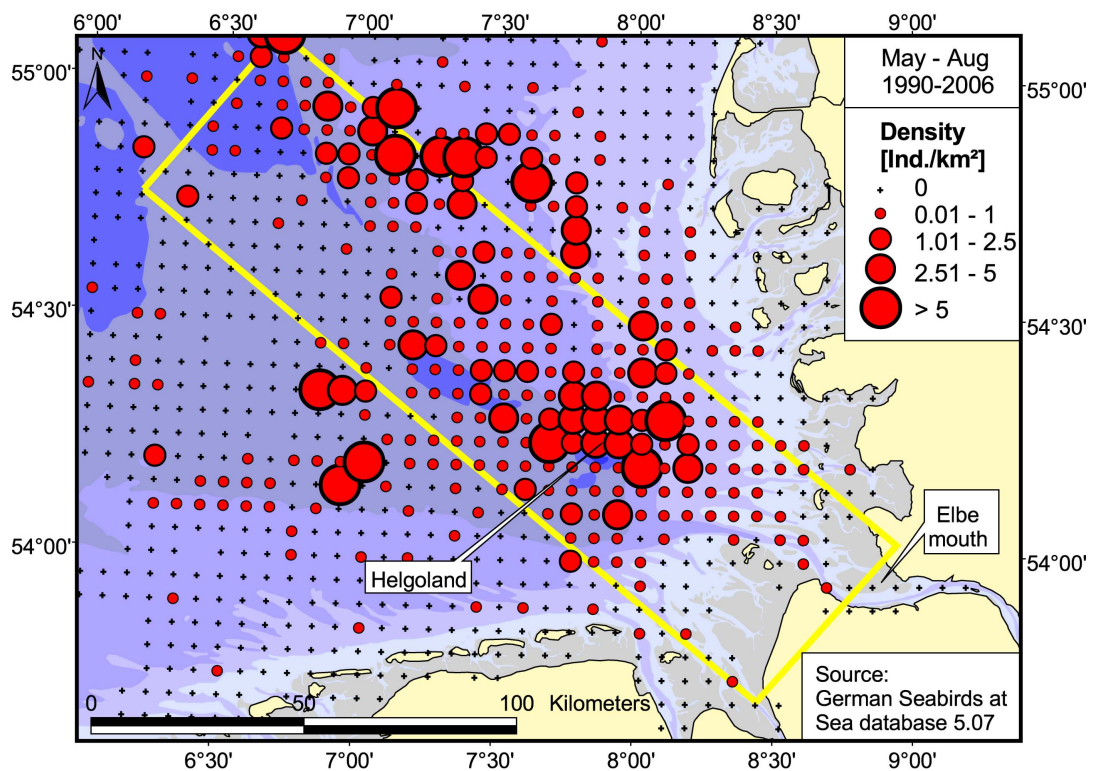


Figure 2.2: Mean distribution pattern of Black-legged Kittiwakes during the breeding season and late summer. Data were pooled from ship-based surveys conducted from May to August (1990-2006; Source: German Seabirds at Sea database v5.07). Note the location of the post-glacial river Elbe valley (indicated by the yellow box) that can be recognised by the higher water depth.

2.4.2 Implications for conservation

Seabird distribution in the German Bight is linked to habitat characteristics that were shown to exhibit high temporal variation. A strong habitat-bird relationship therefore contributes to temporal variation in seabird distribution patterns. This variation in time and space complicates conservation efforts such as the identification and management of Important Birds Areas. Unlike terrestrial ecosystems, the marine environment provides highly dynamic habitats exhibiting moving boundaries and short-lived structures driven by wind and currents. ‘Considering the temporal when managing the spatial’ (Wilson et al. 2004) should thus be a fundamental goal during the set up and management of protected areas. During this process, it is essential to reveal the exact parameters and processes that drive seabird distribution patterns. Future studies should apply appropriate sampling and analysing methods to assess the importance of habitat characteristics at all concerned scales.

Acknowledgements

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3 A menu of winners? - Diet composition of Black-legged Kittiwakes *Rissa tridactyla* in the breeding colony at Helgoland, south-eastern North Sea

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Abstract

In contrast to the situation in the northern North Sea, the breeding colony of Black-legged Kittiwakes *Rissa tridactyla* at Helgoland in the south-eastern North Sea did not exhibit severe declines since the 1990s but instead numbers increased and only lately stagnated. Declines of Kittiwakes in the northern North Sea are attributed to a lower abundance and lower quality of sandeel, their key prey. Consequently, we hypothesise that Kittiwakes at Helgoland do not rely as heavily on sandeel as their conspecifics.

To assess possible reasons for this positive development, we analysed diet composition of Kittiwake nestlings and adults of the years 2001, 2002, 2004 and 2006. According to stomach contents, diet was dominated by fish prey. In concordance with earlier studies of the 1980s and 1990s, young Whiting *Merlangius merlangus* was the most important prey species in 2001, 2002 and 2004 regarding frequency of occurrence, numbers and consumed biomass. Clupeids and sandeels were consumed in lower proportions. While Whiting was believed to originate from fisheries discard in earlier studies, evidence now supports that it represents a natural food source and was preyed upon by Kittiwakes in areas characterised by high incidence of hydrographic fronts. Contrastingly, no Whiting was recovered in samples of 2006 and the proportion of fish prey was low. Main prey items with respect to frequency of occurrence and numbers were polychaete worms (Nereidae), which were presumably consumed as swarming Heteronereis stages. Samples of 2006 originated from a period of exceptionally high temperatures with water temperature rising above 20°C. High levels of direct solar radiation and high temperature presumably

have caused observed high mortality of Kittiwake nestlings. Additionally, the strong rise in water temperature presumably drove fish such as Whiting to deeper cooler layers and thus out of reach of surface-feeding Kittiwakes. Temperature might have further influenced food availability of Kittiwakes by inducing swarming of Nereidae. Overall, Kittiwakes breeding on Helgoland showed a positive population trend for several decades while mainly feeding on Whiting.

3.1 Introduction

In the North Sea, breeding numbers of Black-legged Kittiwakes *Rissa tridactyla* (hereafter 'Kittiwakes') have declined by more than 50% since 1990 (Frederiksen et al. 2004, Heubeck 2004). The reasons for this severe decline are still not explained in detail. In most areas however, a distinct decrease of breeding success has been recorded (Wanless et al. 2005, ICES-WGSE 2006), which was probably connected to low food availability and low food quality (Frederiksen et al. 2004, Wanless et al. 2005, 2007). The Kittiwake's surface-feeding foraging technique restricts it to prey concentrations at the sea surface and thus renders this species more vulnerable to food reductions than most other seabird species (Monaghan 1996, Furness and Tasker 2000). The insufficient food availability, which has also led to breeding failure and negative population trends of other seabird species (Mavor et al. 2005), is assumed to result mainly from ecosystem changes (Heubeck 2004). At the Isle of May, breeding success and population trend of Kittiwakes was strongly influenced by the availability of sandeel (Frederiksen et al. 2004). Sandeel availability is influenced by oceanographic parameters such as sea surface temperature in winter and by fishing activity. In the last decades, the oceanographic situation in the North Sea has changed distinctly with respect to physical as well as biological aspects (Beaugrand 2004). Thus, mean water temperature in winter has increased, leading to depressed recruitment of sandeels (Arnott and Ruxton 2002). Moreover, a stronger inflow of warm water from the Atlantic led to changes in phytoplankton communities which resulted in deteriorated food availability for sandeel larvae (Arnott and Ruxton 2002, Wanless et al. 2007).

In the south-eastern North Sea, Kittiwakes occupy a single colony of at present approximately 7,500 breeding pairs on the small offshore island Helgoland (54°11'N, 7°53'E). Although oceanographic changes resulting in a warmer, more marine situation have been recorded in the sea area around Helgoland as well (Wiltshire and Manly 2004), neither elevated breeding failure nor a distinct decline of breeding numbers have been recorded for this colony so far. In contrast to other colonies, the breeding numbers of Kittiwakes at Helgoland did not decrease since 1990 but instead doubled. Thus, the situation of Kittiwakes breeding in the south-eastern North Sea apparently is up to now favourable. As diet is regarded to be one of the key factors influencing breeding performance and trends in numbers, we assumed that the success of the Kittiwakes breeding at Helgoland could be explained by analysing the diet of chicks and adults. In particular, we hypothesised

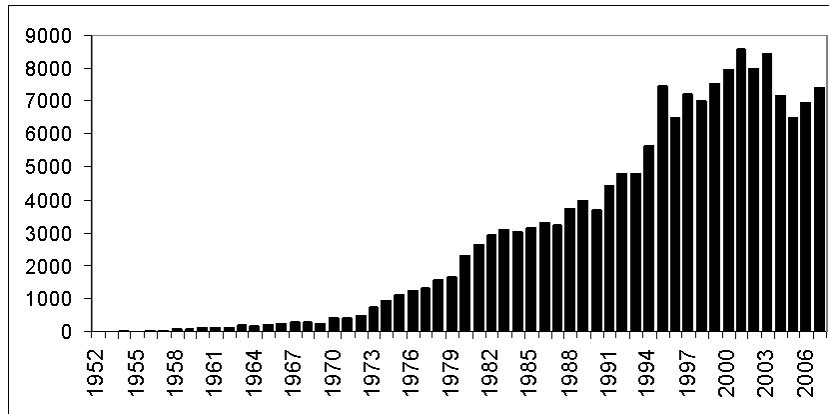


Figure 3.1: Numbers of breeding Black-legged Kittiwakes at Helgoland from 1952 to 2007. (Data: O. Hüppop / IfV unpubl. data)

that Kittiwakes at Helgoland might not be as dependent on sandeel as their conspecifics in the northern North Sea and thus should be less vulnerable to reductions in this prey species.

Samples consisted of birds found dead in the colony in the breeding season. Birds breed in highly eroding sandstone cliffs making nests inaccessible to humans and handling of birds to get diet samples only exceptionally possible. Killing of birds was not considered appropriate due to ethical reasons and conservation aspects. Moreover, inaccessibility of nests would have strongly hampered a collection of chicks by shooting. However, during most years, a considerable number of chicks, which fell out of the nest, and some dead adults could be found beneath the cliffs. Results of analyses of stomach contents are discussed in comparison to earlier studies and with respect to current population trends.

3.2 Material and Methods

3.2.1 Population trend of the breeding colony on Helgoland

After about 150 years of absence most likely due to strong human persecution, Kittiwakes recolonised Helgoland in 1938. Continuous data on breeding numbers is available since 1952 (Fleet 1984, Hüppop 1997). Numbers showed a strong increase especially during the 1970s, 1980s and 1990s and reached a maximum of 8,600 pairs in 2001. The last years showed a stagnation and lately indicate a slight decline (Fig. 3.1).

Table 3.1: Number of stomach samples from the breeding colony of Black-legged Kittiwakes at Helgoland, which were analysed in the present study. Information on age of nestlings could be derived for birds of 2004 and 2006. Age of nestlings ranged between 2 and 40 (median=22) days in 2004 and between 1 and 32 (median=9) days in 2006 respectively.

	2001			2002		2004		2006		Total
	June	July	Aug	June	July	June	July	June	July	
Chicks	5	21	3	0	20	11	22	4	19	105
Adults	2	1	0	0	1	5	5	0	0	14

3.2.2 Samples

In the breeding seasons 2001, 2002, 2004 and 2006, chicks and adult birds found dead beneath the breeding cliffs were collected and stored frozen (Table 3.1). The majority of chicks presumably died due to falling out of the nest. Most of these birds directly die from fractures or internal injuries. However, nestlings which survive the fall die within the next days as adults do not continue to brood, feed or guard these chicks (Vauk-Hentzelt and Bachmann 1983). Falling is caused by accidents, e.g. resulting from antagonistic behaviour or unfavourable weather conditions. In 2002, all chicks but one fell off the cliffs in the course of a heavy storm in early July. In 2006, an exceptional number of more than 100 chicks was found dead during a period of extremely high temperatures. A sub-sample only of these birds was analysed in the present study. Due to low sampling effort, no chicks were collected in 2003 and only one chick was found in 2005, which was not considered in the following analysis.

In 2001 and 2002, birds were dissected prior to storage and stomachs only were preserved for later analyses. The same method was applied to two chicks and one adult bird found dead in 2004. However, all other birds found in 2004 and 2006 were stored completely and later dissected at the Research and Technology Centre (FTZ) following the methods described by Van Franeker (1983, 2004). In the course of dissections, we collected data on biometry, sex and health status. Chicks were aged according to length of lower arm and central tail feathers (Maunder and Threlfall 1972) and grouped within the following age classes: age class 1: 0-9 days, 2: 10-20 days, 3: 21-30 days and 4: >30 days. To derive an index of chick condition, we calculated a 'body mass index' by expressing observed body mass as proportion of body mass of presumably well-nourished chicks of the same age based on data of Kittiwakes from Newfoundland and Norway (Maunder and Threlfall 1972, Barrett and Runde 1980). We tested influence of chick age and freshness of sample on the body mass index applying a Generalized Linear Model (GLM, McCullagh and Nelder 1989) using the Gamma function in R 2.5.0 (<http://www.r-project.org/>).

3.2.3 Analysis of stomach contents

Stomach contents were analysed following Leopold et al. (2000) and Guse (2005). Prey remains were identified to the lowest possible taxon (Ouwehand et al. 2004) by use of undigested hard-parts e.g. of fish skeletons, jaws of Nereidae, claws of crustacea or chitinous remains of insects. Fish species were identified according to otoliths (Härkönen 1986, Leopold et al. 2001), urohyals, premaxillae, vertebrae and otic bullae (Watt et al. 1997, Leopold et al. 2001). Additionally, an own reference collection was used for identifying prey items. Fish remains that could not be identified to species or family level were grouped as ‘fish indet.’. We derived minimum numbers of prey individuals consumed by grouping remains. Thus, right and left hard-parts of the same species or family such as otoliths, premaxillae and nereid jaws were paired based on size, shape and wear. Additional prey remains were only considered in case of proving higher numbers of respective prey species or in case of representing new species / families / prey groups.

Identification of prey remains and measurement of otoliths was performed using a stereo microscope in combination with an attached digital camera (Olympus SZH 10 Research Stereo and Olympus Camedia). Magnification ranged from 10.5 to 100 times and was set to fixed values during measurements. Otoliths were photographed and measured applying Olympus DP-Soft v3.2 software. Accuracy of measurements was 0.05 mm (Guse 2005). We corrected for wear due to digestion by categorizing otoliths within wear classes and by multiplying size measurements of worn otoliths with correction factors to estimate original sizes (Leopold et al. 1998, 2001, Ouwehand et al. 2004). Total length of fish was calculated based on size of otoliths by applying regressions between otolith length / width and total fish length obtained from Leopold et al. (2001). Subsequently, the fresh mass of fish was calculated based on regressions between total length and mass (Leopold et al. 2001). Regressions from Leopold et al. (2001) mainly based on fish data of the North Sea and Wadden Sea and thus were well suitable for our study.

Both samples of adults and chicks comprised 71% of stomachs which contained items classified as prey remains. About 10% of all stomach samples did not contain any objects, neither prey remains nor other items, except for parasites in some cases. Several other samples contained only objects like stones, fragments of mollusc shells or plastic, which were not classified as dietary remains. Overall, of 105 stomachs of nestlings, 57 contained stones (54%), 23 plant material, 8 contained fragments of mollusc shells, 6 feathers, 5 plastic fragments/pellets, 3 contained putative fish prey and 2 sand. In adult Kittiwakes, stones, fragments of mollusc shells and one plastic pellet were each found in only one stomach. Objects such as plant material, stones, sand and feathers were not considered to represent prey items fed to nestlings. Objects such as plant material, stones, sand and feathers were not considered to represent prey items fed to nestlings. Plant remains and sediment are regularly picked up by nestlings in the nest or its vicinity (Prüter 1989). The same could hold true for fragments of mollusc shells as Kittiwakes use a variety of plant material and hard parts to build their nests (Maunder and Threlfall 1972). However, it remains unclear whether stones and other hard parts are picked up on purpose

to enhance digestion or to cover mineral, e.g. calcium, demands. In contrast, plastic pellets and fragments recovered in stomachs of seabirds presumably represent floating litter particles which are mistaken for food by adults and thus get picked up and are fed to nestlings (Van Franeker and Bell 1988). Nevertheless, plastic fragments/pellets were not classified as dietary remains. Several stomachs were infested by parasites.

Influence of chick age on presence of parasites was tested by applying a GLM using the Binomial function in R. Furthermore, we tested the influence of chick age and condition on quality and quantity of stomach contents, i.e. presence of prey remains, number of species recovered and number of prey individuals recovered using Generalized Linear Mixed Models (GLMM, e.g. Faraway 2006) applying the library lme4 (Bates and Sarkar 2007) and the Binomial or quasi-Poisson function, respectively, with year as random effect in R. We tested for differences in fish length between adults and chicks and between different age classes of chicks by applying GLMMs using the Gamma function in case of skewed data or the Gaussian function with year and/or month as random effects. Furthermore, we tested for influence of month on fish length applying GLMMs with year, age and age of chicks as random effects.

3.3 Results

3.3.1 Body condition

Of 31 and 23 chicks recovered in 2004 and 2006, respectively, which were dissected at the Research and Technology Centre (FTZ), 11 (36%) chicks of 2004 and 10 (44%) of 2006 exhibited fractures of wings, legs or other bones. Eight of the remaining chicks showed injuries of internal organs that might have been caused by the drop from the breeding cliff. All chicks aged 10 days or older exhibited body mass values below those of presumably well-nourished chicks collected in boreal climates (Maunder and Threlfall 1972, Barrett and Runde 1980). Body mass index was higher in 2006 (median=78%) compared to 2004 (median=55%). This index was significantly influenced by freshness of samples ($p=0.0007$) and age of birds ($p(\text{age})=0.0002$, $p(\text{age}^2)=0.002$). The model however was underdispersed ($\ll 1$) as age and freshness were not the most important controlling factors of body mass. Body mass of all age classes decreased with increasing signs of decay resulting in most decayed bodies weighing less than 60% of fresh bodies of the same age class. Differences in mass compared to well-nourished chicks from boreal climates were low for birds younger than 10 days, and increased with age.

Of the nine adult birds found dead in 2004, which were dissected at the FTZ, only one male bird exhibited a brood patch. Three birds possessed healthy organs but low fat deposits. The remaining six birds possessed good fat deposits and exhibited body masses in the range of healthy birds (350-430 g). However, lungs of all six birds were severely inflamed.

Table 3.2: Stomach contents of nestlings and adult birds of Kittiwakes from the breeding colony at Helgoland in the different study years.

		2001	2002	2004	2006	Total	
Nestlings	Total number of stomachs	29	20	33	23	105	100%
	Parasites only	4	2	2	2	10	10%
	With contents	25	18	31	21	95	90%
	Containing prey items	16	13	26	19	74	71%
	Containing fish remains	16	12	25	9	62	59%
Adults	Total number of stomachs	3	1	10	0	14	100%
	Parasites only	0	0	2		2	14%
	With contents	3	1	8		12	86%
	Containing prey items	3	1	6		10	71%
	Containing fish remains	3	1	6		10	71%

3.3.2 Stomach contents

Overall, diet composition of Kittiwakes was dominated by fish prey. Fish did not only account for the maximum number of individual prey items but was also the most frequently consumed prey being found in most of the birds' stomachs. Exceptional in this respect were the samples of 2006, which exhibited an occurrence of fish in less than half of the stomachs (Table 3.2). Presence of prey remains, number of species per stomach and number of individual prey items per stomach did not differ between chicks and adults (level of significance: 0.05). Regarding chick samples, presence of prey remains, number of species per stomach and number of individual prey items per stomach were not influenced by chick age and condition.

The most frequent prey with respect to absolute numbers of prey individuals were polychaete worms of the family Nereidae with a total of at least 259 individuals based on recovered jaws. About 80% of these Nereidae (206 ind.) were found in 16 stomachs of nestlings from 2006. Lower numbers were recorded for earlier years with 40 and 12 individuals (14%, i.e. 5%) from three chick samples of 2002 and 2004, respectively. No Nereidae were recovered in 2001 samples and only one stomach of an adult bird contained remains of one nereid worm. In the years 2001, 2002 and 2004, gadoids comprising above all Whiting *Merlangius merlangus* represented the most frequent prey by far, both with respect to frequency of occurrence and absolute numbers (Tables 3.3 and 3.4). Clupeids (Clupeidae) and sandeels (Ammodytidae) followed next, both showing the same moderate values of frequency in occurrence (Table 3.3). Yet, overall numbers of clupeids, which comprised mainly Herring *Clupea harengus* and Sprat *Sprattus sprattus*, were higher than total numbers of sandeels recovered (35 vs. 28 individuals, Table 3.4). Fish species of other families as well as other prey species were only exceptionally recorded in single stomachs.

3.3.3 Prey length and biomass

Fish prey was on average rather small with a mean total fish length of 10.7 cm (median=9.5 cm) and a mean biomass of 11.5 g (median=5.7 g). Whiting, Lesser Sandeel *Ammodytes marinus* and Great Sandeel *Hyperoplus* sp. reached maximum lengths of 20 to 23 cm. The maximum biomass values of 70 g were calculated for Whiting (Table 3.4). Fish recovered in stomachs of adult birds tended to be a bit larger, however differences were not significant (Table 3.5). Sample size of sandeels and clupeids was too small for testing influence of chick age on fish length. Fish length of gadoids increased with age of chicks but this relation was not significant. Moreover, length of gadoids was greater in July compared to June. Gadoids and especially Whiting presented the most important prey when considering total biomass of prey fish calculated for the different years both for chicks and adults (Fig. 3.2). The proportion of the single fish families in the diet varied between years and months. Moreover, when comparing data of 2004, total biomass consumed by nestlings was almost entirely based on gadoids while the importance of these fish was slightly lower for adults.

Lengths of Nereidae were not calculated as jaws could not be identified to species level. Moreover, it was assumed that Nereidae were caught as swarming *Heteronereis* stages during their reproductive period. To our knowledge, no regression formulae are available for the calculation of total length of swarming stages on the basis of length of jaws. In addition, gulls preying on swarming *Heteronereis* stages mostly do not catch whole individuals but fragments only (N. Markones and N. Guse, pers. observation). Thus, total length and biomass actually consumed could not be assessed.

3.3.4 Parasite prevalence

Parasite infestation was high with all adult birds and 58% of chicks being infested with parasites, mostly nematodes. Parasite prevalence increased significantly with age of chicks ($n=55$, $p=0.001$) and varied between years. Thus, the proportion of infested chicks in 2001, 2002 and 2004 amounted to 62%, 70% and 73%, and was contrastingly low with 22% in 2006. However, the low value of parasite prevalence in 2006 resulted from a lower mean age of chicks collected. Prevalence did not differ between years when compared for chicks of the same age class in 2004 and 2006.

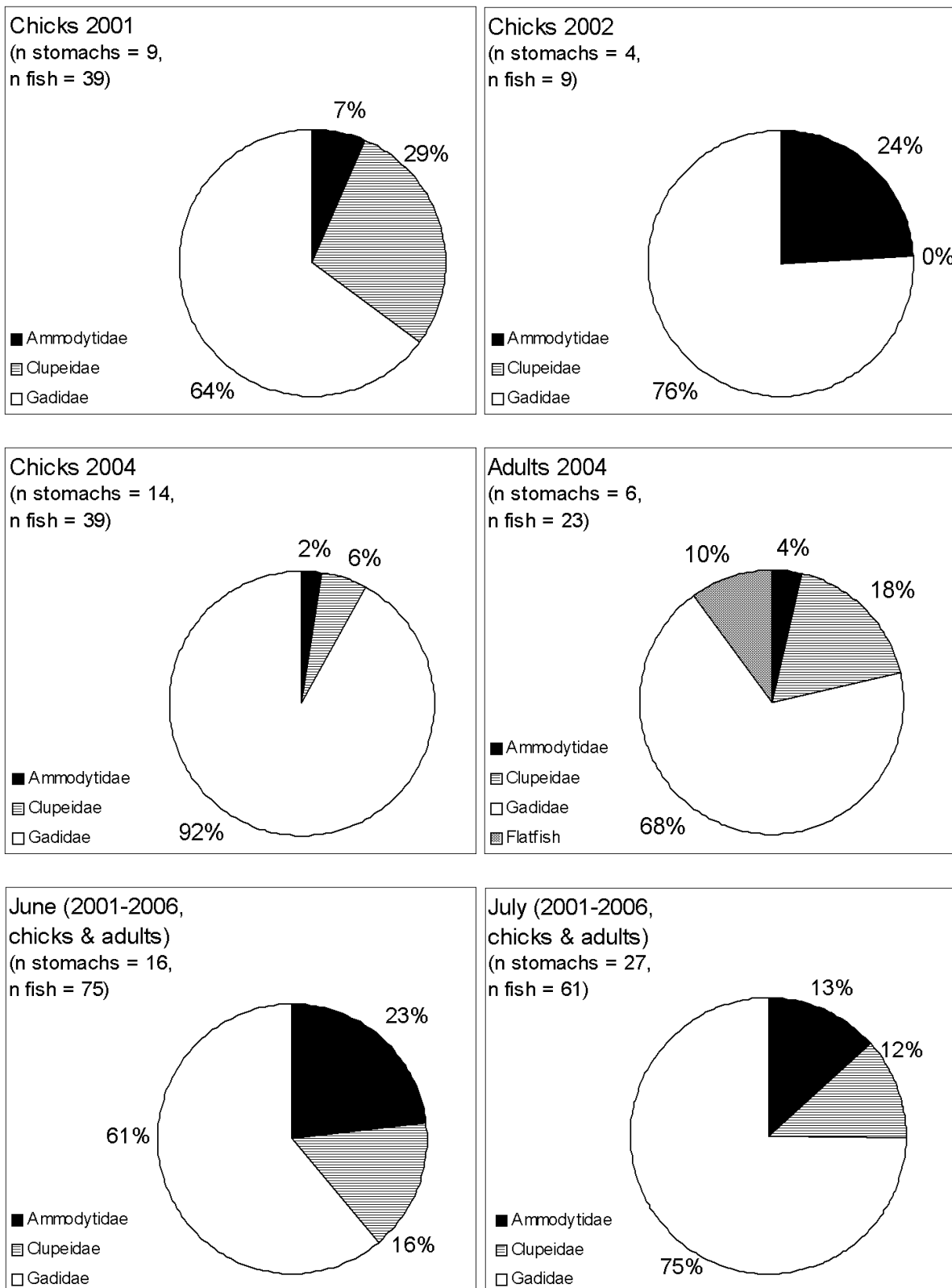


Figure 3.2: Monthly and yearly variation in importance of the main fish families in the diet of Kittiwake nestlings and adults based on calculations of total biomass.

Table 3.3: Frequency of occurrence of prey items in stomachs of Kittiwake nestlings and adults. N = number of stomachs containing the respective prey item; Total N = Total number of stomachs with prey items; % = proportion of stomachs containing the respective prey item of the total number of stomachs with prey items (see Table 3.2). The categories of Gadidae, Ammodytidae, Clupeidae and Pleuronectiformes (only Bothidae and Pleuronectidae) combine results of all identified and unidentified (indet.) species of the respective family as given below.

	2001		2002		2004		2006	2001-2006	
	N chicks (Total N =16)	N adults (Total N =3)	N chicks (Total N =13)	N adults (Total N =1)	N chicks (Total N =26)	N adults (Total N =6)	N chicks (Total N =19)	N chicks (Total N =74)	%
Gadidae	12	2	7	1	21	5	0	40	54%
Whiting <i>Merlangius merlangus</i>	8	1	5	1	14	5	0	27	37%
Poor cod <i>Trisopterus minutus</i>	0	0	0	0	2	0	0	2	3%
Gadoid indet.	6	1	2	0	8	0	0	16	22%
Ammodytidae	1	3	6	0	3	1	6	16	22%
Lesser Sandeel <i>Ammodytes marinus</i>	0	1	1	0	0	1	3	4	5%
Great Sandeel <i>Hyperoplus</i> sp.	0	0	1	0	0	0	0	1	1%
Sandeel indet.	1	2	4	0	3	1	3	11	15%
Clupeidae	7	1	1	0	3	2	5	16	22%
Herring <i>Clupea harengus</i>	1	1	0	0	2	2	1	4	5%
Sprat <i>Sprattus sprattus</i>	2	0	0	0	1	1	2	5	7%
Anchovy <i>Engraulis encrasicolus</i>	0	1	0	0	0	0	0	0	0%
Clupeid indet.	6	0	1	0	1	0	2	10	14%

Table 3.3: (continued)

	2001		2002		2004		2006	2001-2006	
	N chicks (Total N =16)	N adults (Total N =3)	N chicks (Total N =13)	N adults (Total N =1)	N chicks (Total N =26)	N adults (Total N =6)	N chicks (Total N =19)	N chicks (Total N =74)	%
Pleuronectiformes	0	0	0	0	0	1	0	0	0%
Dab	0	0	0	0	0	1	0	0	0%
<i>Limanda limanda</i>									
Scaldfish	0	0	0	0	0	1	0	0	0%
<i>Arnoglossus laterna</i>									
Flatfish indet.	0	0	0	0	0	1	0	0	0%
Goby indet. (Gobiidae)	0	1	0	0	0	0	0	0	0%
Wrasse indet. (Labridae)	0	0	0	0	1	0	0	1	1%
Fish indet.	3	1	1	0	4	2	0	8	11%
Polychaeta (Nereidae)	0	0	3	0	3	1	16	22	30%
Insecta (Coleoptera)	0	1	0	0	0	0	1	1	1%
Crustacea (Brachyura)	1	0	0	0	1	0	1	3	4%

3.4 Discussion

3.4.1 Methodology

The fact that our samples consist of birds that had died due to accident or disease leads to the question whether our results represent or at least correspond to natural diet composition of healthy birds. All adult birds with known body condition were either emaciated or suffered from an inflammation of lungs. Although diseased birds might have altered their foraging behaviour due to infection, we assume that diet recovered in adult birds corresponds to natural diet composition as these birds were not emaciated but well-nourished.

The majority of chicks probably died because of accidents leading to falling or getting pushed out of the nest. However, the question remains whether these chicks correspond to a representative sample. Malnourished birds were observed to show elevated activity and are thus called 'runners' (D. Kildaw, pers. comm.). Consequently, chicks of low-quality parents probably face a higher risk of falling from the nest, which either leads them to adoption by possible higher-quality parents when falling in a neighbouring nest or to death at the bottom of the cliffs. In correspondence, particularly chicks of 2004 weighed considerably less than well-nourished chicks from boreal climates. However, chicks younger than 10 days exhibited body mass more or less equalling that of 'well-nourished birds' (87% in 2004, 112% in 2006). Thus, growth curves of birds from boreal climates in Norway and Newfoundland probably can not be extrapolated to older birds at Helgoland. Growth curves of 10 nestlings from Helgoland raised by hand indeed indicate different growth and lower mean peak masses (363 g, Voss et al. 1987) compared to values of successful colonies in Newfoundland (400 g, Maunder and Threlfall 1972) and Norway (410 g, Barrett and Runde 1980). On the other hand, values of mean peak masses are comparable to more southern colonies from Northern England (350 – 375 g, Coulson and White 1958, Pearson 1968). Nevertheless, older nestlings falling from the nest appear to be individuals of lower body condition as noted already by Köth (1985).

The key question in this context however is the following: Does diet composition of malnourished chicks generally differ from diet of well-nourished birds or are these chicks fed with the same prey species of same length, however less often or by smaller food loads? With respect to the present study, it could be argued that only chicks fed with less energy-rich food died while chicks fed with food of higher energy density faced a lower risk of death. Although Whiting is not as energy rich as clupeids (Herring e.g. 6.5 kJ/g, Garthe et al. 1996), it is comparable to Lesser Sandeel with respect to nutrient composition and energy density (4.41 kJ/g vs. 4.63 kJ/g, Hilton et al. 2000). Overall, we found no indication that body condition of the analysed birds had an influence on presence, quality and quantity of prey remains. Thus, we assume that diet composition of malnourished birds does not differ from diet composition of well-nourished birds. Consequently, we regard our samples to be representative for the chicks of the breeding population.

Table 3.4: Occurrence, length [cm] and biomass [g] of fish prey found in stomachs of Kittiwake nestlings and adults at Helgoland in the different study years. Fish length and biomass were calculated based on otoliths (see Methods) and thus could not be derived for individuals, e.g. one Dab and one wrasse, identified according to objects other than otoliths. Mean no. = mean minimum number of individual fish per stomach containing remains of the respective prey species; Max no. = maximum number of individuals per stomach; N = total number of individuals recovered according to otoliths and other prey remains; No = total number of individual fish used for calculations of fish length and biomass.

	Mean no.	Max no.	N	No	Mean fish length		Range fish length		Mean biomass		Range biomass	
					chicks	adults	chicks	adults	chicks	adults	chicks	adults
Whiting <i>Merlangius merlangus</i>	3.3	1-17	113	86	9	11	6-21	5-21	10	17	1-70	1-68
Poor cod <i>Trisopterus minutus</i>	1	1	2	2	14	-	13-15	-	31	-	25-38	-
Gadoid indet.	1.2	1-4	21	3	12	-	9-15	-	14	-	5-25	-
Lesser Sandeel <i>Ammodytes marinus</i>	1.2	2	7	7	16	15	13-20	15-16	14	11	7-23	9-12
Great Sandeel <i>Hyperoplus</i> sp.	2	2	2	2	22	-	21-23	-	27	-	23-30	-
Sandeel indet.	1.4	1-4	19	7	15	21	13-17	21-21	9	30	6-13	30-31
Herring <i>Clupea harengus</i>	1.3	1-3	9	6	9	11	9-10	9-14	5	11	4-6	4-17
Sprat <i>Sprattus sprattus</i>	2.2	1-3	13	12	11	11	6-13	11-12	10	11	7-18	9-13
Anchovy <i>Engraulis encrasicolus</i>	1	1	1	1	-	15	-	-	-	18	-	-
Clupeid indet.	1.2	1-2	12	5	8	-	6-9	-	4	-	1-5	-
Scaldfish <i>Arnoglossus laterna</i>	4	4	4	4	-	9	-	7-11	-	8	-	3-13
Goby <i>Pomatoschistus</i> sp.	1	1	1	1	-	6	-	-	-	2	-	-

3 Diet composition of Black-legged Kittiwakes at Helgoland

Table 3.5: Factors influencing fish length according to GLMMs. Age = chick or adult; month = June or July; age class = age of chicks (see Methods).

Data set	Predictor variable	Random effect	N observations	N groups	p
Gadoids	Month	Age, year	91	3, 2	0.02
Clupeids	Month	Age, year	24	3, 2	n.s.
Sandeels	Month	Age, year	16	4, 2	n.s.
Gadoids of 2004	Age	Month	48	2	n.s.
Gadoids of chicks 2004	Month	Age class	35	4	0.003
Gadoids of chicks 2004	Age class	Month	35	2	n.s.

However, stomach contents still might not depict a representative picture due to differences in digestibility of species-specific prey remains. Otoliths of clupeids e.g. are smaller and delicate compared to otoliths of similar-sized gadoids and thus are digested within a shorter period of time while prey remains of gadoids persist for longer (see Brugger 1992). Thus, it is likely that higher proportions of gadoids are recovered, leading to an overestimation of their importance regarding diet composition. Correspondingly, Prüter (1989) showed that the proportion of clupeids and sandeels in overall diet composition of Kittiwakes on Helgoland in 1983-85 was higher (and proportion of gadoids lower) when samples were confined to stomachs with completely filled proventriculus exclusively. However, frequency of occurrence of sandeels was very high (>50%) in all samples from 1983-85, while numbers of sandeels and clupeids were low in the present study, and frequency of occurrence was always lower than values of gadoids. Prüter (1989) underlined his findings by the fact that almost all otoliths of gadoids were heavily worn and the majority of stomachs containing gadoid otoliths did not hold other remains of gadoids such as vertebrae. In contrast, the majority of gadoid otoliths recovered in the present study was in good shape (no or only slight wear) and otoliths were often recovered along with vertebrae and other bones of gadoids. Furthermore, unlike otoliths of clupeids, otoliths of sandeels can not be termed delicate and thus digestion time is assumed to be comparable to otoliths of similar-sized gadoids. Finally, sandeel otoliths recovered in the present study were only slightly smaller than gadoid otoliths (median otolith length=2.8 vs. 3.7 mm, but median of clupeid otolith length=1.6 mm). In conclusion, we are confident that bias due to differing digestibility did not constrain our principal result of Whiting being the major prey in the study years 2001-2004.

Table 3.6: Comparison of present results with previous studies: occurrence of fish remains, main prey species and length of consumed Whiting in the diet of Kittiwakes at Helgoland according to food remains in stomach samples. Note that all results refer to nestlings with the exception of the period 1990-92 that contains data of 11 adults additionally (Maul 1994). Stomachs containing fish remains are given in % of stomachs with contents. Calculations of fish length of Whiting consumed in 2001/02 and 2004 based on otoliths of Whiting only equalled calculations based on otoliths of Whiting and unidentified gadoids. Saithe = *Pollachius virens*, Haddock = *Melanogrammus aeglefinus*.

Period	N stomach samples	Stomachs without contents	Stomachs containing fish remains	Main prey species	Length of Whiting consumed	Source
1980-82	113	11.5%	78.0%	Saithe / Haddock, Whiting	min-max: 6-13 cm	Vauk-Hentzelt and Bachmann (1983)
1983-85	560	8.8%	96.7%	Sandeels, Whiting	∅ 16 cm (min-max: <10-23 cm)	Prüter (1989)
1990-92	320	14.0%	62.6%	Whiting	∅ 13 cm (min-max: 7-22 cm)	Maul (1994)
2001	29	13.8%	64.0%	Whiting	∅ 8 cm (min-max: 6-13 cm)	This study
2002	20	10.0%	66.7%	Whiting	∅ 20 cm (min-max: 19-21 cm)	This study
2004	33	6.1%	80.7%	Whiting	∅ 9 cm (min-max: 6-19 cm)	This study
2006	23	8.7%	42.9%	Nereidae	<i>not found</i>	This study

3.4.2 Comparison to earlier studies

The diet composition in the years 2001, 2002 and 2004 assessed in this study corresponds well to earlier studies on food of Kittiwake nestlings at Helgoland (Table 3.6). With the exception of 2006, Whiting was always the major or one of the main prey species in the diet of chicks at Helgoland. Moreover, the size of fish consumed was more or less the same over the different study periods, implying that mostly Whiting of age class 0 were preyed upon (following Knijn et al. 1993). No information of parasite infestation was given in studies of the 1980s. Parasite prevalence of birds from 1990-92 however was with 9% substantially lower than the values recorded for chicks and adults in the present study (58% and 100%, respectively). Proportion of infested birds varied between years both within the early 1990s (range: 7-16%) and 2001-2006. Infection of chicks with parasites can either result from larval stages in prey such as fish, which are intermediate hosts of parasites recorded in Kittiwakes (Maul 1994), or chicks can obtain parasites directly with prey loads delivered by infested parents. Thus, the probability of infection rises with the total sum of feedings and thus the age of chicks. However, differences between the 1990s and the present study are substantial and it is unlikely that samples collected in 1990-92 comprised youngest chicks only. Thus, this result could either represent an artefact due to different methods of preparation of samples or parasite load of birds indeed increased over the years. Parasite infection might be influenced by differences in prey species due to host-specific parasites (not applicable in this case) or by parasite prevalence of prey.

3.4.3 Whiting: discard or natural prey?

As gadoids are generally classified as demersal fish species (Muus and Nielsen 1999), Whiting and other gadoid species were believed not to be naturally available for the surface-feeding Kittiwake, which reaches a maximum diving depth of 1-2 m only during surface plunging (Burt 1974). Earlier studies consequently assumed Whiting to be mainly accessible to Kittiwakes in form of fisheries discard (Vauk-Hentzelt and Bachmann 1983, Prüter 1989, Maul 1994). Thus, Kittiwakes were believed to rely heavily on fisheries and thus were supposed to be highly vulnerable to reductions in this anthropogenic food source (Camphuysen et al. 1995). However, only a very low percentage of Kittiwakes was actually observed at fishing vessels in the German Bight (<5%, Jan-Dec 1990-2006, German Seabirds at Sea database v5.07). In the breeding season of 2006, the at-sea distribution of Kittiwakes in the sea area around Helgoland was studied intensively (chapter 4, page 49) and not a single individual was recorded at fishing vessels. In conclusion, Kittiwakes do not seem to spend a high percentage of their time feeding on discards. Instead, analyses of dedicated cruises depicted an association of Kittiwakes with hydrographic fronts during summer. In correspondence, the major concentration areas of Kittiwakes coincide with areas of high frontal activity during the breeding season (chapter 2, page 13). Most interestingly, young Whiting (<15 cm total length) were

found to concentrate in frontal areas of the North Sea (Flöter 2005). Moreover, the German Bight represents one of the concentration areas of juvenile Whiting within the North Sea in summer (<http://www.ices.dk/marineworld/fishmap/ices/pdf/whiting.pdf>). Juvenile gadoids are characterised by a pelagic phase, which extends over a longer period in the case of Whiting (Muus and Nielsen 1999). In correspondence, dense schools of juvenile Whiting were recorded in the upper water column of the sea area around Helgoland in August 2004 in the course of a fisheries research cruise (D. Stepputtis, pers. comm.). These findings lead to the assumption that juvenile Whiting are indeed available in high concentrations near the sea surface in frontal areas of the German Bight, where they can be preyed upon by foraging Kittiwakes. Consequently, we consider Whiting in the diet of Kittiwakes at Helgoland to originate from a natural feeding area independent of commercial fishing activities.

3.4.4 Diet composition in 2006

Our samples of 2006 comprise three unusual aspects contrasting earlier results: (1) An exceptionally high number of chicks died within a few days although weather conditions were not stormy. (2) No Whiting was found in stomach samples. (3) The main prey item according to stomach contents were polychaetes (Nereidae).

Nereidae are benthic polychaetes and thus are like benthic fish, usually out of reach for surface-feeding Kittiwakes. During reproduction however, most Nereidae evolve epitokous Heteronereis stages swarming in the surface layers which simultaneously release gametes within a few days ('epidemic spawning', Watson et al. 2000). These ephemeral patches of swarming Nereidae have been found to attract high numbers of gulls (SE North Sea, N. Markones and N. Guse, unpubl. data) and other seabirds, e.g. Surf Scoters *Melanitta perspicillata* (Lacroix et al. 2005). No information was available on energy content of Heteronereis stages, but this prey can be assumed to possess relatively high energy density due to large numbers of mature gametes per individual. Common nereid species in the sea area around Helgoland swarming in June/July comprise *Nereis virens* and *Eunereis longissima* (I. Kröncke, pers. comm.). Due to its small size, the latter probably was not relevant in the present study as jaws recovered in Kittiwake stomachs were relatively large with an estimated mean length of 3 mm. However, Kittiwakes reach maximum foraging distances of 80 km around the colony (Camphuysen 2005) and thus are also able to feed on Nereidae swarming in the coastal zone. Thus, species like *Nereis succinea* and *Nereis zonata* could also be prey of Kittiwakes from Helgoland (following Dankers et al. 1983a). *Nereis diversicolor*, a common species of the Wadden Sea area however does not form epitokous Heteronereis stages (Hartmann-Schröder 1996). On 28 June 2006, smaller concentrations of Kittiwakes were recorded near the 10 m water depth contour at the edge of the Wadden Sea region (Fig. 3.3). Jaws of Nereidae were first recorded in 2006 in one stomach sample of 1 July, while four birds collected on 27 or 29 June either did not contain any prey remains or contained one Sprat or one unidentified clupeid, respectively. Due to resistible chitinous material, digestion of nereid

jaws presumably takes relatively long (see also Leopold and Van Damme 2003) similar to that of cephalopod beaks (Furness et al. 1984). Fish remains on the other hand can be completely digested by Kittiwake chicks (Prüter 1989). Thus, it remains unclear whether birds were already preying on nereid worms on 28 June. In addition, possible feeding flocks over smaller nereid patches might have been missed due to distances of 8 km between the different aerial observation transects.

Did birds feed on Nereidae because of exceptionally high availability of this prey in form of swarming Heteronereis stages or because of exceptionally low availability of fish prey, i.e. of Whiting? It may be speculated that a single factor, i.e. temperature, influenced both availability of Whiting and Nereidae and caused high mortality of Kittiwake chicks. In the respective period, high temperature of air and water was recorded with sea surface temperature in the German Bight rising above 19°C and temperature at the sea bottom around Helgoland rising above 17°C (Wegner 2007). Temperature of the seabird breeding cliffs, which are mainly oriented to SW, presumably reached extremely high values. Direct radiation and high temperatures constrain thermoregulatory abilities and cause heat stress both in adults and chicks of Kittiwakes. Under such circumstances, parent birds are forced to leave the nest, leading to death of chicks due to heat stress or lack of food (Barrett and Runde 1980). In correspondence, Becker et al. (1997b) reported high mortality of fledged chicks of Common Terns *Sterna hirundo* at the German North Sea coast in summer 1989 and 1992, when water temperature reached values of >20°C. Mortality, which was accompanied by low values of growth and body mass in 1989, was not referred to direct heat stress but rather to food shortage. In that study, the main prey, Herring, had deserted the Wadden Sea area during the heat wave, leading to a depressed supply of energy and water for the chicks. Most interestingly, low body mass values and increased mortality were also recorded for Kittiwake chicks at Helgoland in the same year (O. Hüppop in Becker et al. 1997b).

Like Herring and Cod *Gadus morhua*, which strive to remain in water bodies of stable temperature to avoid energetically costly reacclimation processes (Claireaux et al. 1995), Whiting presumably desert water bodies of increasing temperature during periods of extreme heat. On the other hand, swarming of Nereidae is triggered by certain threshold temperature levels. *Nereis succinea* and *N. virens* thus require a rise in water temperature to 16°C or higher and greater than 5-8°C, respectively (reviewed in Watson et al. 2000). Moreover, suddenly raised temperatures can cause swarming in polychaetes independent from other factors such as lunar timing (Hardege et al. 1990). With regard to frequency of occurrence and numbers of Nereidae found in Kittiwake stomachs in 2006, which were all collected between 1 and 4 July, it is highly probable that Kittiwakes preyed upon swarming Heteronereis stages occurring ephemerally at the sea surface. However, it remains unclear whether swarming was actually induced by the observed rise in temperature or whether it was triggered by other parameters, e.g. the lunar cycle (Watson et al. 2000). In conclusion, superabundance of swarming Nereidae and absence of Whiting might explain diet composition of Kittiwake nestlings in July 2006. It can be assumed that Nereidae did not provide comparable values of lipid and above all water content, making them less suitable prey in periods of heat stress.

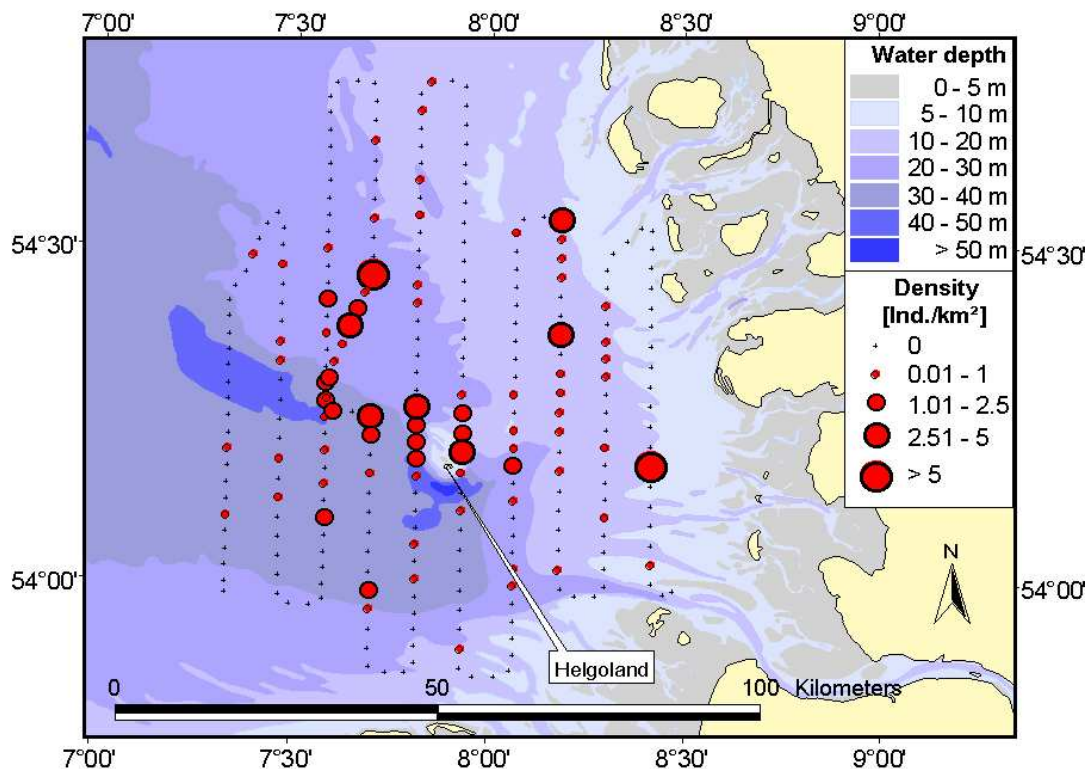


Figure 3.3: Distribution of Black-legged Kittiwakes as recorded during an aerial survey on 28 June 2006. (Flight route had to be slightly altered due to an active danger zone to the Northwest of Helgoland.)

3.5 Conclusions

3.5.1 Quality of samples

Collection of dead chicks currently represents the only method at the study site to investigate Kittiwake diet. Results of the present study and earlier analyses imply that these samples indeed provide valuable information regarding diet composition of Kittiwakes from the breeding colony on Helgoland. Due to maximum foraging distances of approximately 80 km, Kittiwakes may sample a relatively large sea area around Helgoland. Thus, they provide valuable information for the inner German Bight on the occurrence of pelagic prey, which is generally difficult to sample (Montevecchi 1993). However, results have to be interpreted with care. Thus, there is risk of sampling the 'losers' of the breeding colony, and the availability of samples may be influenced by environmental incidents.

3.5.2 A menu of winners?

The population trend of Kittiwakes at Helgoland differs substantially from the situation of breeding colonies in the northern North Sea. However, the persistent increase in breeding numbers observed in the 1990s might at least partly result from birds immigrating from other colonies as it had been shown for periods of rapid growth in the 1970s and 1980s (Fleet 1984). Although leading to a doubling of breeding numbers at Helgoland, the observed increase by 4,000 breeding pairs is negligible compared to declines in the Northern North Sea (following Heubeck 2004, ICES-WGSE 2006). Unfortunately, no detailed information is available concerning breeding performance of Kittiwakes at Helgoland. Some indications however can be drawn from results of the present study. Thus, the low body condition of chicks in 2004 coincides with devastating breeding performance of Kittiwakes in many British colonies (ICES-WGSE 2006). In contrast, mortality in 2006 can probably be attributed to exceptionally high temperatures whilst overall condition of chicks was good. Overall, the combination of present results and earlier studies leads us to the conclusion that Kittiwakes at Helgoland were well off while consuming predominantly Whiting for several decades.

However, data from fisheries research catches and commercial catches indicate that the Whiting stock of the North Sea has declined since 1991 to a low level compared to earlier years (ICES-WGNSSK 2006). In the German Bight, older/adult Whiting have not been caught in higher numbers in International Bottom Trawl Surveys since 1997 and numbers were already low since 1993. In addition, numbers of young Whiting at age 1 decreased substantially in IBTS catches since 2003 at the level of the entire North Sea (S. Ehrich, pers. comm.). However, trends vary spatially probably due to the fact that Whiting forms two separated stock units in the northern and the southern North Sea (ICES-SGSIMUW 2005). There are indications that the abundance of Whiting in the southern part of the North Sea increased between 2001 and 2005 while it remained stable or declined in the central and northern part of the North Sea (ICES-WGNSSK 2006). No information could be derived on probable changes in energy density of Whiting, but according to data from landings, mean body mass at age 1 increased from 1995 to 2005 (ICES-WGNSSK 2006). This positive trend indicates good feeding conditions both for young Whiting and its predators.

Differing trends for marine prey stocks in the southern and the northern part of the North Sea are also indicated by an exceptionally high abundance of seabirds and marine mammals in the southern North Sea in recent years (Camphuysen 2006). For the latter group this phenomenon can in particular be observed for Harbour Porpoises *Phocoena phocoena* which showed a shift in their main concentration area from the northern to the southern North Sea between 1994 and 2005 (Hammond and Macleod 2006). Following Clark and Frid (2001), distinct ecosystem changes in the northern, western and central part of the North Sea are generally mainly caused by climatic changes while ecosystem changes in the southern and eastern part are predominantly driven by changes in nutrient input from anthropogenic sources. Thus, current climatic changes like increasing temper-

atures probably led to reductions in food availability for seabirds and marine mammals in the northern part of the North Sea but presumably did not cause significant changes in the southern part. It remains unclear however, whether the latter will persist to provide good foraging grounds for marine top predators or whether comparable ecosystem changes in this region will become evident after a certain time lag. Like seabird research in the northern North Sea, future studies of breeding numbers, breeding performance and diet composition of Kittiwakes at Helgoland could provide the potential to evaluate the situation of marine prey stocks in the German Bight and to identify major ecosystem changes.

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4 Small scale temporal variability of seabird distribution patterns in the south-eastern North Sea

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Abstract

A series of replicate surveys was conducted to assess extent and sources of small scale temporal variability in seabird distribution patterns in the German Bight, south-eastern North Sea. Both aerial and ship-based surveys were applied to focus on the extent of variability in distribution patterns and on the influence of environmental parameters that evoke and shape such variability. Significant changes in distribution and abundance of seabirds were recorded at the order of days and smaller time spans. Interspecific differences in stability of distribution patterns were assumed to result from differences in foraging behaviour. Abundance, distribution and behaviour of birds were significantly influenced by a variety of environmental parameters, such as hydrographic fronts, wind speed, tidal stage and time of day. These environmental factors vary at periodic or stochastic intervals and thus have the potential to evoke predictable and unpredictable variation in seabird distribution patterns. Knowledge of sources of variability is essential for the evaluation of results of past and future studies on seabird distribution patterns, the design of monitoring programmes focusing on changes in distribution and numbers and the evaluation of consequences of anthropogenic impacts.

4.1 Introduction

Seabirds are generally not dispersed uniformly at sea but aggregate at different scales due to individual associations and spatially varying availability of resources (Hunt and Schneider 1987, Brown 1988). Next to this spatial variation, seabird distribution patterns also undergo temporal variation, mostly in response to temporally varying availability of resources (Hunt and Schneider 1987). Temporal variability in distribution patterns

is here above all defined as changes in spatial patterns, e.g. shifts in concentration areas. This temporal variability of spatial aspects is further supplemented by variability in overall density, i.e. changes in total numbers which are caused by individuals emigrating or immigrating into the study area. Like spatial variability, temporal variability occurs at different scales. Thus, seabird distribution patterns change at the order of decades and years (Final EU-Report BECAUSE, in prep.), at the order of seasons and at smaller scales such as days. In the south-eastern North Sea extensive research has focused on seasonal dynamics of seabird distribution patterns (Garthe et al. 2004). At present, mean distribution patterns of all major seabird species can be depicted for each season. However, small and meso scale variability can be substantial, thus constraining explanatory power of mean distribution patterns. To our knowledge, an analysis of extent and sources of small scale variability of distribution patterns was seldom the focus of past seabird studies world-wide (but see Becker et al. 1997a, Speckman et al. 2000). Variability of seabird distribution patterns complicates conservation and management efforts as it constrains (a) the ecological valuation of specific areas, (b) the calculation of total numbers, and (c) the assessment of population trends or shifts in distribution. However, understanding sources of variability enables us to evaluate results of past and future studies on seabird distribution patterns, to design monitoring programmes focusing on changes in distribution and numbers, and to evaluate consequences of anthropogenic impacts.

In the south-eastern North Sea, plans for offshore wind farms necessitated an ecological accompanying research evaluating the construction, maintenance and operation of wind farms with respect to impacts on seabirds amongst others to enable an ecologically sound and sustainable utilisation of offshore wind energy (Kellermann et al. 2006). Next to an assessment of general distribution patterns, a description of small to meso scale variability within areas of concern was required to complete mean distribution patterns with respect to the ecological valuation of specific areas.

For a number of reasons, the south-eastern North Sea represents both an exceptional and highly suited study area with respect to research on small scale variability of seabird distribution patterns. First, its hydrography, which forms main habitat structures influencing seabird distribution (Garthe 1997, Skov and Prins 2001, chapter 5, page 71, and chapter 2, page 13) is characterised by high small to meso scale spatial and temporal variability (Becker and Prahm-Rodewald 1980, Dippner 1993). Secondly, its seabird community mostly comprises gulls (both truly marine species such as Black-legged Kittiwakes *Rissa tridactyla* and coastal species such as *Larus* gulls) and terns which are highly mobile opportunistic foragers. Gulls and terns predominantly spend their time flying and thus change position rapidly compared to species swimming most of their time. Moreover, gulls in particular use a variety of different food sources, ranging from fisheries discards and offal to pelagic fish, crustaceans and benthic invertebrates of the Wadden Sea mud flats, and may include even terrestrial organisms from agriculturally dominated habitats. The different food sources are characterised by varying availability changing either at periodic intervals, such as benthos availability influenced by tidal rhythms, or irregular intervals such as fisheries discards. Due to their high mobility, gulls are able to respond to changing prey availability within short time spans and thus

are able to exploit the different habitats very effectively. Thus, it is assumed that gulls exhibit higher levels of variability in distribution patterns than e.g. Common Guillemots *Uria aalge* which spend most of their time swimming (chapter 6, page 89).

To analyse extent and sources of variability in seabird distribution patterns, we applied a series of replicate surveys. Emphasis was laid on aerial surveys as they offer the possibility of sampling large areas within short periods of time. Aerial surveys enabled Nettleship and Gaston (1978) to describe substantial changes in distribution of foraging seabirds within a few days. These shifts in distribution would most probably not have been recognised in the course of ship-based studies as these are progressing at the same temporal scale as potential movements of seabirds (following Brown 1980). However, during ship-based studies a variety of parameters, e.g. with respect to hydrography and food availability, can be sampled simultaneously along with seabird counts. These additional data represent the possibility to gain insight into sources of variability by describing factors influencing occurrence and thus variability of seabird distribution. We consequently applied aerial surveys to assess the extent of variability in large scale distribution patterns and carried out ship-based studies to focus on the influence of various environmental parameters.

Thus, the present study was set to meet the following objectives: We wanted to

- (1) test the stability of seabird distribution patterns and to investigate whether temporal variability is a major characteristic of seabird distribution patterns in the study area,
- (2) test for temporal variability at different scales (i.e. at the order of weeks, days and time spans shorter than days),
- (3) evaluate whether single species exhibited higher temporal variability in distribution patterns than others and try to explain possible differences,
- (4) identify parameters evoking and shaping variability in the study area.

4.2 Material and Methods

In the German Bight, seabird distribution patterns were recorded by aerial and ship-based surveys as described in chapter 1.3.3, page 8. Aerial surveys were only carried out during low wind conditions (Table 4.1) to obtain good observation conditions. Estimating temporal variability in animal abundances is constrained by sampling variance, i.e. sampling inexactness and spatial variance (Mönkkönen and Aspi 1997). In the ‘Seabirds at Sea’ programme, sampling inexactness is accounted for by avoidance (intercalibration of observers, snapshot method) and correction / mitigation (Buckland distance correction). Spatial variance results from the fact that the size of the sampling unit is inadequate to depict the distribution pattern of individuals in the sampling area (Mönkkönen and Aspi 1997). However, this problem is most relevant with respect to

4 Small scale temporal variability of seabird distribution patterns

Table 4.1: Dates of aerial surveys during the breeding season of 2006 and respective breeding stages of the two most common breeding species on Helgoland. Classification of breeding stages follows Dierschke et al. (2004), Grunsky-Schöneberg (1998), OAG Helgoland and pers. observations.

	7 Jun	9 Jun	19 Jun	28 Jun	12 Jul	13 Jul	12 Aug
Wind	NW 2-3 / N 1-2		S-SW 1-3	NW 3-4	S 1-2/ SW-W 1-3		N 1-3
Black-legged Kittiwake	Late incubation period		Hatching / Early chick-rearing	Chick-rearing	Late chick-rearing / Fledging		Colony deserted
Common Guillemot	Chick-rearing		Late chick-rearing / Chicks leave ledge	Colony mostly deserted, begin of moult	Colony mostly deserted, begin of moult		Colony deserted, moult

assessing numbers, i.e. variability in density. Although spatial variability can be confused with temporal variability in certain situations, this aspect is not considered to be relevant in the present analysis.

We carried out several dedicated surveys to assess variability of seabird distribution patterns at different temporal scales. In the breeding and immediate post-breeding period of 2006, aerial surveys were conducted along a specifically designed survey route focusing on the waters around the small offshore island Helgoland. The transect course was designed with regard to the breeding species of the seabird colony on Helgoland and covers in particular the central part of the mean distribution area of Black-legged Kittiwakes during the breeding season (Fig. 4.1). Distance between single transects was set to 8 km. Following the method described above, the entire route was sampled within one survey day. Surveys were carried out at different stages of the breeding period to assess differences in distribution patterns at the order of weeks. In addition, we also repeated surveys twice within one or two days, respectively, to assess small scale variability at the order of days (Table 4.1). Distribution patterns of Common Guillemots were derived by combining data on Common Guillemot and ‘Razormots’ (Common Guillemot / Razorbill *Alca torda*). This method was considered appropriate as numbers of Razorbills make up less than 1% of numbers of Common Guillemots in summer in the German Bight (Garthe et al. 2007). We tested differences in distribution of Kittiwakes and Common Guillemots between single surveys by modelling the occurrence of the species using the observation position. Thus, a spline of the latitude and longitude values formed the predictor variable in a Generalized Additive Model (GAM, Hastie and Tibshirani 1990, Wood 2006) using the quasi-Poisson function and the MGCV package (Wood 2000) in R 2.5.0 (<http://www.r-project.org/>). We compared models that based on data of two survey days with models that were fitted using the data of one of the survey days by

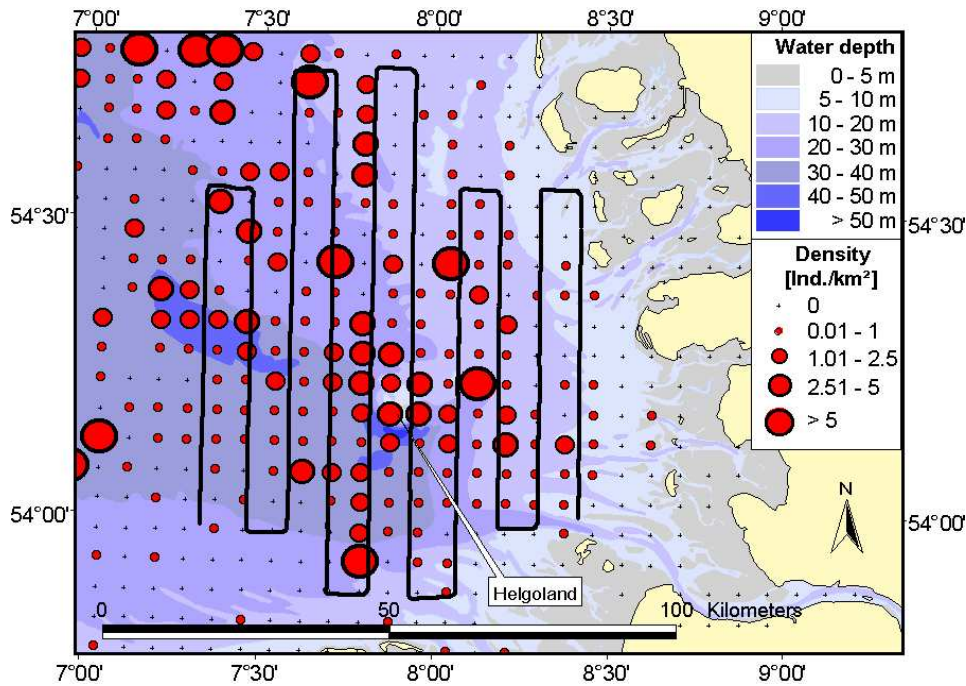


Figure 4.1: Transect lines of aerial surveys for studying the temporal variability of seabird distribution patterns. Additionally depicted is the mean distribution pattern of Kittiwakes during the breeding period (May-July, data source: German Seabirds at Sea database 5.07, comprising ship-based surveys from 1990-2006). Total length of survey transects \approx 840 km.

applying the ANOVA function (Wood 2006). Thus, we tested differences in the distribution of Kittiwakes between the survey days of 9 June, 19 June, 28 June, 12 July and 12 August to assess variability at the order of weeks. Bonferroni correction was applied to account for multiple testing. In addition, we tested differences in distribution patterns of Kittiwakes and Guillemots between 7 and 9 June, and 12 and 13 July, respectively, to get an indication of variability at the order of days.

A comparison of the same survey route was also carried out during a ship-based survey on 3 and 4 May 2006 in the vicinity of Helgoland ($54^{\circ}11'N$, $7^{\circ}55'E$). On both days, we recorded Kittiwake occurrence on a transect in north-westerly direction from the breeding colony. Sea surface hydrography (temperature and salinity) was assessed simultaneously along with bird counts using Ferrybox instrumentation (<http://www.ferrybox.org/>, Petersen et al. 2005). Additionally, bird counts were interrupted every 3 nautical miles to record vertical profiles of temperature and salinity continuously from sea surface to sea bottom using a CTD-cast. Stations were sampled at the same positions on both days. However, due to unfavourable weather conditions, two stations could not be sampled on 4 May, resulting in a total of 20 stations on 3 May and 18 stations on 4 May. Differences of Kittiwake distribution between the two survey days were tested by use of GAMs following the method described above for aerial surveys. To correlate Kittiwake distribution with hydrography, we divided the seabird survey route into transect

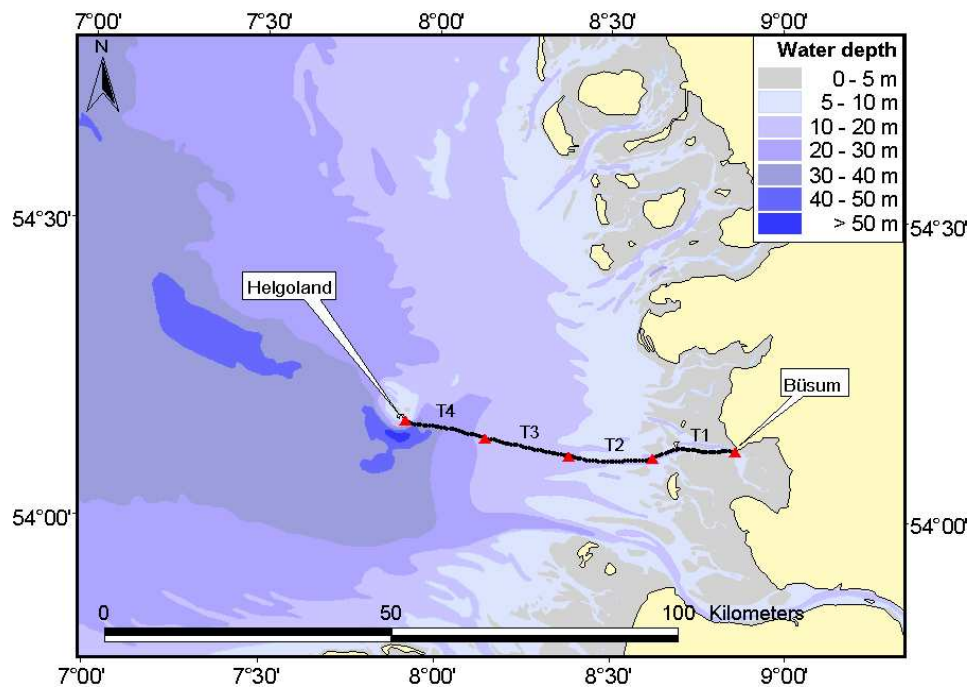


Figure 4.2: Survey route of ship-based studies between Helgoland and Büsum and classification of count sections T1-4.

segments prefacing and following a respective hydrographic station to obtain sampling units that were representative of the Kittiwake occurrence at the station or in its immediate vicinity. Segments were confined to a maximum of 12 min sampling time following or prefacing the hydrographic station. Thus, bird density was calculated for counting intervals covering a sampling area from 0.94 km² to 2.18 km² around (i.e. prefacing or following) the corresponding hydrographic station. We obtained indicators of frontal occurrence by calculating the average difference between consecutive sea surface salinity and temperature measurements per minute for the respective sampling unit around the hydrographic station. The difference between measurements at the surface and the seabed acted as indication of stratification. Next to these indicators of fronts (T_{front}, S_{front}) and stratification (T_{diff}, S_{diff}), we used sea surface temperature (SST) and sea surface salinity (SSS) as predictor variables in a GAM modelling the distribution of Kittiwakes. The model was fitted using five knots for each parameter and by applying the quasi-Poisson function. The model was selected using backward selection (applying the ANOVA function in R).

Small scale temporal variability of seabird distribution was additionally studied during ship-based studies in the coastal area between Büsum (54°08'N, 8°52'E) and Helgoland (Fig. 4.2). Bird counts were carried out along a regular ferry route on ten consecutive days in late summer 2003 from 12 to 21 August. The ferry travelled from Büsum to Helgoland in the morning between 7:30 h and 10:15 h UTC and returned from Helgoland

to Büsum in the afternoon between 14:15 h and 17:00 h UTC. However, on 15 August, the outbound survey had to be interrupted due to unfavourable weather conditions. The survey transect presented a section over different habitats such as the Wadden Sea region, the subsequent Elbe plume and the area around Helgoland which represents a more marine habitat. The route was divided into 4 sections, each comprising 16 km transect length. Thus, seabird distribution could be compared between days, different times of day (morning vs. afternoon) and count sections.

Dominant seabird species recorded during the survey between Büsum and Helgoland on the ten ship-based survey days in August 2003 consisted of six gull species and three tern species: Black-headed Gull *Larus ridibundus*, Common Gull *Larus canus*, Lesser Black-backed Gull *Larus fuscus*, Herring Gull *Larus argentatus*, Great Black-backed Gull *Larus marinus*, Black-legged Kittiwake, Sandwich Tern *Sterna sandvicensis*, Common Tern *Sterna hirundo* and Arctic Tern *Sterna paradisaea*. The latter two species were grouped as ‘Commic Terns’ due to identification difficulties. Differences in daily numbers of each species (group) were tested separately for different count sections and times of day. We applied a Pearson correlation with a 1-day time lag, i.e. tested for correlation of seabird occurrence on a given day with numbers of the following day. Due to missing data (see above) 15 August was ignored in the analysis, treating 16 August as successor of 14 August. Tests were only carried out for species exhibiting at least one positive occurrence (>0) in more than one of nine data pairs.

Furthermore, we tested the influence of several environmental parameters on the occurrence of the four most common species, Black-headed Gull, Common Gull, Lesser Black-backed Gull and Herring Gull, during the nine complete survey days. Trawler abundance was recorded simultaneously along with bird counts to investigate the influence of fishing activity on the occurrence of the four species, which are known to feed regularly on discard and offal. Data on wind speed was obtained from the meteorological station at Research and Technology Centre (FTZ) in Büsum. We incorporated maximum wind speed in the analyses as we expected a stronger influence of strong gusts compared to mean wind speed on gull mobility and thus gull occurrence. According to tide forecasts of the Federal Maritime and Hydrographic Agency (BSH), the tidal stage of each count section was classified as flood tide or ebb tide separately for each day and time of day. Analyses comprised data of count section 1 and 2 only as gulls predominantly occurred in this area (see Fig. 4.9). Moreover, trawlers were exclusively recorded in count section 1 and 2. We first tested influence of time of day, count section (= transect), tidal stage and maximum wind speed on trawler abundance applying a Generalized Linear Mixed Model (GLMM, e.g. Faraway 2006) in R using the package lme4 (Bates and Sarkar 2007). The model was set as follows: response variable = trawler number, predictor = daytime + transect + tide + wind, random effect = day, family = quasi-Poisson. The influence of time of day, count section, tidal stage and maximum wind speed on gull occurrence was tested independently from trawler abundance separately for each species applying a GLMM of the following kind: response variable = bird number, predictor = daytime + transect + tide + wind, random effect = trawler number, family = quasi-Poisson. Influence of trawler abundance on numbers of gulls was tested by comparing these GLMMs

4 Small scale temporal variability of seabird distribution patterns

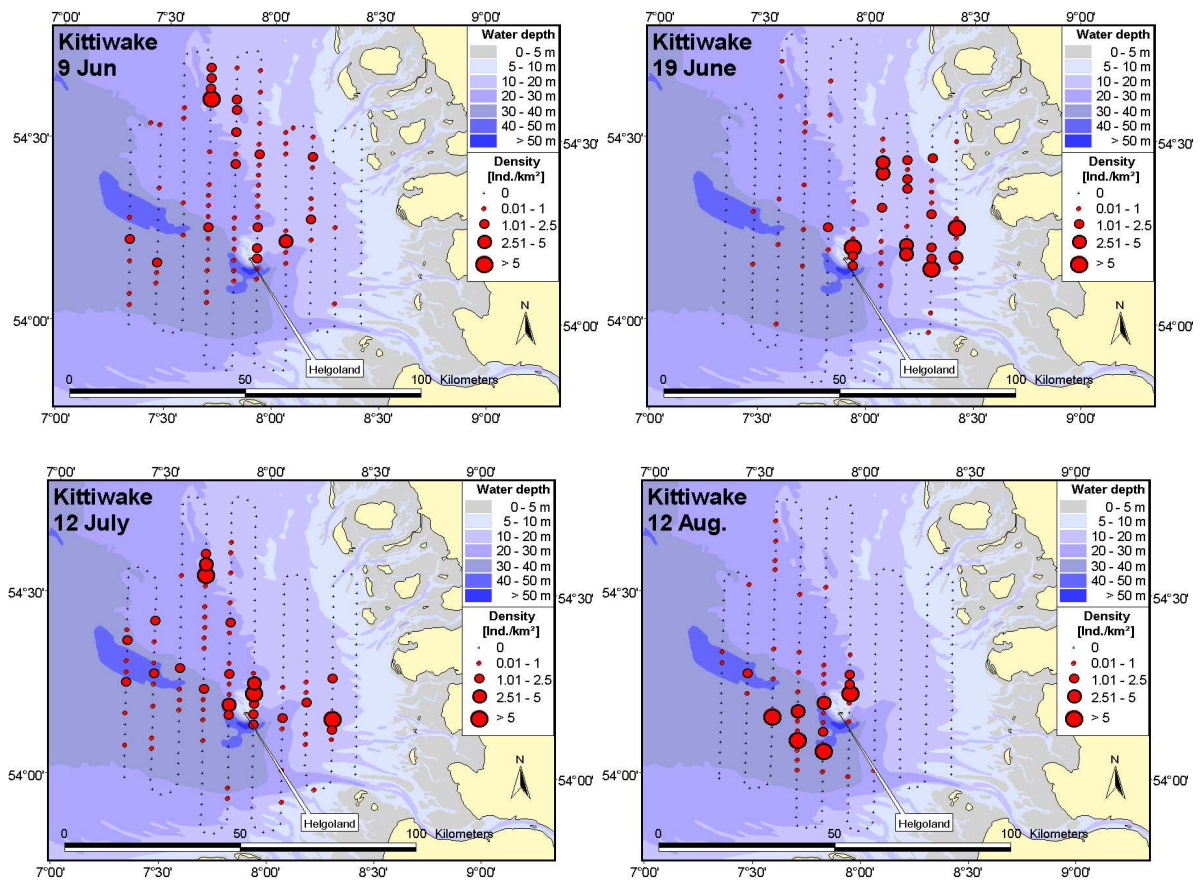


Figure 4.3: Temporal variability of seabird distribution patterns in the breeding and post-breeding period of 2006 in the south-eastern North Sea. Distribution of Black-legged Kittiwakes on 9 June, 19 June, 12 July and 12 August as recorded during aerial surveys.

with GLMMs incorporating no random effect (only one group) by applying the ANOVA function in R. Influence of trawler abundance on gull occurrence was regarded significant in case of significant differences between corresponding models. In addition, we tested the influence of daytime, count section, tidal stage and maximum wind speed on resting and scavenging behaviour applying a GLMM of the following kind: response variable = resting / vessel association, predictor = daytime + transect + tide + wind, random effect = day, family = binomial. For the analysis of behaviour, we incorporated data from all ten survey days. Models were selected using backward selection (applying the ANOVA function in R).

Influence of time of day was also tested for the distribution of Black-legged Kittiwakes during the breeding season (May-July) within the area 53.35° to 55.2° N and 5° to 9° E. Thus, we derived mean distribution patterns of this species for 6 different time periods, 2:30-5:59, 6:00-8:59, 9:00-11:59, 12:00-14:59, 15:00-17:59 and 18:00-20:30 h UTC, according to long-term ship-based surveys (1990-2006, data source: German Seabirds at

Sea database v5.07). Time periods were hereafter termed as 2-5, 6-8, 9-11, 12-14, 15-17 and 18-20 h UTC. No surveys had taken place before 2:30 h UTC and after 20:30 h UTC due to darkness. Distribution patterns were mapped in ArcView GIS 3.2 by calculating densities per 3' latitude x 5' longitude grid. Kittiwakes were recorded in distances up to 200 km from the breeding site. However, maximum foraging ranges of breeding Kittiwakes in the North Sea amount to 80 km (Camphuysen 2005). We thus tested differences in distribution within 80 km around Helgoland between different daytimes applying GAMs. We compared models that were based on the data of two different times of day with models that were fitted using the data of one specific daytime by applying the ANOVA function (Wood 2006). Thus, we tested for differences between each possible pair of times of day. Bonferroni correction was applied to account for multiple testing. We then analysed the occurrence of breeding Kittiwakes within different distance classes from the breeding colony on Helgoland. We considered individuals occurring in distances >80 km to be entirely independent of the Helgoland breeding colony and distinguished between distance classes of 0-20 km, 20-40 km, 40-60 km and 60-80 km. Mean densities were calculated separately for each class of daytime for the four different distance classes on the basis of grid data described above. The influence of daytime and distance from colony was tested on the basis of original data applying a GAM.

4.3 Results

The at-sea distribution of Black-legged Kittiwakes around the colony on Helgoland differed substantially between the four different survey days that took place in different stages of the breeding season of 2006. High numbers of Kittiwakes were always recorded in the vicinity of the breeding colony on Helgoland. On 9 June and 12 July, distinct concentrations were additionally observed along the 20 m depth contour in the north-west of the study area. High densities were also recorded in the Elbe outflow region east of Helgoland on 12 July. This area along the coast held the majority of Kittiwakes on 19 June. In contrast, it was completely deserted in the post-breeding period on 12 August, as Kittiwakes concentrated in the vicinity of Helgoland and further west and south-west (Fig. 4.3). Distribution patterns differed significantly between single surveys. Only the distribution patterns of 28 June (Fig. 3.3) and 12 July were not significantly different, yet both surveys differed significantly from the rest of the days. Significant differences were also detected between consecutive days (Fig. 4.4). The distribution of Common guillemots did not differ between 7 and 9 June ($p=0.4$) and was relatively similar between the surveys on the 12 and 13 July 2006 ($p=0.06$, Fig. 4.4, bottom). In contrast, the distribution of Kittiwakes differed significantly between 7 and 9 June ($p=0.0002$) and 12 and 13 July ($p=0.02$), showing e.g. a concentration area along the 20 m depth contour to the north-west of Helgoland on 12 July that had disappeared the next day (see Fig. 4.4, top).

4 Small scale temporal variability of seabird distribution patterns

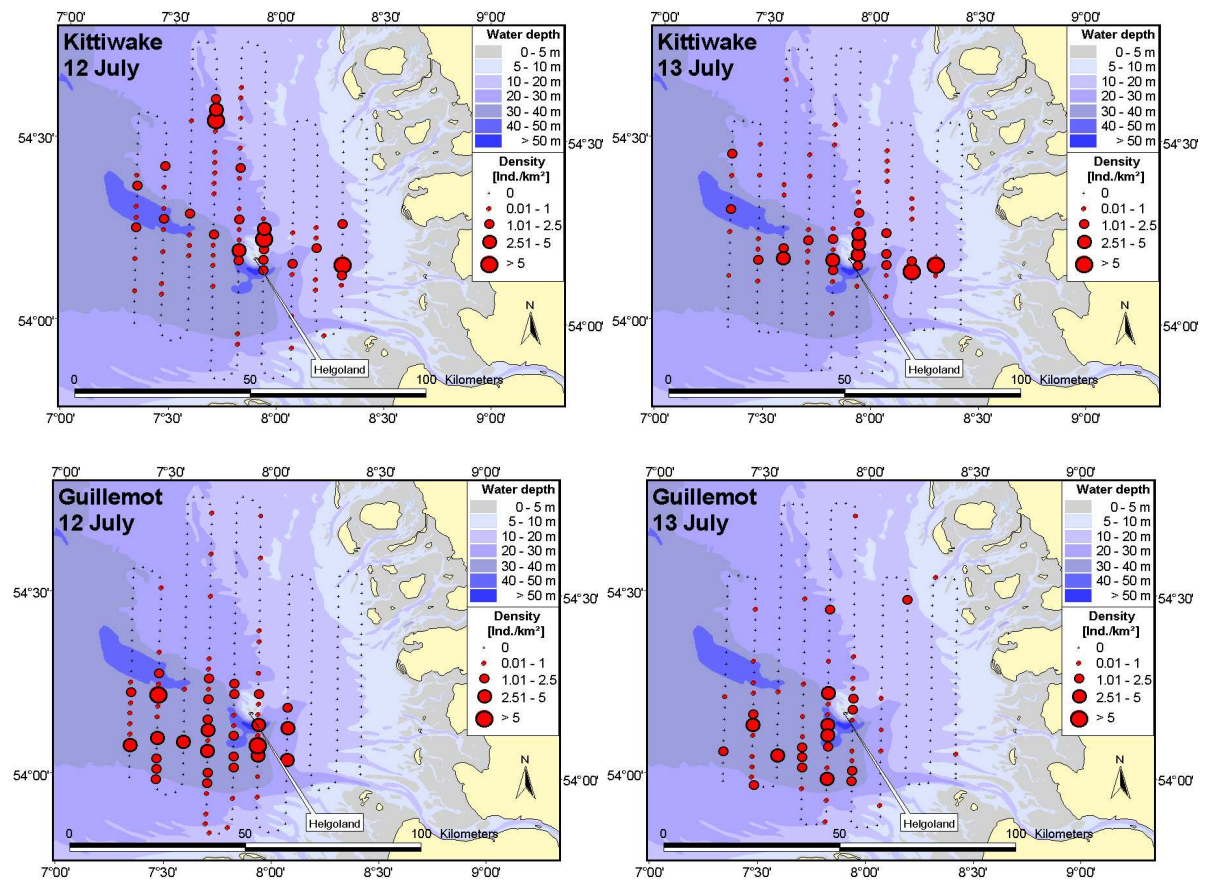


Figure 4.4: Small scale temporal variability of seabird distribution patterns in the breeding period of 2006 in the south-eastern North Sea. Distribution of Black-legged Kittiwakes (top) and Common Guillemots (bottom) on 12 (left) and 13 (right) July as recorded during aerial surveys.

Significant differences in Kittiwake distribution were also recorded between 3 May and 4 May 2006 during ship-based surveys ($F=8.387$, $p<0.0001$). On both days, high numbers were recorded in the vicinity of the colony. The second concentration area at sea however shifted further to the north-west from 3 to 4 May (Fig. 4.5). The occurrence of Kittiwakes was best explained by a GAM comprising sea surface salinity (SSS), and indicators of salinity fronts (Sfront) and temperature stratification (Tdiff). All parameters influenced Kittiwake occurrence significantly (variance of the intercept: -2.586 , $p=0.02$; SSS: $F=5.091$, $p=0.031$; Sfront: $F=5.156$, $p=0.003$; Tdiff: $F=5.030$, $p=0.003$). High intensity of salinity fronts had a distinct positive effect on Kittiwake distribution (Fig. 4.6). The model explained 65.8% of the total variance of the data. However, the model was based on 38 data points only and removing the data point of maximum density resulted in less significant effects (Figs. 4.6 and 4.7) and a lower value of 52.4% variance explained by the model.

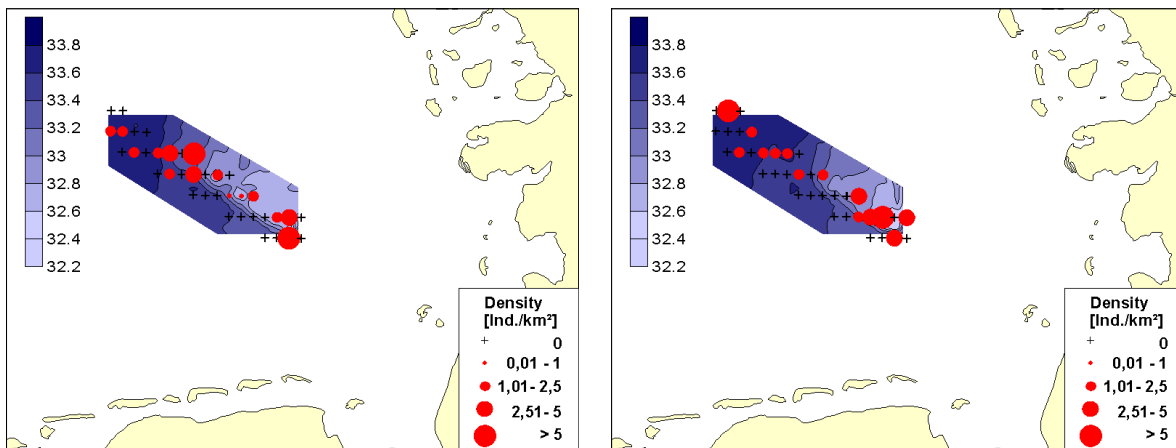


Figure 4.5: Sea surface salinity [psu] and distribution of Black-legged Kittiwakes on 3 (left) and 4 (right) May 2006 as recorded during ship-based surveys. Sea surface salinity was recorded simultaneously along with bird counts and was mapped by interpolating measurements via the kriging method in Surfer 8.01 (Anonymous 2002).

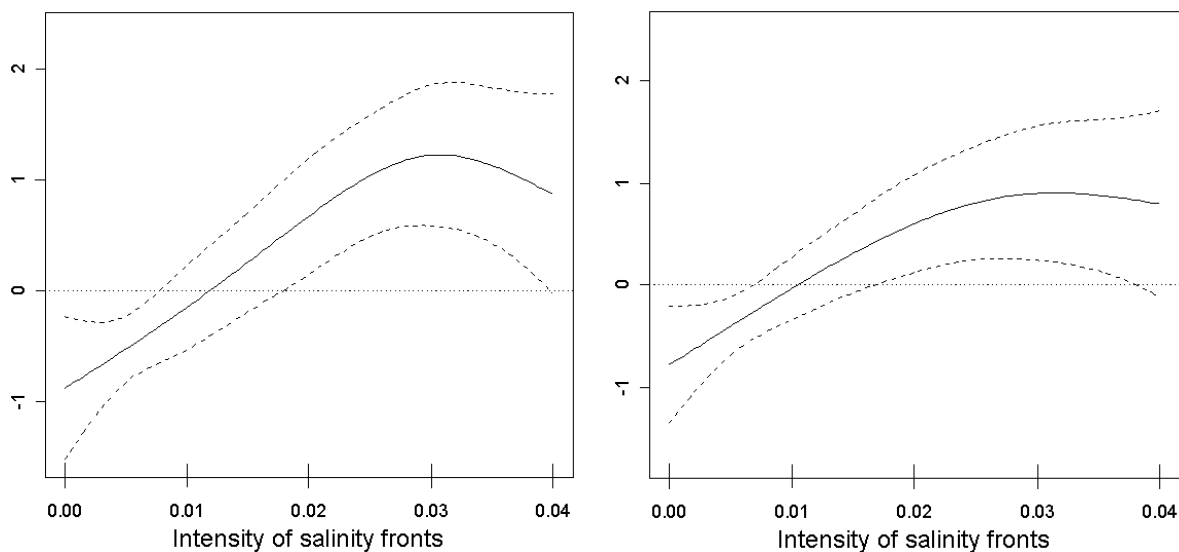


Figure 4.6: GAM smoothing curves fitted to partial effects of explanatory variables on density of Black-legged Kittiwakes during ship-based studies on 3 and 4 May. Density is represented as a function of intensity of salinity fronts depicted for a GAM based on complete data of both study days (left; $F=5.156$, $p=0.003$) and for a GAM based on data lacking the data point of maximum density (see Fig. 4.7; $F=2.989$, $p=0.03$; right). Dashed lines represent 95% confidence intervals around the main effects. High intensity of salinity fronts had a positive effect on Kittiwake distribution. Frontal intensity represents an indication of gradient strength and frequency of frontal incidents (see Methods).

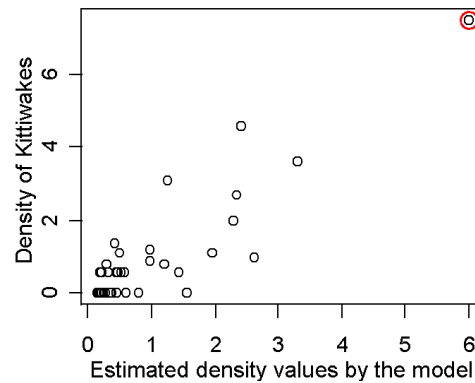


Figure 4.7: Estimated density by GAM versus measured density. High correlation is caused by the data point of maximum density encircled in red.

The occurrence of seabird species between Büsum and Helgoland on the ten ship-based survey days in August 2003 was characterised by high variability. Numbers of different species peaked at different times, and patterns of occurrence differed between the morning and afternoon trip and between consecutive days (Fig. 4.8). In accordance, analyses revealed no correlation of the occurrence of all eight gull and tern species (groups) between consecutive days: Only two of 55 Pearson correlation tests produced a significant result, making up a proportion of less than 2%. Thus, the proportion of significant results falls within the expected range ($<0.05\%$) of a dataset holding no effect. In addition, the mean correlation coefficient (mean rho) equals approximately 0, implying no trend. However, numbers did not vary randomly but were correlated to a variety of factors. Thus, trawler abundance correlated significantly positively with the occurrence of Black-headed, Common, Lesser black-backed and Herring Gulls. Trawler occurrence itself was significantly influenced by time of day, count section and wind, but not by tidal stage. Numbers of trawlers were higher in the second count section further offshore and decreased with time of day and with increasing wind speed. Thus, the influence of the factors time of day, count section, tidal stage and wind had to be tested independently from influence of trawler abundance. All four factors had a significant influence on the occurrence of all four species (significant at 0.05 level, n observations = 36, n groups of trawler abundance = 8). Numbers of all four gull species decreased with increasing wind velocity and were higher during flood tide compared to ebb tide. While numbers of Black-headed, Common and Herring Gulls correlated positively with time of day and negatively with distance to coast, Lesser Black-backed Gulls showed an inverse relationship with higher numbers in the morning and in the second count section further offshore. An overview over total numbers of gulls in each count section during the different times of day depicted striking spatio-temporal differences in area usage (Fig. 4.9). All species predominantly occurred in the first and second count section in the Wadden Sea region. In the morning, highest gull numbers occurred in count section 2 whereas in the afternoon most gulls occurred in count section 1 closer to the coast. Trawler numbers were higher in the morning in count section 2 but did not differ between times of day

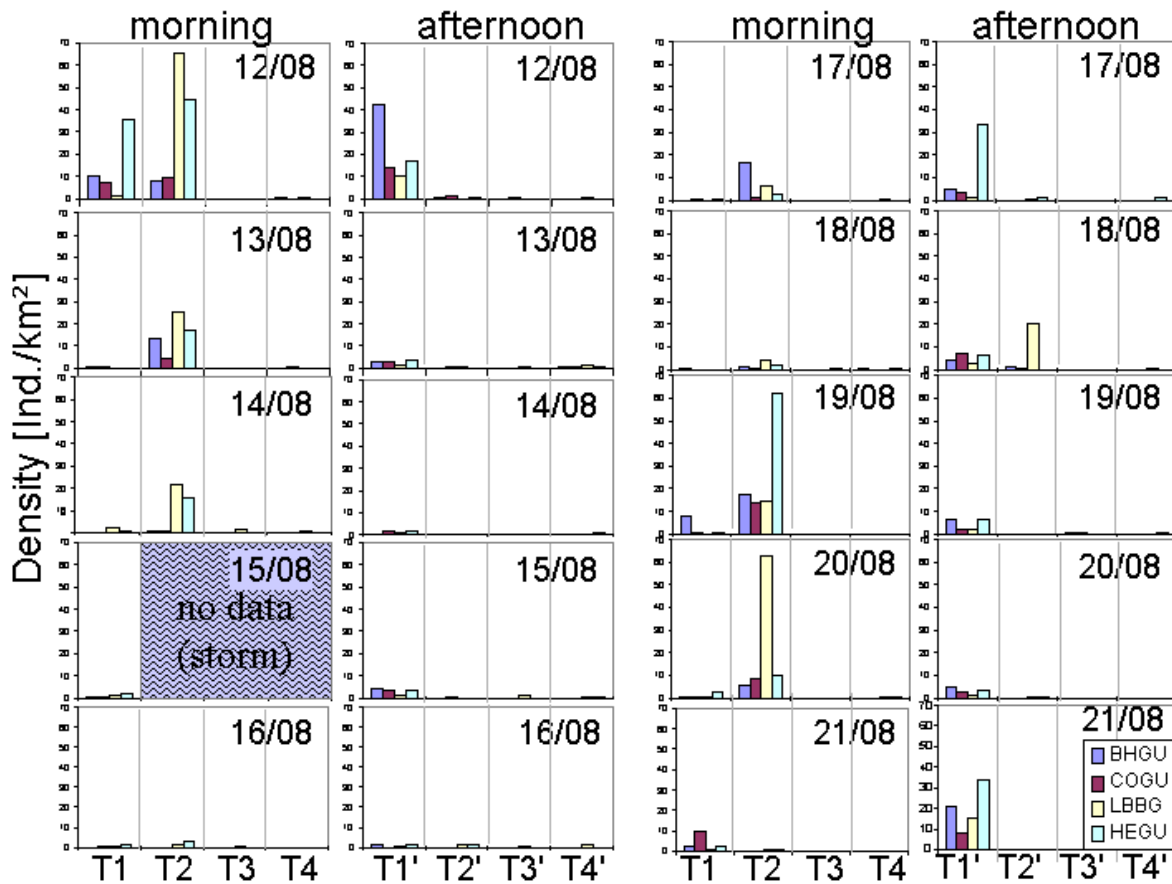


Figure 4.8: Variability of seabird occurrence during repeated surveys in the study area between Büsum and Helgoland in August 2003. BHGU = Black-headed Gull, COGU = Common Gull, LBBG = Lesser Black-backed Gull, HEGU = Herring Gull.

in count section 1. Next to the observed differences in numbers, all four gull species showed also differences in behaviour between times of day (Fig. 4.10). Levels of association with fishing vessels were generally higher in the morning, higher in section 2 and higher during ebb tide and in periods of low winds. Common Gulls however showed highest values of association with vessels in the afternoon. Resting behaviour correlated significantly positive with high winds, flood tide, count section 2 and increased in the afternoon (Table 4.2).

Significant differences between different times of day were also evident for the distribution of Black-legged Kittiwakes in the German Bight during the breeding season with low numbers at sea in the early morning and late evening and high numbers in the middle of the day (Figs. 4.11 and 4.12). According to the GAMs, the distribution pattern of each time of day differed significantly from every other daytime. Density of birds was influenced significantly negative by distance from colony ($F=41.69$, $p<0.0001$) and varied with time of day ($F=12.30$, $p<0.0001$, Fig. 4.12). Being constricted to the ultimate

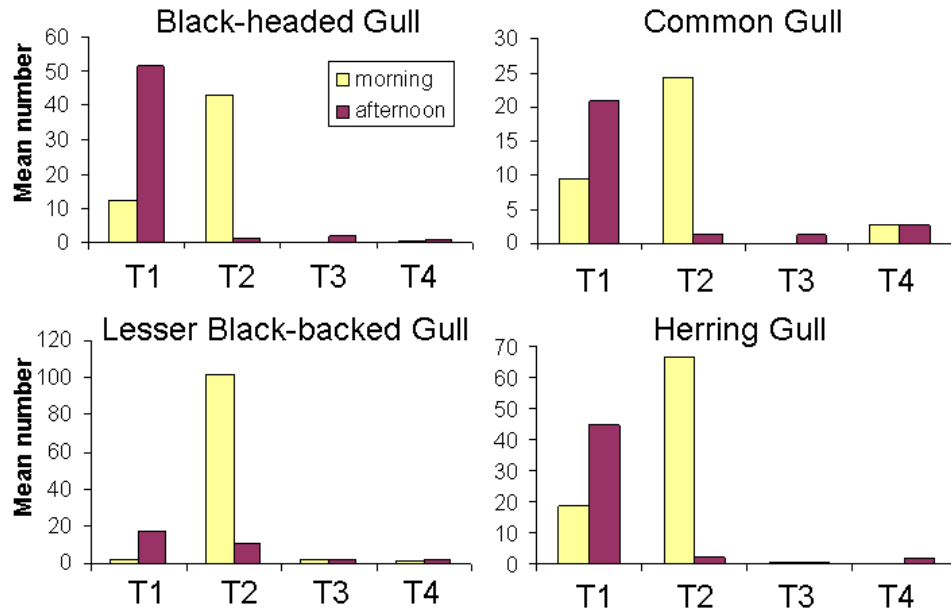


Figure 4.9: Spatially and temporally differing area usage by gulls. Mean abundance of the four most common gulls in count sections T1-T4 during repeated surveys between Büsum and Helgoland in August 2003.

vicinity around the breeding colony in the morning, the main concentration area expands with time of day, apparently reaching a maximum extent between 12 and 14 h UTC and contracting again towards the evening (Fig. 4.11). Accordingly, highest mean densities in the distance classes 40-60 km and 60-80 km were recorded for the period between 12 and 14 h UTC. However, mean density values in the nearest distance class 0-20 km were highest throughout the day, reaching values of 1.8 individuals/km².

4.4 Discussion

4.4.1 Methodology

To discuss the results presented it is important to evaluate whether we assessed representative data during the analysed surveys. Aerial surveys covered the main distribution area of both Kittiwakes and Guillemots in the breeding season. However, to achieve a survey route that could be covered within one day, it was not possible to extend surveys to the maximum foraging distance of 80 km. Instead, maximum distance to the north of the breeding colony reached by aerial surveys amounted to 60 km. Aerial surveys were carried out above all between 7 and 13 h UTC. This implies (a) that distribution possibly varied during the survey according to changing daytime and (b) that surveys took place at least partly within the period of maximum extension of distribution (following

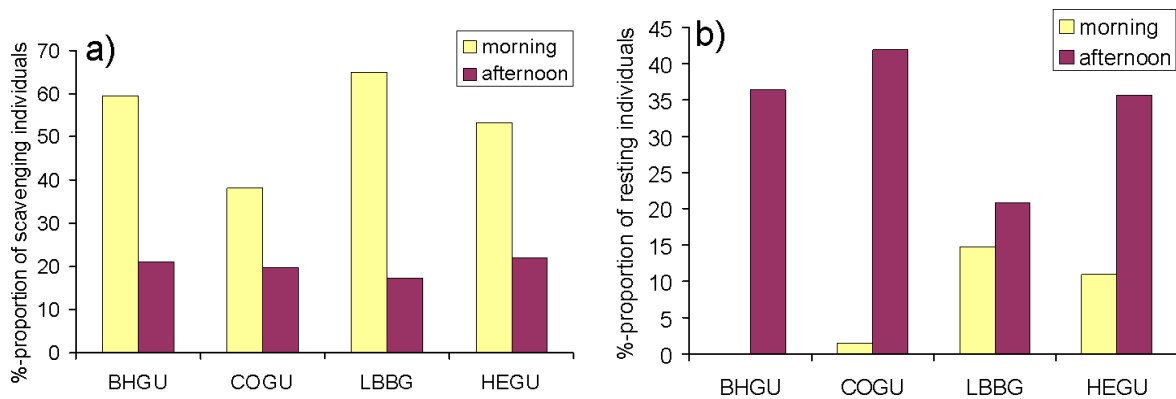


Figure 4.10: Differences in (a) scavenging and (b) resting behaviour between morning and afternoon of Black-headed Gull (BHGU), Common Gull (COGU), Lesser Black-backed Gull (LBBG) and Herring Gull (HEGU) observed during repeated surveys between Büsum and Helgoland in August 2003.

results above). However, single surveys were always carried out at the same time of the day. Thus, we assume that comparisons between single surveys were not constrained by the methodology applied. Another critical aspect concerns the spatial effort. We covered approximately 10% of the survey area. Some sections had to be excluded from analyses due to unfavourable observation conditions. Nevertheless, the overall sampling effort was considered high so that the probability to correctly depict general distribution patterns was high although smaller concentration areas may have been overlooked due to transect layout.

Results of correlation of Kittiwake distribution with hydrographic parameters on 3 and 4 May 2006 were based on a very limited dataset of two days only in a spatially restricted area. Consequently, variance can be assumed to be low. The GAM explained a relatively high proportion of total variance but confidence intervals were rather high (see Fig. 4.6). Removing the data point of maximum density altered results pronouncedly (Figs. 4.6 and 4.7). In conclusion, the significant effects presented here rather have to be regarded as tendencies implying potential interrelations. Nevertheless, our results fit earlier studies based on extensive datasets which also report a significant positive effect of fronts on Kittiwake distribution (see below; chapter 2, page 13).

Ship-based surveys between Büsum and Helgoland covered a very limited proportion of the total area only and thus were not suited to depict distribution patterns. The main focus of this paper however was on temporal variability. The studied species, i.e. gulls and terns, can be assumed to exhibit higher temporal variability in their occurrence than other seabird species due to the fact that they are highly mobile opportunistic foragers. Thus, the results presented can not fully be extrapolated to other seabird species which spend most of their time swimming or which possess a more restricted prey spectrum.

Moreover, most gulls also forage in terrestrial habitats and on mud flats of the Wadden Sea region. Thus, not only distribution but also numbers of gulls at sea vary with time. Finally, the study took place in the post-breeding season, when birds are not bound to the colony anymore but are able to roam freely. Moreover, migration has started, possibly causing changes in numbers of birds. However, results of our study do not refer to actively migrating individuals but rather focus on more or less stationary birds foraging and resting in the area. Overall, our study represents a presumably extreme situation of high variability due to the study period and the species studied. Moreover, applying this method, no reliable information can be derived on changes in numbers of

Table 4.2: Results of GLMMs testing the influence of environmental parameters on the behaviour of the four most common gull species during repeated surveys in the study area between Büsum and Helgoland. Parameters influencing the response variable significantly are listed under predictors (level of significance: 0.05). BHGU = Black-headed Gull, COGU = Common Gull, LBBG = Lesser Black-backed Gull, HEGU = Herring Gull, vessel assoc = vessel association, resting beh = resting behaviour, dtime = time of day (morning / afternoon), tide = tidal stage (ebb tide / flood tide), transect = count section (T1 / T2), wind = maximum wind velocity recorded in m/s.

Species	Response variable	Predictors	Random effect	N observations	N groups / days
All	Vessel assoc	Dtime+transect +tide+wind	Day	3702	10
BHGU	Vessel assoc	Transect+tide+ wind	Day	832	10
COGU	Vessel assoc	Dtime+transect +tide+wind	Day	478	10
LBBG	Vessel assoc	Dtime+wind	Day	1190	10
HEGU	Vessel assoc	Dtime+transect +wind	Day	1202	10
All	Resting beh	Dtime+tide+ transect+wind	Day	3702	10
BHGU	Resting beh	Dtime+transect	Day	832	10
COGU	Resting beh	Dtime+tide	Day	478	10
LBBG	Resting beh	Transect+wind	Day	1190	10
HEGU	Resting beh	Dtime+transect +tide+wind	Day	1202	10

studied species due to our low spatial effort. However, we were able to give information on several aspects of variability in seabird distribution patterns. Thus, we (a) assessed a possible order of magnitude of temporal variability in seabird distribution areas, (b) depicted general shifts in concentration areas, i.e. changes in distribution patterns, with time of day, and (c) identified environmental parameters causing and shaping variability of seabird occurrence.

Influence of time of day on distribution of Kittiwakes was tested using a rather heterogeneous dataset characterised by efforts varying spatially and temporally (Table 4.3). Ideally, the same area should have been sampled repeatedly at all different time periods during one single day. However, a realisation of this method is possible neither by ship nor by plane due to the large foraging area of breeding Kittiwakes. On the other hand, bearing the present results on variability of Kittiwake distribution patterns at the order of single days in mind, mean distribution patterns can be assumed to be less influenced by singular events. Thus, being based upon a high number of different survey days, the dataset used might nevertheless produce reasonable results. Furthermore, we were not able to distinguish between breeding and non-breeding individuals. Thus, distribution patterns especially in the distant areas might have been influenced by birds not breeding on Helgoland. However, bias presumably was low as breeding birds make up the majority of numbers of Kittiwakes in summer during the breeding season (following Garthe et al. 2007).

4.4.2 Scales of temporal variability

Distribution patterns of Black-legged Kittiwakes differed significantly in most cases between the different phases of the breeding season indicating variability of distribution patterns at the order of weeks. However, results from repeated specific surveys on the following day emphasized high variability at the order of days. Thus, as surveys were carried out on single days, variability at the order of weeks as found in this study might in fact also represent variability at the order of days. In this context, it also has to be

Table 4.3: Survey effort of long-term ship-based surveys (1990-2006, German Seabirds at Sea database v5.07) within the four different distance classes around the colony on Helgoland at different times of day. Effort is given as the ratio between the sum of total survey area (including repeated surveying of the same plots) and the area size covered by each distance class.

	2-5 h	6-8 h	9-11 h	12-14 h	15-17 h	18-20 h
0-20 km	0.14	0.41	0.53	0.49	0.16	0.05
20-40 km	0.02	0.19	0.16	0.09	0.1	0.03
40-60 km	0.01	0.08	0.06	0.05	0.06	0.01
60-80 km	0.01	0.02	0.02	0.02	0.02	0.01

noted that weeks do not represent biologically distinct time periods but might rather be considered as multiples of days. The time period of one day on the other hand will be reflected in most species' occurrence as the majority of seabirds exhibits diurnal patterns in activity (e.g. Shealer 2002). Variability at a temporal scale finer than one day is caused by factors varying by hours or minutes such as tidal stage, wind speed and direction.

4.4.3 Interspecific differences

The higher variability found in distribution patterns of Black-legged Kittiwakes compared to Common Guillemots might result from the fact that Kittiwakes are strongly associated with short-lived frontal structures (chapter 2, page 13). In contrast, Common Guillemots are not restricted to prey patches at the sea surface but are able to use the whole water column, i.e. a third dimension of their habitat. Thus, regarding only horizontal distribution patterns, Kittiwakes are likely to exhibit a higher variability than Common Guillemots which may e.g. alter their diving behaviour in response to differing food availability. Moreover, Kittiwakes mostly spend their at-sea time flying (chapter 6, page 89) and thus cover larger distances during a shorter time span. In contrast, Common Guillemots spend the majority of their at-sea time swimming (chapter 6, page 89). Consequently, distribution patterns of Kittiwakes can vary at shorter intervals due to a higher amount of travelling involved.

4.4.4 Influence of environmental parameters

The observed significant variation of seabird distribution patterns at different scales could at least partly be explained by various environmental factors such as trawler abundance, hydrographic parameters, wind speed, tidal stage and time of day. These factors influence seabird occurrence in different ways. Trawler abundance acts as a measure for direct food availability with fishing vessels representing an anthropogenic food source. Hydrography and tide may influence abundance, distribution and behaviour of prey species of seabirds in the south-eastern North Sea such as polychaetes (Esselink and Zwarts 1989), crustaceans (Aagaard et al. 1995) and fish (Valenzuela et al. 1991, Thiel et al. 1995). These factors thus act as indirect indicators of food availability. The correlation of Kittiwakes with frontal structures in the German Bight has been recorded earlier and is assumed to result from enhanced food availability at fronts due to physical and biological mechanisms (chapter 2, page 13). Wind speed influences both mobility of birds and food availability. Thus, medium wind speeds may reduce flight costs (e.g. Furness and Bryant 1996) while strong winds constrain flight performance and thus mobility (Woodcock 1940, Manikowski 1971). Moreover, strong winds reduce fishing activity (e.g. see results) and decrease natural food availability (Dunn 1973, Finney et al. 1999). Time of day may reflect food availability e.g. in case of prey species exhibiting

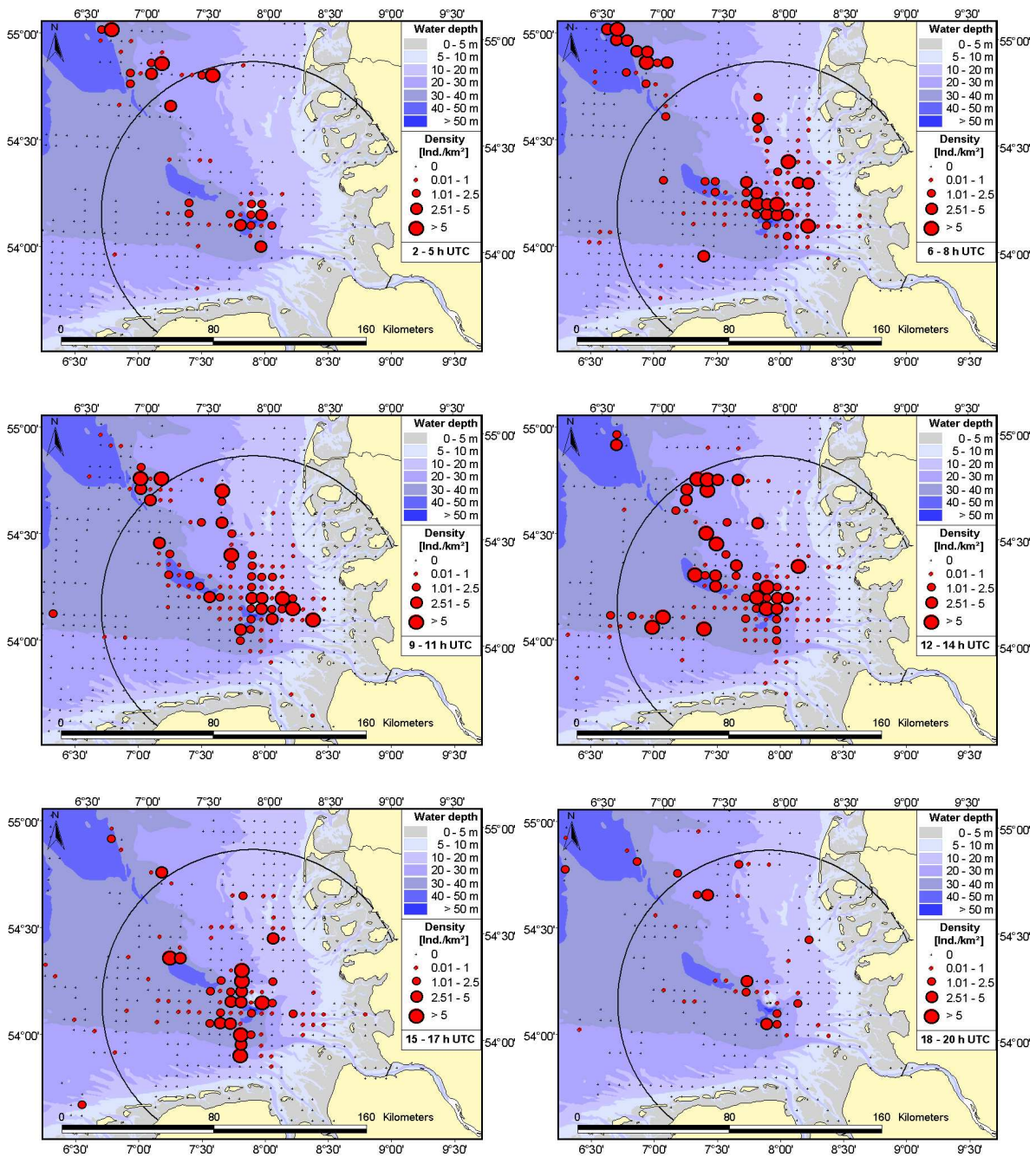


Figure 4.11: Distribution patterns of Black-legged Kittiwakes in the German Bight in summer (May-July) at different times of day: 2-5 h (top left), 6-8 h (top right), 9-11 h (centre left), 12-14 h (centre right), 15-17 h (bottom left) and 18-20 h UTC (bottom right). The circle marks the distance of 80 km around the colony on Helgoland, beyond which birds were considered not to be related to the breeding colony. Data source: German Seabirds at Sea database 5.07 (ship-based surveys from 1990-2006).

diel vertical migration such as zooplankton and fish (Hays 2003). However, the link between time of day and seabird occurrence is additionally influenced by intrinsic factors such as the behaviour of breeding birds to spend the night at the colony. During hours of darkness, Common Guillemots do not forage (Wanless et al. 1988) and Kittiwakes do not fly (Daunt et al. 2002). While resting at sea during the night of the early breeding season (May – mid of June), Kittiwakes spend the night at the colony during chick-rearing (mid of June - mid of July, Glutz von Blotzheim and Bauer 1999). This behaviour is reflected in varying distribution patterns studied at different times of the day during the breeding season (Fig. 4.11). As the distribution ranges furthest from the colony during mid-day, one might conclude that the furthest areas represent especially favourable foraging grounds that are only within reach of Helgoland breeding birds at this time of day because of the long distance from the breeding colony. However, assuming that individuals leave the colony at dawn and travel at an average flight speed of 47 km/h (Pennycuik 1997), the maximum foraging range of 80 km can be reached within less than two hours time, i.e. at approximately 4 h UTC and thus much earlier than observed. A different explanation could lie in prey availability varying with time of day such that birds encounter favourable food availability at noon / early afternoon only. However, this seems unlikely as most prey species of seabirds rather retreat out of reach during daylight (Hays 2003). Large distances from the Helgoland colony reached during 12-14 h UTC however coincide with by far the highest numbers of birds at sea. Thus, birds might simply spread over a larger area to avoid competition with conspecifics.

Our results correspond to other studies that found the early afternoon to be one of the periods of high activity in breeding Kittiwakes (Glutz von Blotzheim and Bauer 1999). However, the early morning, which is generally characterised by highest activity, did not stand out in our study. Chick-rearing Kittiwakes equipped with data loggers showed highest foraging activity and highest amounts of time at sea during the morning (\approx 8-10 h UTC) and high values of colony attendance in the early afternoon (14-15 h UTC Daunt et al. 2002).

Behaviour of Black-headed, Common, Lesser Black-backed and Herring Gulls differing with time of day can be explained by the fact that seabirds - like most birds - show diurnal activity peaks and display e.g. intensified feeding early in the morning and late in the afternoon (Bezzel and Prinzing 1990). The fact that gulls occurred nearer to shore in the afternoon might result from a movement to roosting aggregations at land, where gulls mostly spend the nights outside the breeding season.

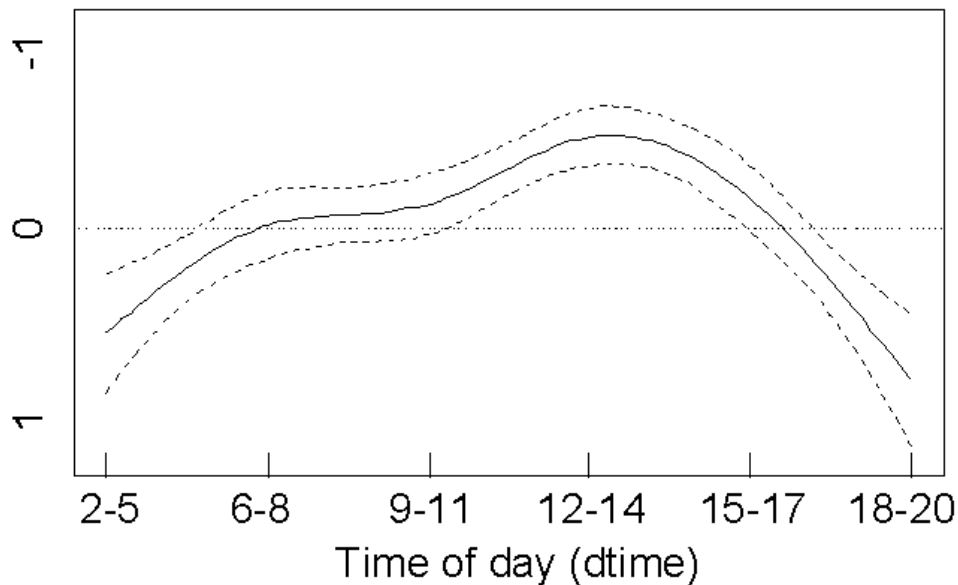


Figure 4.12: GAM smoothing curve fitted to partial effects of an explanatory variable on density of Black-legged Kittiwakes. Density is represented as a function of time of day. Dashed lines represent 95% confidence intervals around the main effects. Maximum densities were recorded between 12 h and 14 h UTC. Data source: German Seabirds at Sea database v5.07.

4.5 Conclusions

Temporal variability has been shown to be a major characteristic of seabird distribution patterns. Some of the environmental factors influencing variability such as season, time of day and tide are of a periodic nature. In contrast, wind speed, hydrography (which is often influenced by wind speed and direction) and trawler abundance are shaped by a variety of different factors and are thus characterised by a more or less stochastic quality. Thus, seabird distribution patterns undergo predictable as well as unpredictable temporal variation at fine scales. Differences can be significant, requiring the consideration of temporal variability during the design and interpretation of surveys and ecological assessments. Future studies have to proceed in identifying other sources of variability and characterising relationships between seabird occurrence and environmental parameters. Knowledge of these effects can e.g. maximize survey effectiveness with respect to estimating numbers and trends by sampling during periods of lowest variability (Becker et al. 1997a, Speckman et al. 2000) and would permit an improved interpretation of survey results.

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5 Seasonality of seabird habitat choice in the German Bight (North Sea)

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Abstract

Seabird distribution patterns undergo distinct seasonal variations which are presumably reflected in seasonally varying habitat choice of birds. Variations in habitat choice are believed to be controlled by seasonally differing demands of birds with respect to resources and by variations in the availability of resources and thus habitat quality. In the German Bight (south-eastern North Sea), habitat choice of several seabird species is related to distinct hydrographic structures such as water masses and fronts. We analysed temporal variation of habitat choice at the order of seasons and years by comparing hydrographic affinities of two dedicated summer cruises and one winter cruise. Several seabird species showed a significant preference for one of the two prevailing water masses of the study area. While the results for a given season (here: late summer) did not differ between years, several aspects of seasonality of habitat choice were noted during this study. No obvious contrasting preferences were revealed between different seasons, however strength of habitat choice varied. Strong habitat bonds were revealed both for non-breeding birds and for birds experiencing spatial constraints. Thus, breeding Black-legged Kittiwakes and flightless Common Guillemots showed particularly strong habitat bonds. These findings contradict the hypothesis of spatial constraints masking habitat preferences. Differences in habitat preferences were believed to result from seasonal variation in habitat quality, i.e. availability of resources.

5.1 Introduction

The main proximate factor controlling habitat choice of birds is believed to be availability of specific resources (e.g. Bairlein 1996). However, both availability of resources and demands of birds vary at temporal scales, e.g. at the level of seasons. Thus, breeding grounds have to provide resources for reproduction (e.g. nesting sites) while wintering grounds are chosen to enhance survival during the non-breeding period (Salewski and Bruderer 2007). These differing demands and varying availability of resources are thought to cause observed distinct seasonal differences in habitat choice (Bezzel and Prinzing 1990). The marine environment which forms the main habitat for seabird species is characterised by high variability at different temporal and spatial scales. Resources like marine prey stocks undergo distinct seasonal variation in availability. Seasonal changes are particularly pronounced at higher latitudes with low to negligible primary production in winter (Ashmole 1971). Moreover, the demands of seabirds with respect to habitat resources differ distinctly between breeding and non-breeding season. In the breeding season, seabirds are central-place foragers (Orians and Pearson 1979) bound to nesting sites at land whereas the entire non-breeding period is spent exclusively at sea by the majority of species (Ainley 1980). These differing spatial constraints are expected to influence quality and strength of habitat affinities of seabirds. On the one hand, Shealer (2002) expects the categorisation of seabirds into coastal, inshore, offshore or pelagic feeders to be valid only during the breeding season as during the rest of the year birds are not bound to the vicinity of their colonies and thus are free to forage in a wide area. In his eyes, the categories of coastal, inshore, offshore or pelagic are ‘artificial’ and not justified due to the pronounced opportunism of seabirds. On the other hand, it is believed that the spatial constraints of seabirds during the breeding season do not cause but rather mask actual habitat preferences, as distance to colony was shown to have a marked influence on the distribution patterns of breeding seabirds (e.g. Garthe 1997).

In the German Bight, few of the regularly occurring seabird species can be termed truly pelagic seabirds which do not return to land at night outside the breeding season (cf. Furness and Monaghan 1987). Only Northern Fulmar *Fulmarus glacialis*, Northern Gannet *Sula bassana*, Black-legged Kittiwake *Rissa tridactyla* and Common Guillemot *Uria aalge* represent pelagic species in the area. Apart from these species, the avifauna of the German Bight is dominated by gulls and terns (Garthe et al. 1995). While some of these species leave the North Sea in winter, Black-headed Gull *Larus ridibundus*, Common Gull *Larus canus*, Herring Gull *Larus argentatus* and Great black-backed Gull *Larus marinus* occur throughout the year in substantial numbers in the German Bight. However, the sea area of the German Bight is used differently within the different seasons by most seabird species. Thus, recent high efforts in at-sea studies have revealed substantial seasonal differences in mean distribution patterns of the common seabird species in the German Bight (e.g. Garthe et al. 2004). The fact that seabird distributions undergo temporal variation is widely recognised and related to variations in their marine habitat.

Changes in species distribution consequently might be explained by analysing habitat choice of seabirds, e.g. by correlating seabird density to physical and biological variables (Ballance et al. 2006). In the German Bight, seabird distribution patterns have been related to distinct hydrographic structures such as water masses (Garthe 1997) and fronts (Skov and Prins 2001, chapter 2, page 13). To analyse seasonality of habitat choice, we compared hydrographic affinities of all common species between two different seasons, winter and summer. In addition, we tested for interannual differences by analysing data sets of two different summers separately. Analyses were carried out for all species occurring in substantial numbers throughout the year and thus included all of the above mentioned species with the exception of Northern Gannets which were observed in low numbers only. We expected habitat affinities to vary between seasons in quality and strength according to variation in availability of resources and according to expected seasonally differing demands.

5.2 Material and Methods

Data material To compare seabird distribution to hydrographic features, we carried out ship-based seabird counts (see chapter 1.3.3, page 8) simultaneously along with hydrographic measurements. Sea surface salinity and temperature were recorded once per minute by a thermosalinograph at a depth of 4 m. Additionally, hydrographic stations were carried out at intervals between 5 and 9 km. During hydrographic stations, vertical profiles of temperature and salinity were obtained using CTD-casts. In addition, water depth was assessed and water transparency was measured by use of a Secchi disk (Pickard and Emery 1990, Aarup 2002). For the present study, we analysed data collected during three cruises of the RV "Heincke" (formerly Biologische Anstalt Helgoland, at present Alfred-Wegener-Institut Bremerhaven): an early winter cruise W (25 October - 02 November 1993, Table 5.1) and 2 summer cruises S1 (18 - 22 July 1994) and S2 (27 July - 06 August 1999).

Table 5.1: Details on the three cruises analysed. The number of hydrographic stations equals the number of corresponding transect segments

Cruise	Date	Distance surveyed (km)	No. of hydrographic stations
W	Oct/Nov 1993	801.6	156
S1	July 1994	642.9	115
S2	Jul/Aug 1999	1779.7	192

Characterisation of major habitat variables In addition to direct hydrographic measurements, we derived indicators for characterising hydrographic structures such as stratification and frontal activities. Horizontal gradients in temperature and salinity were defined as the difference between the start and end point of each counting interval. The average difference between consecutive sea surface hydrography measurements per minute served as an indicator for temperature and salinity fronts, respectively. To assess thermohaline stratification, we calculated differences in salinity and temperature between water surface and sea bottom. We then carried out Principal Component Analyses to identify major habitat variables. Hydrographic parameters that did not meet the assumption of a normal distribution (checked by visual inspection) were either transformed to approach normal distribution or if the latter was not possible omitted from further analyses. The results of corresponding standard measures and tests justified the application of Principal Component Analyses for all three cruises (W: Kaiser-Meyer-Olkin measure of sampling adequacy: 0.629, Bartlett's test of sphericity: $\chi^2=493$, $df=21$, $p<0.001$; S1: Kaiser-Meyer-Olkin measure of sampling adequacy: 0.684, Bartlett's test of sphericity: $\chi^2=855$, $df=36$, $p<0.001$; S2: Kaiser-Meyer-Olkin measure of sampling adequacy: 0.714, Bartlett's test of sphericity: $\chi^2=1041$, $df=36$, $p<0.001$; McGregor 1992). Only principal components with eigenvalues > 1.0 were considered in subsequent analyses. Axes were rotated orthogonally using the VARIMAX option (Backhaus et al. 1996) to facilitate easy interpretation and to allow for independent results of the subsequent computations of correlations between the derived principal components and the abundance of seabirds. An otherwise existing dependency between principal components would complicate the interpretation of correlation coefficients between each of these factors and seabird occurrence.

Correlation of seabird occurrence with habitat variables The sampled transect area was divided into separate counting intervals corresponding to the single hydrographic stations. Each counting interval consisted of one transect segment prefacing the corresponding hydrographic station and one segment following it. In the case of short sampling distances between single hydrographic stations, the extension of each segment corresponded to half of the distance between the hydrographic stations. Otherwise, segments were confined to a maximum of 16 min sampling time following or prefacing the hydrographic station to achieve that counting intervals were representative of the seabird occurrence at the hydrographic station. Segments were excluded if they were temporarily not attached to the hydrographic station. Bird density was calculated for counting intervals covering an area from 2.6 to 11.0 km² (average: 6.9 km²) around (i.e. prefacing and following) the corresponding hydrographic station.

Samples of seabird abundance exhibited two major characteristics: they comprised many zero density values violating the assumption of normality and furthermore, data points were characterised by strong autocorrelation. However, autocorrelation could not be quantified accurately due to the large number of zero values that complicated interpreting the results of autocorrelation analyses. To account for non-independent data and

Table 5.2: Results of Principal Component Analysis for cruise W (October/November 1993). The loadings of the seven hydrographic parameters used for analysis on the first two principal components, derived from the correlation matrix and subsequent rotation, are shown. Rotation method: Varimax with Kaiser normalisation. Eigenvalues and percentages of variation are given for the two principal components. Bold faced values of loadings were used for interpreting and characterising the components. SSS = sea surface salinity in psu; Depth = water depth in m; Secchi = water transparency in m according to Secchi disk measurements; horiz. T-gradient = horizontal temperature gradient in K; horiz. S-gradient = horizontal salinity gradient in psu; T-fronts = indicator of temperature fronts; S-fronts = indicator of salinity fronts. Parameters marked with an asterisk were transformed in order to approach a normal distribution. The parameters ‘vertical temperature gradient’ and ‘vertical salinity gradient’ were excluded from the analysis because of violation of the normal distribution. See Methods for details of parameter calculations

	PC 1	PC 2	
Eigenvalue	3.22	1.48	
% of Variance explained	46.1	21.1	Σ 67.2%
SSS	-0.41	0.81	
Depth	-0.33	0.81	
Secchi	0.23	0.74	
horiz. T-gradient*	0.72	-0.27	
horiz. S-gradient*	0.86	-0.04	
T-fronts*	0.65	-0.08	
S-fronts*	0.86	-0.08	

distributions containing many zero values we used a permutation procedure. To keep the major characteristics constant, the original data set was split up into alternating blocks of cases comprising consecutive zero values and blocks of cases with a consecutive occurrence of birds. During permutation the position of each single block was randomised while the alternating occurrence of ‘zero value’ - blocks and blocks containing seabird density values was kept constant. The sequence of cases containing seabird density values was not altered within each block. Following this method all data sets (i.e. the original data set and all of the permuted data sets) contained the same number of blocks, the same seabird density values and within blocks of seabird occurrence the same sequence of density values.

Correlation between each data set and each principal component derived from the PCA of the hydrographic parameters was tested separately for the three cruises using Spearman’s Rank Correlation analyses. The proportion of absolute correlation coefficients greater than or equal to the absolute correlation coefficient of the original data corresponded to the p-value. The number of permutations was set to 1000, but was elevated to 10,000 (or 100,000 respectively) in cases of p-values lying near 0.05 after the first computations. To correct for multiple testing we applied Fisher’s Omnibus-Test

separately for each principal component and its associated analyses of correlation. This test combines a number of p-values into a single χ^2 -distributed variable with its degrees of freedom equalling twice the number of p-values (Haccou and Meelis 1994).

Analyses of habitat affinities were carried out for all common seabird species that occurred in numbers enabling statistical analyses during all three cruises. A test using log-transformed seabird density values revealed no major differences in results compared to results of analysing absolute density values.

To visualise the relation between seabird distributions and the derived principal components we developed ordinations of analysed seabird species on the basis of their correlation coefficients with the respective components for all three cruises.

Table 5.3: Results of Principal Component Analysis for cruise S1 (July 1994). The loadings of the nine hydrographic parameters used for analysis on the first two principal components, derived from the correlation matrix and subsequent rotation, are shown. Rotation method: Varimax with Kaiser normalisation. Eigenvalues and percentages of variation are given for the three principal components. Bold faced values of loadings were used for interpreting and characterising the components; italicised values were considered additionally. SSS = sea surface salinity in psu; Depth = water depth in m; Secchi = water transparency in m according to Secchi disk measurements; vert. T-gradient = vertical temperature gradient in K; vert. S-gradient = vertical salinity gradient in psu; horiz. T-gradient = horizontal temperature gradient in K; horiz. S-gradient = horizontal salinity gradient in psu; T-fronts = indicator of temperature fronts; S-fronts = indicator of salinity fronts. Parameters marked with an asterisk were transformed in order to approach a normal distribution. See Methods for details of parameter calculation

	PC 1	PC 2	PC 3	
Eigenvalue	3.98	2.19	1.17	
% of Variance explained	44.2	24.3	13	Σ 81.5%
SSS	-0.23	0.93	-0.18	
Depth	-0.02	0.93	0.28	
Secchi	-0.62	<i>0.60</i>	-0.21	
vert. T-gradient	-0.05	0.56	0.79	
vert. S-gradient*	0.24	-0.18	0.91	
horiz. T-gradient*	0.85	0.00	-0.13	
horiz. S-gradient*	0.69	-0.02	0.08	
T-fronts*	0.82	-0.21	0.17	
S-fronts*	0.83	-0.26	0.25	

5.3 Results

5.3.1 Habitat characteristics

Two principal components with an eigenvalue >1.0 explained 67.2% of parameter variance for the winter cruise W (Table 5.2) and three principal components with an eigenvalue >1.0 explained 81.5% of parameter variance and 76.2%, respectively, for the summer cruises S1 (Table 5.3) and S2 (Table 5.4). All Principal Component Analyses stressed the existence of different water masses in the German Bight. The Continental Coast water mass that prevails nearshore in shallow depths is characterised by low values of salinity and transparency. In contrast, the Central North Sea water mass, that dominates towards the deeper north-western part of the German Bight, shows high salinity, high transparency and additionally thermal stratification during the summer months (Becker et al. 1983). Thus, the second principal component of cruise W and cruise S1 and the first component of cruise S2 act as indicators for distance to coast as well as for

Table 5.4: Results of Principal Component Analysis for cruise S2 (July/August 1999). The loadings of the nine hydrographic parameters used for analysis on the first two principal components, derived from the correlation matrix and subsequent rotation, are shown. Rotation method: Varimax with Kaiser normalisation. Eigenvalues and percentages of variation are given for the three principal components. Bold faced values of loadings were used for interpreting and characterising the components. SSS = sea surface salinity in psu; Depth = water depth in m; Secchi = water transparency in m according to Secchi disk measurements; vert. T-gradient = vertical temperature gradient in K; vert. S-gradient = vertical salinity gradient in psu; horiz. T-gradient = horizontal temperature gradient in K; horiz. S-gradient = horizontal salinity gradient in psu; T-fronts = indicator of temperature fronts; S-fronts = indicator of salinity fronts. Parameters marked with an asterisk were transformed in order to approach a normal distribution. See Methods for details of parameter calculation.

	PC 1	PC 2	PC 3	
Eigenvalue	3.62	1.78	1.46	
% of Variance explained	40.3	19.7	16.2	Σ 76.2%
SSS	0.91	-0.23	-0.04	
Depth	0.96	-0.03	-0.01	
Secchi	0.90	-0.15	0.03	
vert. T-gradient*	0.87	0.15	0.13	
vert. S-gradient*	0.23	0.63	-0.09	
horiz. T-gradient	-0.09	-0.04	-0.88	
horiz. S-gradient	-0.01	0.00	0.89	
T-fronts*	-0.17	0.73	0.23	
S-fronts*	-0.30	0.83	-0.04	

the two different water masses. High positive values of these components represent the Central North Sea water mass, plus increasing distance from land, while high negative values indicate presence of the Continental Coast water mass and vicinity of the coast. While thermal stratification (high values of vertical temperature gradient) is incorporated in the water mass gradient (PC 1) in cruise S2 (Table 6 5.4), it acts as a separate component, cleared for effects of water mass and distance from land, in results of cruise S1 (PC 3 in Table 5.3). Furthermore, areas of frontal activity resulting from different mechanisms represented important hydrographic structures during all cruises analysed. The first principal component derived in the analysis of cruise W combines gradients and fronts with high negative loadings of the two factors signalling growing distance to coast, sea surface salinity and water depth (Table 5.2). Therefore, it is regarded as an indicator for the estuarine areas near the coast, where low saline and in the winter months cold river run-off meets the warmer high saline Central North Sea water mass, thereby producing strong gradients and fronts in temperature and salinity. Regarding cruise S1, the first principal component combines high positive loadings of all indicators for temperature and salinity gradients and fronts with high negative loading of water transparency according to Secchi disk measurements (Table 5.3). Low loadings of sea surface salinity and water depth signal that this component is not influenced by distance to land. In conclusion, the first component of S1 most likely represents an upwelling region attached to the post-glacial river Elbe valley with its adjacent fronts, but could also be an indicator for the Elbe river plume. The latter is well described by the second principal component derived in the analysis of cruise S2, combining temperature and salinity fronts with haline stratification. No interpretation could be derived for component 3 of cruise S2 that combines high positive loading of horizontal salinity gradients with a high negative loading of horizontal temperature gradients (Table 5.4).

5.3.2 Water mass affinities of seabirds

Several seabird species of the German Bight showed a significant preference for one of the two prevailing water masses (Tables 5.5, 5.6 and 5.7, Fig. 5.1). The nearshore dominating Continental Coast water mass of low salinity and high turbidity was the preferred habitat of Common Gulls. On the other hand, Northern Fulmars, Black-legged Kittiwakes (during early winter cruise W) and Common Guillemots (during both summer cruises) were significantly associated with the high saline Central North Sea water mass of high transparency, that becomes dominant in the deeper north-western part of the study area.

While the results for a given season (here: late summer) did not differ between years, several aspects of seasonality of habitat choice were noted during this study (Tables 5.5, 5.6 and 5.7, Fig. 5.1). Most important, no obvious contrasting preferences were revealed between different seasons. E.g., Northern Fulmars always showed a strong significant preference for the Central North Sea water mass. Common Gulls showed a likewise strong preference for the Continental Coast water mass as they displayed the same

negative correlation with the component acting as land-sea and water mass gradient for all 3 cruises. Habitat preferences of Common Gulls and Kittiwakes were stronger in early winter while Northern Fulmar and Common Guillemot showed strongest habitat associations in summer. In this context, it is essential to note that the observed patterns of both species were shaped by individuals that were not bound to the breeding colony (anymore). Common Guillemots had already left the colony at the time of the summer cruises and the majority of Northern Fulmars in the German Bight during summer is generally made up by non-breeders (following Garthe et al. 2007 and breeding numbers according to O. Hüppop, pers. comm.). Kittiwakes and Herring Gulls showed a higher association with the Central North Sea water mass in winter as compared to summer. Thus, the majority of Kittiwakes was distributed in areas of median salinity during both summer cruises. Common Gulls, Northern Fulmars and Common Guillemots however occurred in comparatively higher proportions in the Continental Coast water mass in winter than during summer.

Table 5.5: Spearman's Rank Correlations between the distribution of selected seabird species and the two principal components derived from Principal Component Analysis (see Table 5.2) for cruise W in October/November 1993. To account for non-independent data and distributions containing many zero values we used a permutation procedure to calculate adequate p-values for all correlation coefficients (see Methods for more details). nPerm = number of Permutations. Bold values show significant correlations; trends are indicated by italicised values. To correct for multiple testing we applied Fisher's Omnibus-Test separately for each principal component.

	Component 1			Component 2		
	<i>Indicator of estuarine water body with temperature / salinity gradients and fronts</i>			<i>Indicator of Central North Sea water mass and distance to land</i>		
	rs	p	nPerm	rs	p	nPerm
Northern Fulmar	-0.152	<i>0.094</i>	10000	0.22	0.011	1000
Black-headed Gull	0.032	0.741	1000	-0.126	0.127	1000
Common Gull	0.048	0.603	1000	-0.364	0.001	1000
Herring Gull	0.097	0.258	1000	0.081	0.424	1000
Great Black-backed Gull	0.134	0.139	1000	0.107	0.321	1000
Black-legged Kittiwake	-0.071	0.438	1000	0.19	0.042	10000
Common Guillemot	0.038	0.684	1000	0.133	0.213	1000
Fisher's Omnibustest		0.35			0.0002	

Table 5.6: Spearman's Rank Correlations between the distribution of selected seabird species and the three principal components derived from Principal Component Analysis (see Table 5.3) for cruise S1 in July 1994. To account for non-independent data and distributions containing many zero values we used a permutation procedure to calculate adequate p-values for all correlation coefficients (see Methods for more details). nPerm = number of Permutations. Bold values show significant correlations; trends are indicated by italicised values. To correct for multiple testing we applied Fisher's Omnibus-Test separately for each principal component.

	Component 1 <i>Elbe river plume / Upwelling</i>			Component 2 <i>Indicator of Central North Sea water mass and distance to land</i>			Component 3 <i>Stratification</i>		
	rs	p	nPerm	rs	p	nPerm	rs	p	nPerm
Northern Fulmar	-0.331	<i>0.052</i>	100000	0.495	0.004	1000	-0.074	0.88	1000
Black-headed Gull	0.023	0.833	1000	-0.114	0.224	1000	-0.072	0.443	1000
Common Gull	0.276	0.139	1000	-0.387	0.011	1000	-0.172	0.374	1000
Herring Gull	0.081	0.514	1000	-0.266	<i>0.074</i>	10000	-0.173	0.246	1000
Great Black-backed Gull	0.26	0.037	1000	-0.09	0.589	1000	-0.195	0.153	1000
Black-legged Kittiwake	0.256	0.039	10000	0.132	0.424	1000	0.027	0.833	1000
Common Guillemot	-0.055	0.633	1000	0.261	0.036	1000	-0.026	0.844	1000
Fisher's Omnibustest		0.03			0.0006			0.67	

Table 5.7: Spearman's Rank Correlations between the distribution of selected seabird species and the three principal components derived from Principal Component Analysis (see Table 5.4) for cruise S2 in July/August 1999. To account for non-independent data and distributions containing many zero values we used a permutation procedure to calculate adequate p-values for all correlation coefficients (see Methods for more details). nPerm = number of Permutations. Bold values show significant correlations. To correct for multiple testing we applied Fisher's Omnibus-Test separately for each principal component

	Component 1			Component 2			Component 3		
	<i>Indicator of</i>			<i>Elbe river plume</i>			<i>Salinity fronts</i>		
	<i>Central North Sea water mass</i>			<i>and adjacent fronts</i>			<i>in an area of</i>		
	<i>and distance to land</i>						<i>stable temperatures</i>		
	rs	p	nPerm	rs	p	nPerm	rs	p	nPerm
Northern Fulmar	0.551	0.001	1000	-0.184	0.104	1000	-0.003	0.981	1000
Black-headed Gull	-0.11	0.118	1000	-0.046	0.539	1000	0.083	0.241	1000
Common Gull	-0.314	0.007	1000	-0.011	0.918	1000	-0.055	0.536	1000
Herring Gull	-0.135	0.187	1000	-0.06	0.544	1000	-0.059	0.406	1000
Great Black-backed Gull	0.051	0.548	1000	0.011	0.893	1000	-0.039	0.587	1000
Black-legged Kittiwake	-0.086	0.503	1000	0.296	0.006	1000	0.188	0.043	10000
Common Guillemot	0.423	0.001	1000	-0.093	0.383	1000	-0.014	0.847	1000
Fisher's Omnibustest	<0.0001			0.15			0.48		

5.4 Discussion

5.4.1 Data quality

In the study area, a low number of dedicated cruises combining data on seabird occurrence and hydrography comprises a data volume as extensive as presented here. Thus, the cruises analysed in this study offer an exceptionally good opportunity to derive general results on habitat choice of seabirds. However, results from other, shorter research cruises support the findings presented here.

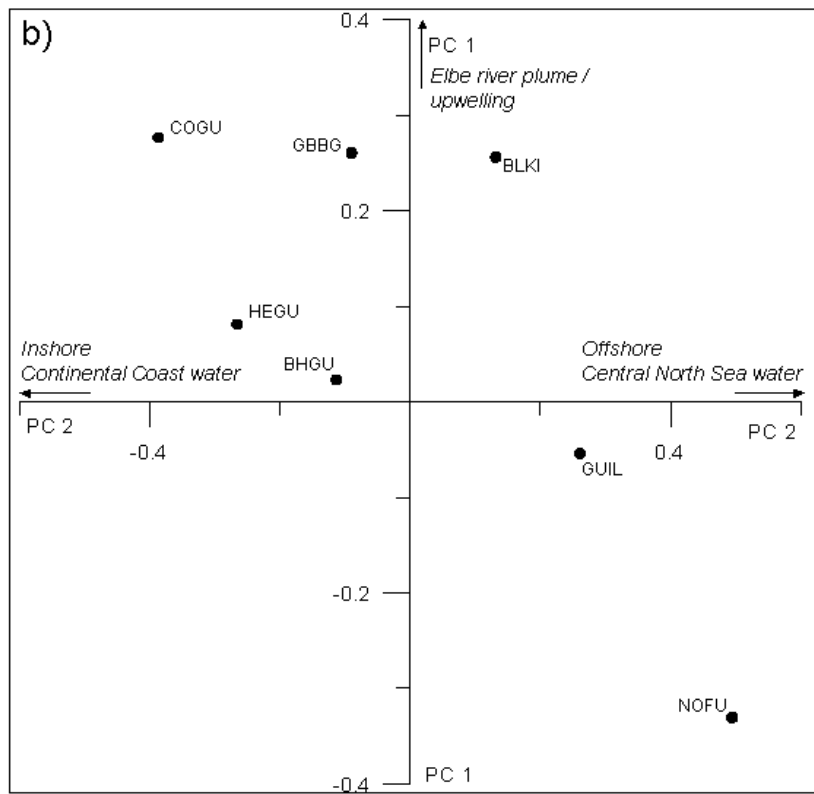
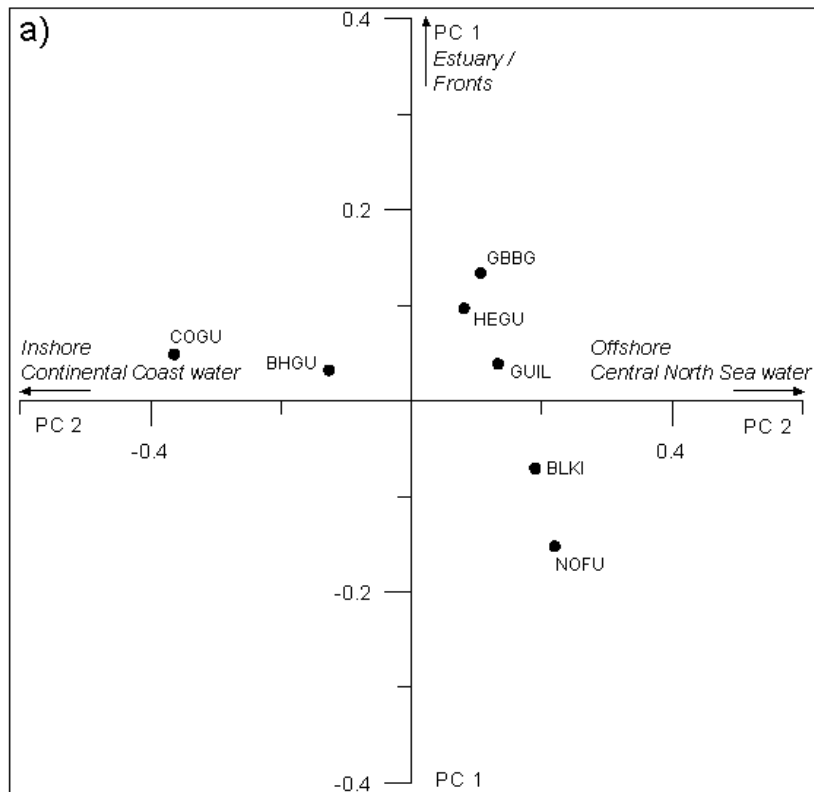
5.4.2 Water mass affinities of seabirds

The differing preferences of seabird species for certain water masses are likely to be explained by the different origin of these water bodies and their distinct physical and chemical conditions resulting in differing biological characteristics.

Several authors speak of different food webs prevailing in the different water masses. According to (Joiris 1978, 1983), the Atlantic water hosts a complete food web consisting of the chain phytoplankton – zooplankton – pelagic fish – seabirds while primary production in the coastal North Sea water is largely consumed by bacteria (80%) and only a small part (20%) is consumed by zooplankton, resulting in comparatively low stocks of pelagic fish and seabirds. Similarly, Fransz et al. (1991) stated that the majority of primary production in shallow North Sea areas is transferred directly to the benthos. It is most likely that the assumed differences result not only in different overall quantity of prey but also in different prey types, sizes and qualities. Thus it was e.g. shown that Atlantic waters host the largest species of zooplankton while the smallest occur in coastal waters (Hansen 1979, Fransz et al. 1991), a relationship that was similarly revealed in the Northern Bering Sea (Elphick and Hunt 1993). This fact gives a reasonable explanation for the preference of Northern Fulmars for the Central North Sea water mass in the German Bight, which shows the strongest influence of Atlantic waters in this area. The Fulmar which feeds amongst others on zooplankton should select for bigger prey in order to gain most profitable foraging results as has been shown for other seabird species feeding on zooplankton (Vermeer et al. 1987). Thus the Central North Sea water mass likely provides better foraging opportunities for seabirds as well as fish species depending on larger zooplankters.

The coastal zone of the German Bight is in contrast strongly influenced by the presence of the Wadden Sea area and several larger estuaries, which have various biological functions. Both the Wadden Sea and estuaries are important feeding grounds and nursery areas for juvenile fishes and also act as spawning sites and important migration areas (Dankers et al. 1983*b*, Vorberg and Breckling 1999, Elliot and Hemingway 2002). With high densities especially of young fish and fish larvae prevailing in the coastal areas (Dankers et al. 1983*b*, Vorberg and Breckling 1999), the Continental Coast water mass

5 Seasonality of seabird habitat choice in the German Bight



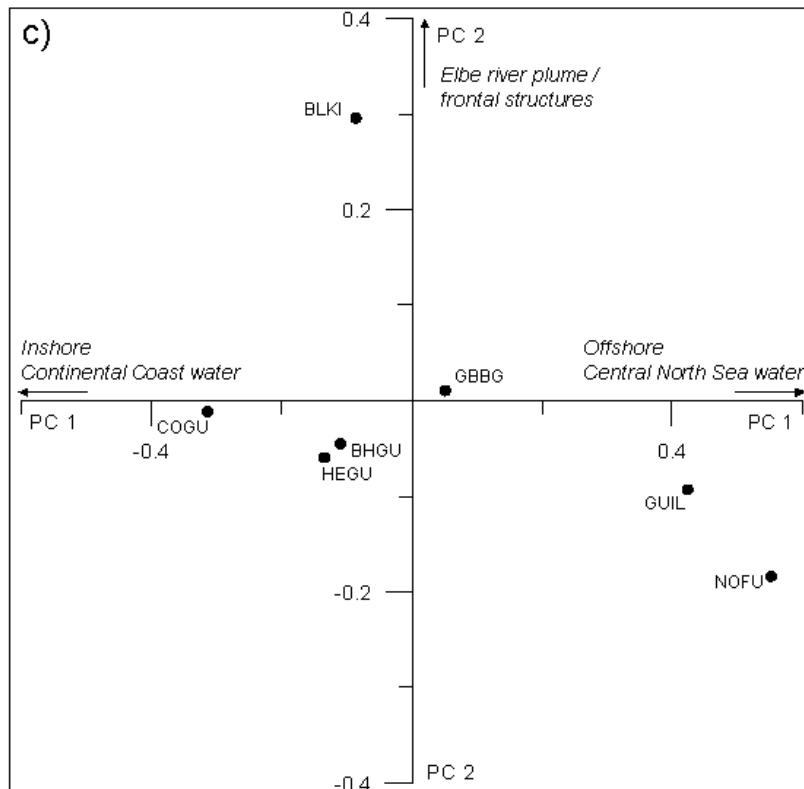


Figure 5.1: Ordination of seabird species on the basis of their correlation coefficients with principal components 1 and 2 from Tables 5.2, 5.3 and 5.4, respectively, for cruise W in Oct/Nov 1993 (a), cruise S1 in July 1994 (b) and cruise S2 in Jul/Aug 1999 (c). For levels of significance see Tables 5.5, 5.6 and 5.7. BHGU = Black-headed Gull, BLKI = Black-legged Kittiwake, COGU = Common Gull, GBBG = Great Black-backed Gull, GUIL = Common Guillemot, HEGU = Herring Gull, NOFU = Northern Fulmar

hence also hosts an important type of prey for seabirds in high numbers. Both water masses consequently offer potentially good feeding grounds for many seabirds but differ in quantity and quality of available prey and food web structure.

A physical effect of water clarity on seabird distribution as proposed by Ainley (1977) could not be observed in the present study. Following Ainley's hypothesis, pursuit diving species should favour turbid waters that allow a closer approach to the prey. In our study, the pursuit diving Common Guillemots clearly showed no preference for turbid waters but actually favoured areas of high transparency during summer.

5.4.3 Seasonality of habitat choice

Two distinct mechanisms might be responsible for the observed seasonality of habitat choice that is likely to be reflected also in seasonal differences in diet as have been described e.g. for Northern Fulmars (Phillips et al. 1999) and Common Guillemots (Blake et al. 1985, Ainley et al. 1996). First, variation in habitat choice can be caused by seasonally differing demands. Thus, breeding seabirds are spatially restricted to the sea area in the vicinity of the breeding colony during summer but are able to roam freely during the rest of the year. In this study, strongest water mass affinities were revealed for non-breeding birds. However, breeding Kittiwakes showed strong associations to small scale hydrographic structures. Moreover, particularly strong habitat affinities of Common Guillemots were revealed in late summer. Both summer cruises coincided with the period of moulting and chick-guarding in Common Guillemots. Thus, Guillemots were flightless during the summer studies (see also chapter 6). It can be expected that birds stayed within favourable feeding areas due to their low mobility. Consequently, spatial constraints led to a particularly strong habitat bond in this species.

Secondly, variation in habitat choice might result from differences in habitat quality, i.e. in the availability of resources and in temperature and weather conditions. A distinct seasonality can be observed at different levels of the environment. The North Sea exhibits a seasonally varying distribution of water masses showing a retreat of Atlantic water to the North and a bigger extension of coastal water during summer (Otto et al. 1990, Fransz et al. 1991), probably triggered by the precipitation over the European continent and thus river runoff that reaches highest intensity during the summer months (Otto et al. 1990). Moreover, the different seasons are characterised by differing temperature, wind stress, solar activity and nutrient availability (Körner and Weichart 1992, BSH 1994, Loewe et al. 2003) leading to the observed distinct seasonal variation in abundance and distribution of phytoplankton and zooplankton (Krause and Martens 1990, Fransz et al. 1991, Poremba et al. 1999).

Though biological activity during winter is generally low, the German Bight seems to be an area of relatively high productivity in the North Sea. While zooplankton species of the northern North Sea migrate into deeper water and enter a torpid period, many southern species keep on feeding and reproducing throughout the winter months and thus show a less distinct seasonality (Broekhuizen and McKenzie 1995). In accordance, by

far the highest numbers of copepods in the North Sea can then be found in the German Bight (Fransz et al. 1991). During winter studies, densities of phytoplankton as well as zooplankton communities were twice as high in the coastal mixed water compared to the North Sea water (Hesse et al. 1989a), and centres of high biomass were located off the mouth of the rivers Weser and Elbe (Krause and Martens 1990). Moreover, according to Fransz et al. (1991), the Continental Coast water mass hosts species that are of considerable size or of particular importance as prey species for fishes (that themselves make up suitable prey for seabirds). It is possible that these characteristics of prey quantity and quality favour the stronger use of the Continental Coast water mass by Northern Fulmars and Common Guillemots during winter.

Northern Fulmars could also take advantage of higher mean wind velocities during winter that allow them to extend their foraging ranges without investing too much energy (cf. Furness and Bryant 1996). Furthermore, it is likely that the association between Northern Fulmars and the Central North Sea water mass is stronger during summer due to the then existing thermal stratification. Stratification improves feeding conditions of planktivores like Fulmars through an increased density of plankton biomass due to individuals aggregating at the thermocline (Hunt 1990). On the other hand, Common Guillemots as piscivorous pursuit divers may take advantage of the colder water temperatures of the Continental Coast water mass in winter. As temperature influences both the physiology of fishes and the physics of the water flow and thus has a strong influence on the swimming performance of fishes (e.g. Hunt von Herbing 2002), pursuit diving seabirds might benefit from lower reaction rates and swimming speeds of exotherm fishes in cold water areas (Montevecchi 1993).

The result of the Herring Gull showing a stronger affiliation with the Central North Sea water mass in winter is in accordance with observations of this species' higher densities in the offshore areas during the winter months (Camphuysen et al. 1995, Stone et al. 1995) and is probably linked to the observed stronger use of food gained from fishing trawlers (Camphuysen et al. 1995). The preference of Black-legged Kittiwakes for the Central North Sea water mass in winter could rely on the same relationship, as this species also makes higher use of discard and offal during winter (Garthe 1999). On the other hand, Kittiwakes are known as truly marine seabirds and thus, it is not so much the observed winter habitat preference that needs explanation but the concentration of this species in medium saline waters not far from the coast during the summer months. Vicinity to the breeding colony is not regarded as the main shaping factor in this context, as Black-legged Kittiwakes exhibit maximum foraging ranges of approximately 80 km (Camphuysen 2005) that easily allow them to reach areas of the Central North Sea water mass. However, the distribution pattern was shown to be linked to the occurrence of ephemeral structures such as fronts (see chapter 2). It is known that thermal stratification occurs only during the summer months but no information was available on the frequency of occurrence of upwellings and the importance of river plume fronts in different seasons. It might be speculated that these ephemeral structures have a higher influence on biological mechanisms during summer as biological activity is generally higher in this period and thus presumably more sensitive to disturbance or alterations.

5.4.4 Conclusions

A temporal variation of habitat affinities was revealed between summer and winter. Driving forces of this temporal variation were believed to result from seasonal variation in habitat quality and seasonally differing demands of birds. While some species showed a higher strength of habitat affinities in early winter, other species exhibited stronger habitat preferences in summer. Particularly strong habitat bonds were found for breeding Kittiwakes and flightless Common Guillemots, i.e. birds experiencing spatial constraints. These findings contradict the hypothesis that spatial constraints of seabirds mask actual habitat preferences. Non-breeding birds however showed distinct habitat preferences, too. These findings contradict Shealer's (2002) hypothesis that habitat preferences are caused by spatial constraints only.

Acknowledgements

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6 Seasonal differences in at-sea activity of seabirds underline high energetic demands during the chick-rearing period

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Abstract

We assessed seasonal differences in at-sea activity of Lesser Black-backed Gulls *Larus fuscus*, Black-legged Kittiwakes *Rissa tridactyla* and Common Guillemots *Uria aalge* in the south-eastern North Sea by analysing long-term data of aerial and ship-based surveys. We differentiated between active (flying or scavenging at fishing vessels) and inactive behaviour (swimming). This method was considered appropriate for surface feeding seabirds like both gull species but was assumed to produce less pronounced results for Guillemots which are mostly engaged in active foraging behaviour while swimming. Next to estimating activity budgets of all species for the different seasons, we tested for differences between age classes and for long-term trends in activity during the breeding season. All species and most age classes exhibited seasonal differences in activity. Adults of both gull species showed highest levels of activity during the breeding season while immature gulls did not exhibit seasonal differences in activity or exhibited highest levels of activity in winter. Adult but not immature Lesser Black-backed Gulls showed highest levels of vessel association during the breeding season. Common Guillemots also showed significantly higher proportions of flying individuals in summer, whilst numbers of flying auks were exceptionally low in autumn due to moult and guarding of not-yet fledged chicks at sea. The proportion of flying individuals of Lesser Black-backed Gulls and Black-legged Kittiwakes in the breeding season increased significantly over the three periods 1990-1995, 1996-2000 and 2001-2006 as did the proportion of vessel association of adult Lesser Black-backed Gulls. Our results underlined the high energetic demands of the breeding season that lead to increased foraging and travelling activity. In addition, trend analyses imply an increase in foraging efforts from the late 1990s onwards that corresponds to strong increases in breeding numbers and might thus be explained by higher levels of intraspecific competition. Furthermore, ecosystem changes might have caused reduced food availability.

6.1 Introduction

Activity budgets, in combination with knowledge of energetic costs, provide information on resource allocation of seabirds (Goldstein 1990). They may thus be used as indicators of food availability (Cairns 1987) and provide a basis for ecological energetics models (Tasker and Furness 1996). However, information on activity of seabirds at sea is still scarce although the sea represents the major feeding habitat for seabirds and their exclusive habitat outside the breeding season. Data logger studies have started to fill this gap in our knowledge (e.g. Benvenuti et al. 2001, Garthe et al. 2003*a*, Ropert-Coudert et al. 2004) but usually sample sizes are low and studies have so far mostly covered temporally restricted periods at the order of hours or days. Both interannual variability of extrinsic parameters and individual differences though may significantly influence the level of reproductive costs in the breeding season and thus necessitate multi-year comparisons (Golet and Irons 1999). Moreover, logger studies mostly deal with breeding birds due to the need of recatching birds for the detachment of loggers. Due to technological constraints, only few studies focusing on activity of birds so far took place during the non-breeding season (e.g. Daunt et al. 2006) or concerned non-breeding birds (but see ‘Outlook’). However, activity budgets of breeding and non-breeding birds are assumed to differ. Bioenergetics models covering the whole year generally extrapolate data of breeding birds and are thus likely to overestimate energy requirements of seabirds (Ellis and Gabrielsen 2002). Hence, data on activity of non-breeding birds and on activity outside the breeding season are needed to minimise errors in bioenergetics models. Thus, to our knowledge, no information on long-term trends of at-sea activity budgets was so far made available in the course of these studies.

So far, data on seabird occurrence and behaviour collected in the course of surveys at sea has seldom been used to gain information on activity of seabirds (but see Camphuysen 1998). At-sea surveys of seabird abundance though have been carried out in many sea areas over the world and studies often cover several decades. In the south-eastern North Sea, the German Bight, Seabirds at Sea surveys have been carried out by ship and plane since 1990 and 2002, respectively, following internationally standardised methods. Surveys took place throughout the year and activity of seabirds was recorded at least by differentiating between swimming and flying behaviour. For the present analysis, we thus assessed activity of selected species in all four seasons on the basis of their behaviour as recorded during aerial and ship-based surveys.

The null-hypothesis implies no differences between activity levels of different seasons and between activity budgets of birds of different status (age, breeding/non-breeding). However, we expect elevated activity levels in the breeding season as parent birds need to maintain self-provisioning and additionally have to raise their young by commuting between the colony and often remote foraging areas at sea (Ricklefs 1984). During at-sea surveys, it is difficult to gain information on the breeding status of birds unless they are observed carrying prey in direction of the colony. To get a reasonable indication

of the differences in activity between breeders and non-breeders in the breeding season, we distinguished between immature birds which can be equated with non-breeders and birds in adult plumage that primarily comprise breeding birds. Next to the breeding period, winter is expected to impose highest energetic costs due to low food availability, harsh climatic conditions and short day lengths (Daunt et al. 2006). Conditions are presumably more severe for immature seabirds that exhibit lower foraging abilities than adults (Burger 1987). Ship-based surveys in the study area comprise data of 17 years, enabling analyses of long-term trends in activity. In the last years, the situation of breeding seabirds in parts of the North Sea changed dramatically taking a turn to the worse, apparently due to ecosystem changes. Low breeding numbers and extraordinarily low breeding success connected to low food availability and low food quality were recorded especially in the northern North Sea (Frederiksen et al. 2004, Mavor et al. 2005, ICES-WGSE 2006). No such breeding failures or declines in breeding numbers have been registered for truly marine seabirds in the study area so far (O. Hüppop, pers. comm., ICES-WGSE 2006) although ecosystem changes have taken place in the German Bight as well (Wiltshire and Manly 2004). Instead, the breeding numbers of Black-legged Kittiwakes *Rissa tridactyla* at Helgoland have doubled since 1990 (chapter 3) and numbers of Lesser Black-backed Gulls *Larus fuscus* even increased by factor 10 (following Garthe et al. 2000, Koffijberg et al. 2006). The size of breeding populations has been shown to correlate positively with foraging trip duration of breeding birds (Ashmole 1963, Lewis et al. 2001), presumably due to local prey depletion (Ashmole 1963, Birt et al. 1987) or prey disturbance (Lewis et al. 2001). Thus, we expect increasing activity levels with growing population size for both gull species due to higher intra-specific competition evoking increasing foraging efforts. However, no such trend is expected for the Common Guillemot which exhibited relatively stable breeding numbers throughout the study period (O. Hüppop, pers. comm.).

Our study aims to assess reasonable indications of time-activity budgets of selected species for each season in the study area. Furthermore, we focus on differences in activity between birds of different age and breeding status and on differences in activity over time. In this context, we formulated the following specific hypotheses:

- (1) Due to the high energetic demands of the breeding season, we expect a higher amount of actively foraging or travelling birds during the breeding season compared to the other seasons.
- (2) In contrast to adult birds, immatures should not meet higher energetic demands during the breeding period as they are not engaged in breeding behaviour.
- (3) Instead, immature birds are likely to face an energetic bottleneck during winter and thus are expected to show highest activity during this season.
- (4) Differences in activity are expected to turn out less pronounced in diving species like alcids due to low proportions of resting behaviour while swimming (following Tremblay et al. 2003). Thus, activity can not be expressed properly by merely

considering the behaviour ‘flying’. Nevertheless, the proportion of flying behaviour should be higher due to breeding birds commuting to and from the colony.

- (5) We expect an increase in activity levels of breeding birds over the last years due to strong increases in breeding numbers of several species presumably resulting in higher intraspecific competition.

6.2 Material and Methods

Studies were carried out in the German Bight which is defined here as the area between 53° 21’ and 55° 01’ N and 05° to 09° E in the south-eastern North Sea. Only breeding species of the study area which forage virtually exclusively at sea were considered appropriate for the analyses. Northern Gannet *Sula bassana* and Northern Fulmar *Fulmarus glacialis* meet this criterium but their breeding population comprises an insignificant share of the total numbers in summer in the German Bight due to large numbers of non-breeding individuals (following Garthe et al. 2007 and breeding numbers according to O. Hüppop, pers. comm.). Thus, only Lesser Black-backed Gull, Common Guillemot *Uria aalge* (hereafter ‘Guillemot’) and Black-legged Kittiwake (hereafter ‘Kittiwake’), whose breeding populations comprised 50% or more of the total summer populations respectively (following Garthe et al. 2007 and breeding numbers according to Koffijberg et al. 2006 and O. Hüppop, pers. comm.), were considered appropriate for the study. While the latter two occupy a single breeding colony on the small offshore island Helgoland in the study area, Lesser Black-backed Gulls breed in several large colonies along the coast line.

Seabirds at Sea data Data on seabird occurrence has been recorded by seabirds at sea counts in the German Bight since 1990 during ship-based surveys and since 2002 during aerial surveys. Aerial and ship-based surveys followed the internationally standardised methods described in chapter 1.3.3, page 8. Both survey methods included the recording of information on vessel association of species feeding on discard and offal. Distance correction to data from ship-based studies (see chapter 1.3.3, page 8) was applied in the same way to all different seasons and different age classes. Thus, comparisons of activity between seasons and age classes were not constrained.

Aerial surveys sampled a total area of circa 24,600 km² while ship-based surveys covered an area of more than 28,000 km². Aerial surveys were carried out in recent years only, covering large sampling areas during single surveys. Ship-based surveys comprise a longer period and thus a higher number of years. However, single ship-based surveys mostly covered only small fractions of the study area. Ship-based surveys took place at different times of day or covered longer periods of single days, respectively, while aerial surveys were mostly restricted to the late morning and noon (Table 6.1). Thus, data from aerial surveys are more homogeneous with respect to spatial and temporal effort compared to ship-based surveys. Ship-based surveys though offer data over a longer period of time and

a higher data quality due to better observation and identification conditions. In contrast to aerial surveys, it is e.g. possible to identify age classes on the basis of the respective plumages. Immature Common Guillemots however can not be identified properly at sea once they are fully grown and thus can not be recognised by size-differences. By applying the ratio of adult to immature birds recorded in ship-based surveys (86:14% for Lesser Black-backed Gulls and 90:10% for Kittiwakes) to aerial surveys, results of all birds from aerial surveys can be assumed to mirror the situation of adult birds of both species. Due to identification difficulties during aerial surveys, we combined data of Guillemot, Razorbill *Alca torda* and ‘Razormot’ (Common Guillemot/Razorbill) to get an indication of activity budgets of Guillemots. This group is termed as Razormots in the following. We considered this method appropriate as breeding numbers of Razorbills are very low compared to numbers of Guillemots (18 compared to 2655 apparently occupied nests (AON) in 2006, O. Hüppop, pers. comm.). Razorbill numbers comprise less than 5% of Guillemot numbers in the German North Sea during spring, summer and autumn. During winter they make up a share of about 23% compared to numbers of Guillemots (following Garthe et al. 2007). However, we assumed that activity budgets of wintering Razorbills and Guillemots do not differ significantly, and are thus confident that the combined data set produces representative results for the Guillemot population of the study area. To compensate for the inconspicuousness of swimming auks at sea especially during rough conditions, we only included data of relatively calm conditions (sea state <5 for ship-based surveys and sea state <4 for aerial surveys).

To test our hypotheses, we analysed data from aerial surveys to get a general picture of the seasonality of activity budgets in recent years and further on analysed data from ship-based surveys to test differences between adult and immature birds and to check for possible trends in activity levels.

6.2.1 Seasonal differences in activity

We assessed activity of selected species in all four seasons by distinguishing between flying and swimming individuals and between individuals associated with vessels and those that were not. For the interpretation of our results, we took the proportion of individuals exhibiting a specific behaviour as an indicator for the proportion of time being spent with this behaviour of the respective species in the studied season to get an indication of time-activity budgets (instantaneous sampling, Altmann 1974). We considered flying behaviour and vessel-association to be active (foraging) behaviour. This classification is regarded appropriate in particular for seabirds that forage mainly at the sea surface like gulls and terns and mostly sit on the water surface during resting. Seasons were classified for each species according to timing of breeding, moulting and migration (Table 6.2). We assessed the ratio of flying and swimming individuals for each season, year and species. Only individuals recorded within the counting transect were included. Lesser Black-backed Gulls are frequently associated with vessels feeding on discard and offal. Scavengers at the stern are mostly recorded swimming (pers. observation). We

Table 6.1: Seasonal survey effort and main day periods sampled by aerial surveys (2002-2006) and ship-based surveys (1990-2006, German Seabirds at Sea database ship v5.07 and plane v5.06) in the German Bight. Classification of seasons as defined for Black-legged Kittiwakes (see Table 6.2)). $CV_{area/year}$ = Coefficient of variation of area surveyed in the different years (=standard deviation/mean area surveyed per year)

	Season	Area surveyed [km ²]	$CV_{area/year}$	Earliest start time [UTC]	Latest stop time [UTC]	Main time of day sampled [UTC] (>80% of area surveyed)
Aerial surveys	Winter	6327	69%	08:46	16:13	10-13
	Spring	9797	60%	06:39	17:54	8-14
	Summer	5023	178%	06:50	13:25	8-11
	Autumn	3448	80%	06:15	14:59	7-11
	Total	24595				
Ship surveys	Winter	4630	100%	06:30	17:11	7-13
	Spring	3737	81%	04:16	18:29	7-15
	Summer	11967	70%	02:38	20:27	7-15
	Autumn	7692	73%	03:27	19:52	7-16
	Total	28026				

consequently incorporated information on vessel association of single individuals in our analyses of Lesser Black-backed Gulls to test an influence of vessel association on activity as well. Moreover, this method allowed us to distinguish between swimming birds that were associated with vessels and thus active foragers and those swimmers which were not associated with vessels and thus presumably resting. Very few Kittiwakes (less than 5%, German Seabirds at Sea ship database, version 5.07) and only one Guillemot were recorded in association with vessels. Thus, we ignored this parameter for the latter two species.

Seasonal differences in the ratio of flying and swimming birds and in the proportion of vessel association were tested independent of interannual variability applying a Generalized linear mixed model (Faraway 2006, GLMM,) in R Version 2.4.1 (<http://www.r-project.org/>) using the library lme4 (Bates and Sarkar 2007). The model was set as follows: response variable = activity[/vessel association], predictor = season or breeding/non-breeding period (& vessel association), random effect = year, family = binomial. Using data from aerial surveys (German Seabirds at Sea aerial database, version 5.06), we tested whether the ratio of flying and swimming birds differed significantly between seasons. We then tested whether the species studied showed higher proportions of flying individuals during the breeding season (or autumn in case of auks) compared to the rest of the year. Furthermore, we tested the influence of season and breeding season/non-breeding season on vessel association of Lesser black-backed gulls.

Table 6.2: Classification of species-specific seasons for the analysis of activity. Spring covers the return to the breeding site and egg laying while summer comprises the incubation and chick-rearing period in all three species (Prüter 1989, Grunsky-Schöneberg 1998, Glutz von Blotzheim and Bauer 1999)

	Winter	Spring	Summer	Autumn
Lesser Black-backed Gull	01/11 – 15/03	16/03 – 15/05	16/05 – 15/07	16/07 – 31/10
Black-legged Kittiwake	01/11 – 29/02	01/03 – 30/04	01/05 – 31/07	01/08 – 31/10
Common Guillemot	01/10 – 29/02	01/03 – 15/04	16/04 – 15/07	16/07 – 30/09

Using data on Lesser Black-backed Gulls and Kittiwakes from ship-based surveys (German Seabirds at Sea ship database, v5.07), we distinguished adult and immature birds according to plumage differences. Following the different plumages, the class of immature birds comprised 1 to 2 year old Kittiwakes and 1 to 5 year old Lesser Black-Backed Gulls, respectively. However, note that mean age of first breeding is 4-5 years in Black-legged Kittiwakes (Glutz von Blotzheim and Bauer 1999, Rothery et al. 2002). Thus, birds identified as in adult plumage possibly comprise a substantial proportion of non-breeding immatures and adults. We tested whether the ratio of flying and swimming birds differed significantly between seasons for adults and immatures separately. In case of significant seasonal differences, we tested whether proportions of flying individuals differed between the breeding season and the rest of the year. Furthermore, we tested whether proportions of flying immature Kittiwakes differed between winter and the rest of the year. No immature Lesser Black-backed Gulls were recorded during winter.

6.2.2 Long-term trends in activity

To check for long-term trends in activity, we tested whether the proportion of flying adult Lesser Black-backed Gulls, Kittiwakes and Guillemots in the breeding season increased significantly over the three periods 1990-1995, 1996-2000 and 2001-2006. Thus, we applied a Generalized Linear Model (GLM, McCullagh and Nelder 1989) in case of Kittiwakes and a GLMM for Lesser Black-backed Gulls to compensate for influence of vessel association in case of the latter species. The models were built as follows: response variable = activity, predictors = period + period², [random effect = vessel association], family = binomial. In addition, we tested whether the extent of vessel association of adult Lesser Black-backed Gulls in the breeding season increased significantly over time using a GLM (response variable = vessel association, predictors = period, family = binomial). Models were selected using backward selection (applying the ANOVA function in R).

6 Seasonal differences in at-sea activity of seabirds

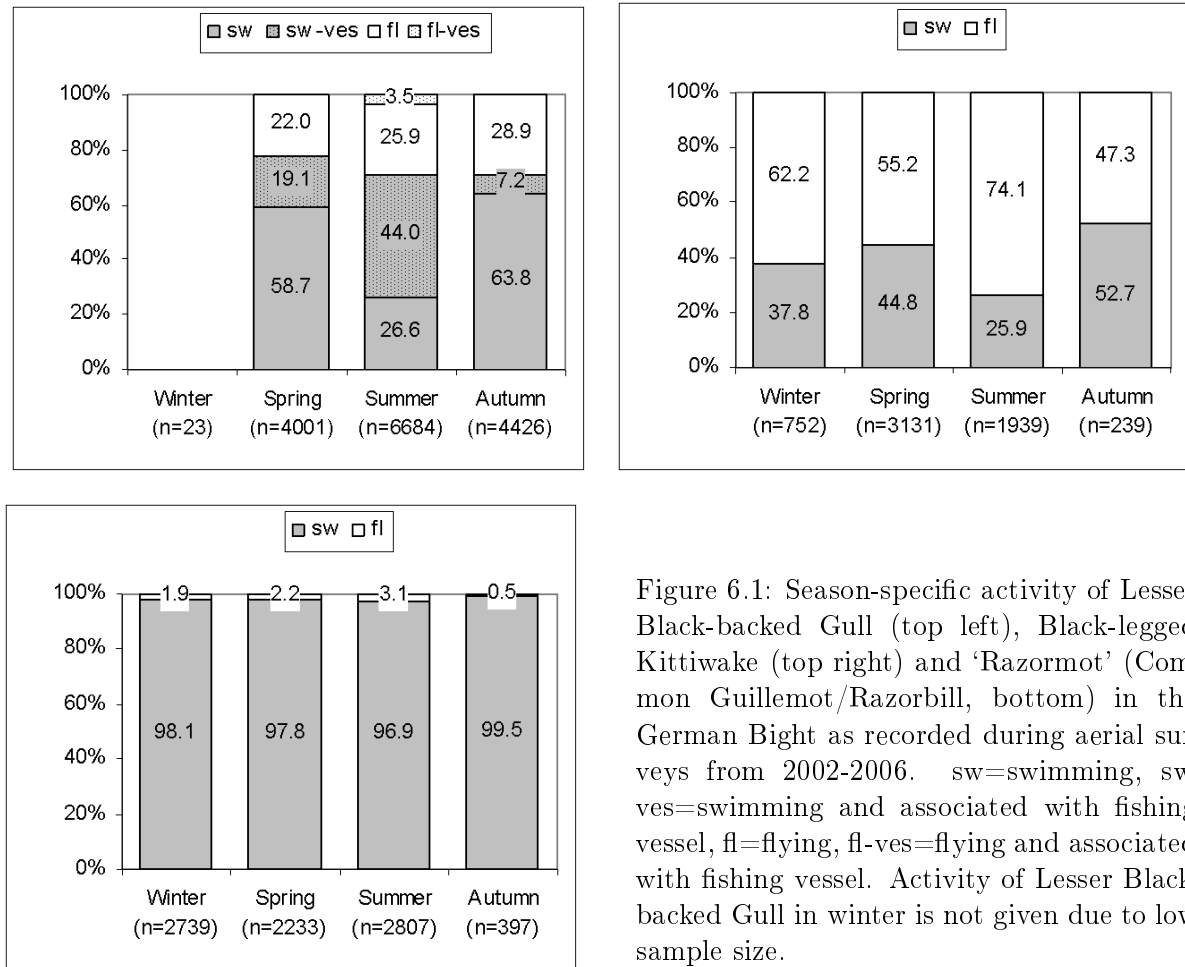


Figure 6.1: Season-specific activity of Lesser Black-backed Gull (top left), Black-legged Kittiwake (top right) and 'Razormot' (Common Guillemot/Razorbill, bottom) in the German Bight as recorded during aerial surveys from 2002-2006. sw=swimming, sw-ves=swimming and associated with fishing vessel, fl=flying, fl-ves=flying and associated with fishing vessel. Activity of Lesser Black-backed Gull in winter is not given due to low sample size.

6.3 Results

6.3.1 Seasonal differences in activity

Seasonal differences in at-sea activity were evident for all species and most age classes. Analyses of data from aerial surveys revealed significantly higher proportions of active individuals in summer compared to the rest of the year for all three species. According to data of gulls from ship-based surveys, this pattern holds only true for adult birds of both gull species, while immature Lesser Black-backed Gulls showed no seasonal differences in activity and immature Kittiwakes showed highest proportions of flight activity in winter. In summer, adult, but not immature Lesser Black-backed Gulls were associated with vessels to a much higher extent than during in the rest of the year. Kittiwakes and Razormots observed during aerial surveys showed highest proportions of flying birds in summer (Fig. 6.1). An exceptionally low proportion of potentially resting individuals (=swimming, but not associated with a vessel) was recorded for Lesser Black-

backed Gulls in summer. In contrast, the proportion of flying and swimming individuals associated with vessels was by far highest in summer (Fig. 6.1).

According to the GLMM, Razormots showed significant differences in activity between seasons (Table 6.3). The proportion of flying birds was significantly higher during breeding season and was significantly lower during autumn with only 2 flying individuals of a total of 397 (0.5%). In correspondence, only 13 individuals out of 1929 (0.7%) were recorded flying during ship-based surveys in autumn. Activity of Kittiwakes differed significantly with season and was significantly highest during summer. Activity of Lesser Black-backed Gulls differed significantly with season and vessel attendance. The proportion of flying individuals was highest during summer and decreased with increasing vessel association (Table 6.3). Analyses of ship data revealed distinct differences between season-specific activity of the different age classes (Fig. 6.2). In accordance with aerial survey data, activity of adult Lesser Black-backed Gulls differed significantly with season and vessel attendance with highest proportions of flying individuals in summer and an inverse relationship between flying behaviour and vessel association. Activity of immature Lesser Black-backed Gulls was also significantly influenced by vessel association but did not differ with season. Likewise, activity of adult Kittiwakes differed seasonally and was highest during summer. Immature Kittiwakes also showed significant seasonal differences in activity. However, the proportion of flying birds was not higher during the breeding season but was significantly lowest during winter (Table 6.3). Both aerial data and ship-based data revealed significant seasonal differences in proportion of vessel association of adult Lesser Black-backed Gulls with highest values recorded in summer. The proportion of vessel association of immature Lesser Black-backed Gulls recorded during ship-based surveys also differed significantly with season but was not significantly higher in summer (Table 6.3).

6.3.2 Long-term trends in activity

Proportion of vessel association and proportion of flying individuals of adult Lesser Black-backed Gulls as well as proportion of flying individuals of Kittiwakes increased significantly in summer over the three periods 1990-1995, 1996-2000 and 2001-2006 (Fig. 6.3, Table 6.3). The relationship between time and flying activity was best described by a quadratic model implying a substantial difference between the first and second period and a weaker between second and third. No such trend was found for Guillemots although levels of activity varied significantly between the three periods. Flight activity was highest in the period 1996-2000 which exhibited lowest mean breeding numbers (2060 AON vs. 2250 AON in 1990-1995 and 2360 AON in 2001-2006, O. Hüppop, pers. comm.) and lowest in the period of highest breeding numbers.

Table 6.3: Temporal variation of seabird activity. Results of GLMMs and GLMs (for details see Methods). *** = significant at 0.001 level, ** significant at 0.01 level, * significant at 0.05 level, n.s. = not significant at 0.05 level.

Species	Data source	Model	Response variable	Predictor variable(s)	Random effect	p	N observations	N groups
LBB gull	plane-all	GLMM	activity	season+vessel association	year	season*** vessel***	15134	5
LBB gull	plane-all	GLMM	activity	summer/rest of year + vessel association	year	summer*** vessel***	15134	5
LBB gull	ship-ad	GLMM	activity	season + vessel association	year	season*** vessel***	22615	17
LBB gull	ship-ad	GLMM	activity	summer/rest of year + vessel association	year	summer*** vessel***	22615	17
LBB gull	ship-im	GLMM	activity	season + vessel association	year	season n.s. vessel***	3819	17
LBB gull	plane-all	GLMM	vessel association	season	year	***	15134	5
LBB gull	plane-all	GLMM	vessel association	summer/rest of year	year	***	15134	5
LBB gull	ship-ad	GLMM	vessel association	season	year	***	22615	17
LBB gull	ship-ad	GLMM	vessel association	summer/rest of year	year	**	22615	17
LBB gull	ship-im	GLMM	vessel association	season	year	***	3819	17
LBB gull	ship-im	GLMM	vessel association	summer/rest of year	year	n.s.	3819	17

Table 6.3: (continued)

Species	Data source	Model	Response variable	Predictor variable(s)	Random effect	p	N observations	N groups
LBB gull	ship-ad-summer	GLMM	activity	period + period ²	vessel association	period ^{***} period ^{2***}	8252	2
LBB gull	ship-ad-summer	GLM	vessel association	period	-	***	8252	-
Kittiwake	plane-all	GLMM	activity	season	year	**	6061	5
Kittiwake	plane-all	GLMM	activity	summer/rest of year	year	***	6061	5
Kittiwake	ship-ad	GLMM	activity	season	year	***	8836	17
Kittiwake	ship-ad	GLMM	activity	summer/rest of year	year	***	8836	17
Kittiwake	ship-im	GLMM	activity	season	year	**	1021	17
Kittiwake	ship-im	GLMM	activity	summer/rest of year	year	n.s.	1021	17
Kittiwake	ship-im	GLMM	activity	winter/rest of year	year	**	1021	17
Kittiwake	ship-ad-summer	GLM	activity	period + period ²	-	period ^{***} period ^{2**}	4860	-
Razormot	plane-all	GLMM	activity	season	year	**	8176	5
Razormot	plane-all	GLMM	activity	summer/rest of year	year	**	8176	5
Razormot	plane-all	GLMM	activity	autumn/rest of year	year	*	8176	5
Razormot	ship	GLM	activity	period + period ²	-	period ^{***} period ^{2***}	3227	-

6.4 Discussion

6.4.1 Methodology

It has to be noted that results on proportions of flying and swimming behaviour can not fully be equated to absolute activity budgets. Considering flying and swimming behaviour only, it is not possible to differentiate between specific foraging behaviours like plunge diving, surface dipping, etc. over the entire data set, although such behaviour has been regularly recorded in most recent years (Camphuysen and Garthe 2004). Furthermore, no information can be collected on frequency and length of dive bouts of Razormots from a moving observation platform. However, we analysed at-sea surveys only and thus are not able to incorporate information on length of time spent on land/in the colony and activity at this site. Lesser Black-backed Gulls usually rest on land throughout the whole year and we assumed that no differences exist between time spent on land between breeding season and the rest of the year. Common Guillemots and Black-legged Kittiwakes though are truly pelagic seabirds as they do not return to land at night outside the breeding season (Furness and Monaghan 1987). However when breeding, they are bound to spend time in the colony to defend their nest sites, incubate and to feed and guard the chicks. Thus, breeding birds could restrict resting time to time at the colony to increase their presence at the nest site while non-breeding birds both forage and rest at sea. On the other hand, due to dense breeding colonies, much time at the colony is spent with antagonistic and thus presumably costly behaviour (Glutz von Blotzheim and Bauer 1999). Unfortunately, we had no information on the proportion of resting behaviour and thus energy expenditure at the colony. However, we assumed that time spent at the colony can not be fully attributed to resting, i.e. low-cost behaviour. Moreover, according to long-term studies, colony attendance of Kittiwakes is assumed to be only slightly lower in spring compared to summer (Tasker and Furness 1996). Our results though reveal clear differences between the two seasons (see Fig. 6.1 and 6.2). Thus, we are confident that the high values of at sea-activity recorded in summer correspond well to an overall increase of activity and thus energy demands during the breeding season.

We also have to bear in mind that not all birds wearing adult plumage in the study area in summer are engaged in breeding activities as they also comprise immature birds (>1 or 2 years) in the case of Kittiwakes, and summering birds or individuals which aborted breeding. Like shown in this study for immatures and in contrast to breeding birds, these non-breeding individuals presumably do not meet higher energetic demands in summer. Consequently, our estimates of the proportion of active foraging behaviour of adult birds in summer might underestimate actual values of breeding birds. On the other hand, immatures which represent our control-group of non-breeders in summer, might have to invest more effort in foraging activities due to low experience (following Burger 1987) and thus, our estimates of the proportion of active foraging behaviour of immature birds in summer presumably overestimate values of older non-breeding

birds. As a consequence, differences in at-sea activity budgets between breeders and non-breeding birds are presumably larger than recorded in our study.

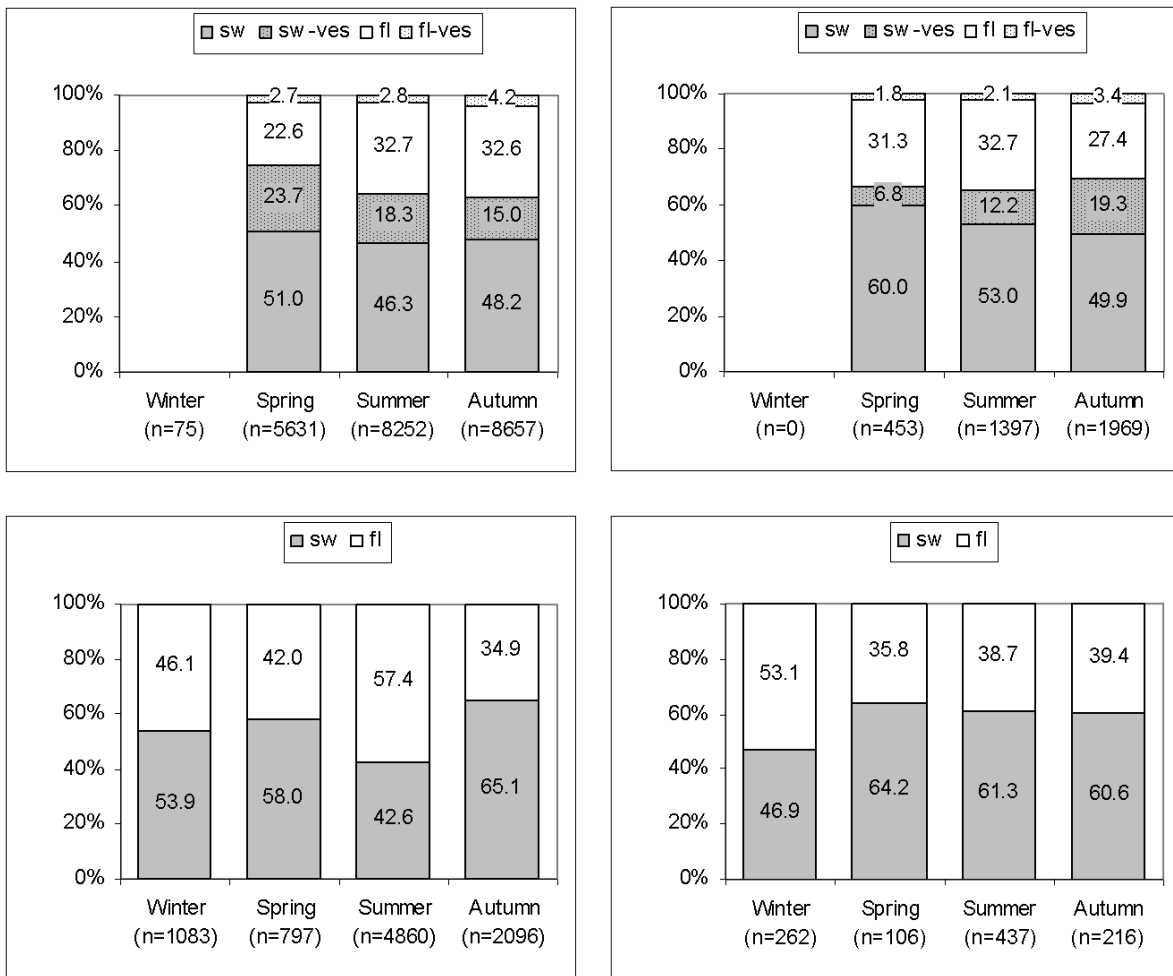


Figure 6.2: Differences in season-specific activity between adult (left) and immature (right) gulls in the German Bight as recorded during ship-based surveys from 1990-2006. Top: Lesser Black-backed Gull, bottom: Black-legged Kittiwakes; sw=swimming, sw-ves=swimming and associated with fishing vessel, fl=flying, fl-ves=flying and associated with fishing vessel. Activity of Lesser Black-backed Gull in winter is not given due to low sample size.

The three periods used for the trend analyses of activity, 1990-1995, 1996-2000 and 2001-2006, differed slightly with respect to area covered. With a total of 3425 km², the first period holds a significantly lower spatial effort than the second and third period (4247 and 4294 km², respectively). This lower value is in particular caused by lower sampling effort in the nearshore area <20 km from the coast (816 km² compared to 1676 and 1837 km²). Sampling effort in the offshore region >80 km from coast was generally low with particularly low efforts in the third period (215 km² compared to 487 km² in the first period and 408 km² in the second). However, sampling effort in the distance classes 20-40 km and 40-80 km from coast did not differ substantially between the three periods. In a case study in 2002, Lesser Black-backed Gulls showed highest numbers of vessel association in a distance of 40-60 km from coast (Schwemmer and Garthe 2005). Thus, the main concentration areas of Kittiwakes as well as of Lesser Black-backed Gulls in summer and the main region of vessel association of the latter species (following Dierschke et al. 2004, Schwemmer and Garthe 2005) were sampled with similar efforts throughout the three periods. We consequently assume our results on trend analyses not to be biased by differences in spatial effort.

Next to spatial aspects of survey efforts, timing of surveys with respect to time of day also influences results on distribution (chapter 4) and activity due to the fact that most seabirds exhibit diurnal patterns in activity (Shealer 2002). This problem will be highlighted in the following for the example of the Kittiwake but is assumed to be valid for other species in a similar manner. Breeding Kittiwakes in Scotland showed distinct diurnal differences in activity according to logger data with highest flight activity in the morning between 8 and 13 UTC and during late evening (Daunt et al. 2002). Thus, aerial surveys of the present study covered exclusively periods of highest activity in summer (see Table 6.1). Consequently, estimated activity budgets are likely to overestimate actual values of the whole day period. Ship-based surveys covering a broader range of time of day (Table 6.1) accordingly produced lower activity values for all seasons (compare Figs. 6.1 and 6.2). However, the general picture of differences between seasons is strikingly similar when comparing results of both survey types. Overall, we assume that our results give reasonable estimates of activity budgets and of the differences between seasons and breeders/non-breeders.

6.4.2 Seasonal differences in activity

Our results confirmed hypothesis (1) by assessing higher proportions of flying or actively foraging birds in summer compared to the rest of the year. In correspondence to hypothesis (4), activity of Razormots was only slightly (but still significantly) elevated in summer. This corresponds to alcids mainly foraging while swimming and the proportion of flying being generally low in this species. Tremblay et al. (2003) found that breeding Guillemots were resting in only 17% of the time they spent at the surface and thus were active in the majority of the time they spent swimming. Nevertheless, our results imply

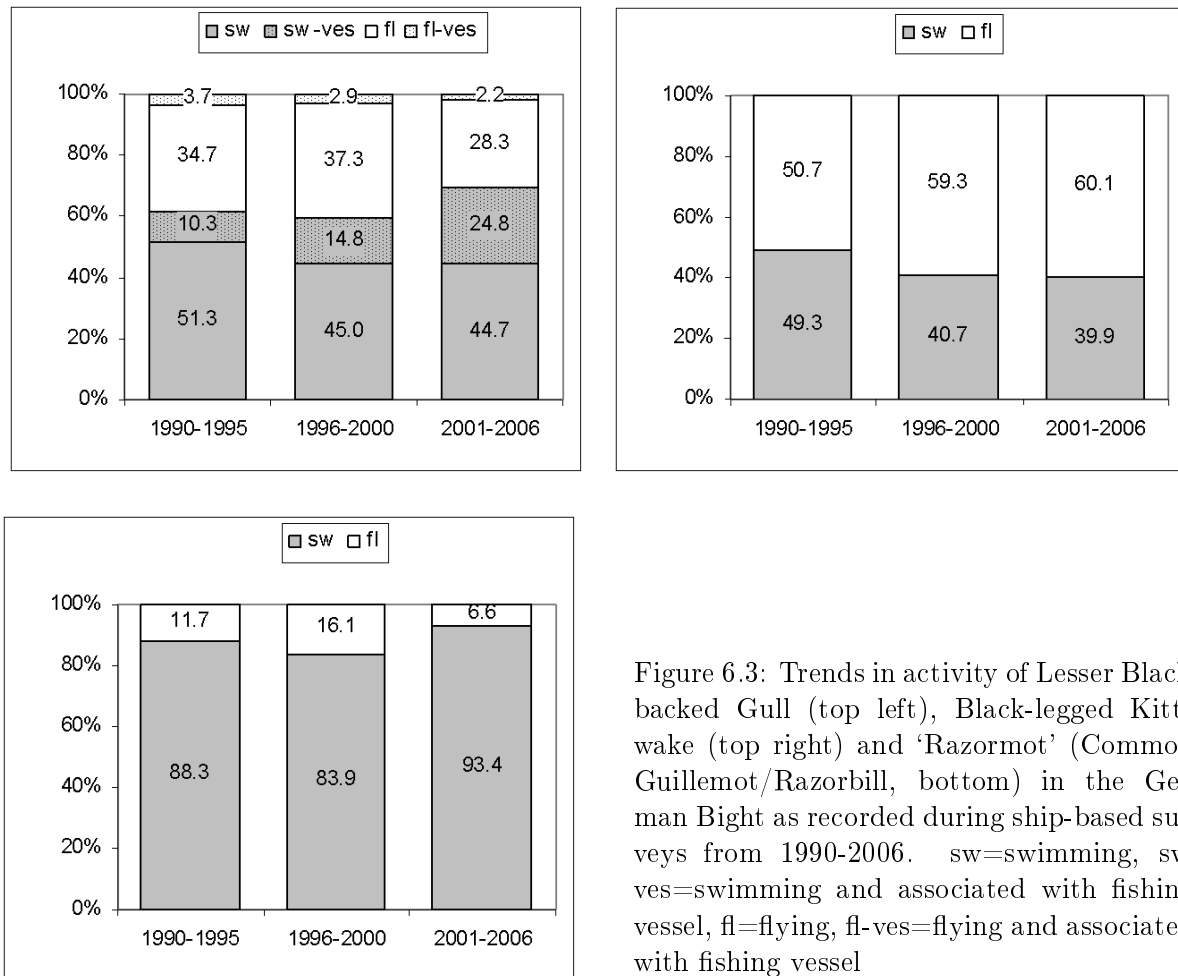


Figure 6.3: Trends in activity of Lesser Black-backed Gull (top left), Black-legged Kittiwake (top right) and 'Razormot' (Common Guillemot/Razorbill, bottom) in the German Bight as recorded during ship-based surveys from 1990-2006. sw=swimming, sw-ves=swimming and associated with fishing vessel, fl=flying, fl-ves=flying and associated with fishing vessel

that travel time does indeed comprise a substantial share of total time for Guillemots, although this species exhibits a mean foraging radius of 5-10 km only around the single breeding colony in the German Bight on Helgoland (Dierschke et al. 2004). Guillemots on Helgoland exhibited mean feeding rates of 4.5 fishes/day/chick (Grunsky-Schöneberg 1998). Assuming even shares of feeding bouts for both sexes, total daily travel length of one parent bird mounts up to 23-45 km ($= 4.5 * 2 \text{ ways} * 5 \text{ or } 10 \text{ km} / 2 \text{ parents}$). With a flight speed of 69 km/h (Pennycuik 1987), each parent bird thus spends 20-40 minutes travel time per day, about 2-4% of total day length assuming a mean day length of 17 h (Grunsky-Schöneberg 1998). This value corresponds well to the proportion of flying individuals (3.1%) recorded in our study for the summer period although the latter probably doubles the proportion of daily travel time assuming a colony attendance value of 50% (following Tasker and Furness 1996). In contrast, breeding Guillemots mounted with activity recorders in Newfoundland and Norway spent 10% and 11% respectively of their time at sea flying (Cairns et al. 1987, Tremblay et al. 2003). The study site in Newfoundland however hosts 77,500 pairs (BirdLife International 2007). Thus, higher values of travel time at this site can be explained by longer distances travelled due to

high densities in the vicinity of the colony (following Ashmole 1963, Lewis et al. 2001). Breeding numbers at the study site in Norway however were of the same size as at Helgoland (Sandvik et al. 2005). Our results do not imply a positive correlation between colony size and foraging activity for Guillemots. In contrast, highest levels in activity coincided with lowest values of breeding numbers at Helgoland. Overall differences in breeding numbers though were low and consequently do not allow further conclusions. The recorded low values of flying Razormots in autumn correspond to the moulting and chick-guarding period of Guillemots. It is striking that virtually no flying individuals were recorded within a period of 76 days (16 July – 30 September) although adults are flightless for a period of only 45-50 days (Glutz von Blotzheim and Bauer 1999). However, Guillemot chicks, exhibiting an intermediate post-hatching development, still need approximately 70 days after leaving the colony to fledge completely (Glutz von Blotzheim and Bauer 1999).

In contrast to adults, the proportion of neither flying individuals nor vessel association of immature gulls was significantly elevated in summer (confirming hypothesis 2). With immatures corresponding to non-breeding birds and the majority of adults comprising breeding birds, our results support the assumption that breeding birds spend higher proportions of time per day for foraging activities (a) compared to non-breeding birds in the same period and (b) compared to the non-breeding period. Chick-rearing birds thus do not only carry out longer foraging trips (Golet et al. 1998) but also allocate time at sea differently. These findings reveal two aspects: In comparison to non-breeders, (1) breeding birds need to exhibit higher foraging efforts to meet self-provisioning plus chick-rearing demands, and (2) breeding birds spend more energy by being engaged in high-costly behaviour like flying and foraging at vessels. It is known that chick-rearing birds increase their working level by 33-50% compared to the non-reproductive level (Drent and Daan 1980). Correspondingly, the proportion of flying Kittiwakes recorded in summer during aerial surveys of our study was nearly 20% higher compared to spring and more than 25% higher compared to autumn.

A quarter of all Kittiwakes observed in summer during aerial surveys in our study was swimming. This value is well in accordance with the proportion of the foraging trip spent on the sea surface recorded by activity loggers for breeding Scottish Kittiwakes (25.0% during daytime, Daunt et al. 2002) and Kittiwakes in Alaska ($21.4\% \pm 15.8\%$, Jodice et al. 2003).

As hypothesized, immature Kittiwakes showed highest activity budgets in winter indicating an energetic bottleneck in this season. Correspondingly, adult Kittiwakes showed second-highest activity during winter following values of the breeding season (Figs. 6.1 and 6.2). The winter period generally represents an extremely demanding season for seabirds of the temperate zone due to low food availability, high frequency of adverse weather conditions, high thermoregulatory costs due to low temperatures of water and air and short day length (summarized in Daunt et al. 2006). In accordance, highest

mortality of Kittiwakes is recorded in winter and mortality rates of inexperienced one-year olds exceed values of older birds (Coulson and White 1959, Aebischer and Coulson 1990). Kittiwakes experience high thermoregulatory costs in winter due to low water temperatures and are thus expected to compensate these costs by suitable behaviour (Humphreys et al. 2007). In accordance with the adaptations of animals coping with cold stress predicted by Scholander et al. (1950), one could assume Kittiwakes to exhibit higher proportions of active behaviour in winter to minimize thermoregulatory costs by increasing heat production. Yet, this seems rather unlikely as flight costs of Kittiwakes are comparatively high (6-7x BMR, Jodice et al. 2003). Besides, thermoregulatory costs should be of the same height concerning both adults and immatures. Portions of flying immatures though were substantially higher than those of adults (53% compared to 46%). Likewise, wintering immature Common Cranes *Grus grus* have to spend more time feeding than adults to achieve the same daily food intake rates (Alonso and Alonso 1993). Age-related foraging success was found in a variety of birds, e.g. in songbirds and waders (Puttick 1984, Desrochers 1992). Thus, the observed high proportions of flying behaviour of immature Kittiwakes presumably reflect the need for intensified foraging efforts due to lower foraging abilities.

6.4.3 Long-term trends in activity

Our study revealed increasing levels of foraging activity for the two gull species both with respect to vessel association and flying individuals over the three periods 1990-1995, 1996-2000 and 2001-2006. However, the increase of flight activity was most definite between the first periods, 1990-1995 and 1996-2000, and less pronounced or not present between 1996-2000 and 2001-2006. This increase presumably reflects higher intraspecific competition due to strong increases in breeding numbers (following Ashmole 1963, Lewis et al. 2001). In accordance, no such trend was revealed for Guillemots which exhibited relatively stable breeding numbers.

In addition, food availability might have deteriorated due to ecosystem changes. Thus, Weijerman et al. (2005) identified a possible regime shift in the North Sea and the Wadden Sea in 1998 on the basis of various physical and biological parameters though results were not as distinct as for earlier regime shifts in 1979 and 1988. This analysis incorporated amongst others data on fish abundance, a factor that is most likely to influence food availability and thus foraging behaviour of Kittiwakes and Lesser Black-backed Gulls in the study area as both species feed on fish to a high extent (Kubetzki and Garthe 2003, chapter 3). In conclusion, major ecosystem changes indeed took place in the late 1990s, being reflected in the occurrence of plankton and fish and thus probably influencing activity budgets of seabirds. However, the situation of top predators in the southern and eastern part of the North Sea still seems to be very well when compared to the northern North Sea as indicated by exceptionally high numbers of seabirds in the southern North Sea in the last years (Camphuysen 2006) and a shift of the main

concentration area of Harbour Porpoises *Phocoena phocoena* from the north to the south of the North Sea from 1994 to 2005 (Hammond and Macleod 2006).

6.5 Outlook

To the best of our knowledge, our study is the first to provide information on activity of selected seabird species in a given study area throughout the year using data on the whole regional population. The applied method qualified above all in assessing activity budgets of surface-feeding species but was also suited to depict elevated activity in a diving species. We were able to specify differences between age classes and seasons. We recorded high foraging activity in the breeding season due to high demands, i.e. reproductive costs (self-provisioning plus chick-rearing), and high foraging activity in winter presumably due to reduced food supply and high costs. Moreover, it was possible to disclose elevated activity levels from the late 1990s onwards in comparison to the early 1990s indicating higher levels of intraspecific competition or reduced food availability.

Results on activity of Kittiwakes correspond well to activity budgets reported in logger studies. Thus, our analyses of at-sea activity apparently give reasonable estimates of time-activity budgets. Analyses of aerial and ship-based surveys provided comparable results proving both data sets suitable for this kind of objectives. Regarding comparisons of different years or periods, the comparison of activity possibly forms a better indicator of food availability than provisioning rates as activity presumably corresponds better to effort spent.

The extensive dataset used thus allows the testing of basic theories and provides estimates of energy expenditure at the level of seasons and for different age classes separately. It fills a gap in existing studies of seabird biology as information on activity and energy expenditure is mostly collected in the colony and thus only covers the time period of birds being present in the colony. Data logger studies can give information on both periods, time at the colony and time at sea, simultaneously. However, numbers of samples are mostly small in these studies while our study gives an overview over the at-sea activity of an entire region. Moreover, most logger studies have generally covered only a short period of a specific breeding season while our study provided general information on the whole breeding season and even more on every other season of the year. However, further progress in microtechnology has recently enabled attachments of devices to seabirds the whole-year round. In those cases, individuals can be tracked over vast ocean areas (e.g. Croxall et al. 2005), and detailed activity data can be derived, often even including feeding and diving behaviour (Catry et al. 2004, Shaffer et al. 2006). Nevertheless, it has to be taken into account that such studies deal with handled birds carrying extra weight and thus may not always produce unbiased results (e.g. Ropert-Coudert and Wilson 2004). On the other side, it is possible to study individuals that move over a much larger area than can be covered by ship-based and aerial surveys.

While results on activity of adults in summer lack information on time spent at the colony

and thus can not be equated to actual activity budgets, results on activity budgets of non-breeding birds (immatures and birds outside the breeding season) can be directly incorporated in models of energy expenditure and food consumption. However, it is recommended to complement results of Lesser Black-backed Gulls by logger studies to obtain data on time spent on land.

Acknowledgements

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7 General conclusions

Several fundamental aspects of the at-sea distribution and habitat choice of seabirds in the German Bight were so far known but more information is needed to fully understand seabird distribution patterns and the factors that drive and control them. Temporal variation of distribution patterns was mainly known at the order of seasons. Less information was available concerning the extent of temporal variability of seabird distribution patterns at smaller time scales. Concerning habitat choice, the distribution of several species had been shown to be linked to the occurrence of different water masses. However, the influence of smaller hydrographic structures was not assessed in detail before. Little information existed on the connecting link between seabird distribution and hydrography. It is expected that this link is formed by the hydrography-dependent availability of prey. Furthermore, habitat choice with respect to water mass associations was so far only assessed during summer while almost no information existed on habitat choice during the rest of the year. Seasonality of habitat choice was not yet studied with respect to the quality and the strength of habitat affinities.

This thesis aimed at filling some of the important gaps described above. I therefore focused on habitat choice of seabirds in the German Bight and on temporal variability of seabird distribution patterns. The following objectives were addressed by analysing dedicated surveys and long-term seabirds at sea survey data:

- (1) Identification of factors controlling and shaping seabird distribution patterns with focus on hydrography, in particular on the influence of small scale hydrographic structures such as fronts;
- (2) Identification of the connecting link between hydrography and seabird distribution;
- (3) Assessment of the extent of temporal variability at smaller time scales and identification of possible controlling factors;
- (4) Assessment of the seasonality of habitat choice with respect to differing preferences and varying strength of habitat bonds, and assessment of the seasonally varying demands of seabirds.

7.1 Small scale temporal variability of distribution patterns

Small scale temporal variability was above all assessed by repeatedly surveying specific transect routes on consecutive days and on the same day. Furthermore, we studied differences in distribution patterns of Black-legged Kittiwakes *Rissa tridactyla* between different times of day on the basis of long-term ship-based survey data (chapter 4).

Seabird distribution patterns in the German Bight were shown to vary substantially at smaller temporal scales, i.e. at the order of days or hours (chapter 4). According to ship-based and aerial surveys, distribution and abundance especially of gulls and terns varied significantly between consecutive survey days. In contrast, distribution patterns of Common Guillemots *Uria aalge* did not differ between consecutive survey days or were relatively similar. This higher stability might be explained by the fact that Guillemots forage while diving and spend far more time swimming than flying. Gulls on the other hand are surface-feeders which are restricted to prey concentrations at the sea surface. While Guillemots exploit the third dimension of their marine habitat, gulls have to sample large areas in search for food two-dimensionally. Time of day had a significant influence on the distribution and abundance of gulls. Thus, the at-sea occurrence of Kittiwakes was restricted to the vicinity of the colony in the morning and evening and reached highest abundance values as well as maximum distance from the colony in the early afternoon.

7.2 Environmental factors influencing seabird distribution patterns

In the course of this thesis, the following factors were found to influence seabird abundance and distribution significantly:

- large scale hydrographic structures, i.e. water masses (chapter 5),
- small scale hydrographic structures, i.e. fronts (chapter 2),
- tidal stage (chapter 4),
- maximum wind speed (chapter 4),
- fishing activity (chapter 4).

A significant association with a specific water mass was in particular found for all truly pelagic species, i.e. Northern Fulmar *Fulmarus glacialis*, Northern Gannet *Sula bassana*, Black-legged Kittiwake and Common Guillemot all of which were associated with the Central North Sea water mass at least in one studied season. Coastal species with an affinity for the Continental Coast water mass comprised Common Gull *Larus canus*,

Sandwich Tern *Sterna sandvicensis* and Common Tern *Sterna hirundo*. The distribution of all other gull species was not significantly correlated to a specific water mass but Herring Gulls *Larus argentatus* showed a trend for an association with the Continental Coast water mass. This low influence of hydrographic structures might be explained by the highly opportunistic foraging behaviour of gulls. All resident *Larus* gulls exploit a variety of food sources and are able to switch between different foraging habitats such as the neritic, the intertidal and the terrestrial habitat (e.g. Kubetzki and Garthe 2003, Schwemmer and Garthe 2005, 2008). Moreover, the distribution of Black-headed Gull *Larus ridibundus* and Herring Gull is restricted to the vicinity of the coast and is thus less influenced by the marine habitat and its hydrography.

With respect to the whole seabird community, small scale hydrographic structures did not play a role as important as larger hydrographic structures, i.e. water masses, in the German Bight. However, the influence of fronts can be substantial as revealed by Skov and Prins (2001) for Red-throated *Gavia stellata* and Black-throated Divers *Gavia arctica* and as could be shown in this thesis in particular for Black-legged Kittiwakes (chapters 2 and 4). A significant influence of fronts was also recorded for Great Black-backed Gulls *Larus marinus*. In addition, Lesser Black-Backed Gulls *Larus fuscus* and Herring Gulls were observed to concentrate at these structures. The observed fronts were either short-lived or highly dynamic in location and strength. Thus, distribution patterns of seabird species such as gulls and divers which concentrate along the described fronts undergo spatio-temporal variation, following variation of the frontal system. In accordance, high variability at the order of days was recorded for distribution patterns of Black-legged Kittiwakes (chapter 4).

An influence of tidal stage on the abundance of Black-headed, Common, Lesser Black-backed and Herring Gull can at least partly be explained by the high importance of the intertidal habitat for foraging *Larus* gulls (Kubetzki and Garthe 2003). Thus, lower numbers of gulls in the gullies at ebb tide can presumably be related to higher foraging activity on the surrounding mud flats. Colony-based observations in the study area indeed revealed highest flight activity towards the mud-flats during ebb tide for Black-headed Gulls (Schwemmer and Garthe, in press). This tidal stage offers profitable foraging conditions for seabirds due to high availability of benthic animals exposed by the retreating waterline (following Gibson 2003). Accordingly, the higher numbers of gulls in the gullies during flood tide coincided with a higher amount of resting behaviour during this tidal stage. On the other hand, flood tide could also be related to higher numbers of prey such as fish and larger crustaceans active in the water column of the water body (following Del Norte-Campos and Temming 1994, Aagaard et al. 1995).

Strong wind had a negative effect on the occurrence of Black-headed, Common, Lesser Black-backed and Herring Gull. An avoidance behaviour to strong winds is also known for Kittiwakes (Manikowski 1971). Strong winds constrain flight performance and increase flight costs (Woodcock 1940, Manikowski 1971). Kittiwakes avoid flying in strong gusts and endure periods of strong winds swimming in a ducked position (Glutz von

Blotzheim and Bauer 1999). In accordance, the proportions of resting behaviour of the four *Larus* gulls was higher during strong winds. In addition, natural food availability is reduced by strong winds (Dunn 1973, Finney et al. 1999). Thus, gulls most probably shifted to the more sheltered terrestrial habitats during periods of strong winds.

Fishing activity had a significant positive influence on the occurrence of Black-headed, Common, Lesser Black-backed and Herring Gulls. All gulls are generally known to feed on discards but an influence on distribution is seldom found. However, Garthe (1997) revealed a significant influence of trawler abundance on the distribution of Black-headed and Herring Gull during summer in the German Bight.

In addition, analyses of long-term activity data indicated a higher importance of fisheries discards for Lesser Black-backed Gulls during the breeding season (chapter 6). This trend however was not reflected in long-term studies of diet composition of Lesser Black-backed Gulls breeding in two of the largest colonies of the German North Sea coast (FTZ, unpublished data).

Studies on the influence of environmental factors on seabird distribution are complicated by the fact that these factors are interrelated, i.e. can not be studied independently. Thus, numbers of trawlers decreased with increasing maximum wind speed (chapter 4) and no fishing takes place during stormy periods. Consequently, strong winds cause a reduction of natural and anthropogenic food sources for seabirds.

Moreover, the influence of fishing activity interacts with the influence of hydrography on the distribution of seabirds. During the winter cruise studied in chapter 5, single individuals of Northern Fulmar and Common Gull which occurred in their respective non-preferred habitat type were nearly always associated with actively fishing trawlers (Fig. 7.1a,b). Earlier studies of the distribution of Northern Fulmars in the North Sea concluded that, although the Fulmar regularly feeds on discard and offal, the observed distribution pattern of this species was hardly influenced by fishing activity itself, but was rather well-explained by hydrographic parameters (Camphuysen and Garthe 1997). This relation was already presumed by Brown (1970) and later confirmed again by Skov and Durinck (2001). The latter found higher numbers of ship-following individuals of both Fulmars and Common Gulls in their preferred habitat types. However, the findings presented here favour the assumption that, despite occurring in lower absolute numbers in their respective non-preferred habitats, both species are more dependent on anthropogenic food sources like discard in these areas, possibly because of lack of suitable natural food sources. Thus, the distribution of Northern Fulmars and presumably also Common Gulls seems to be primarily driven by hydrography and secondarily influenced by fishing activity.

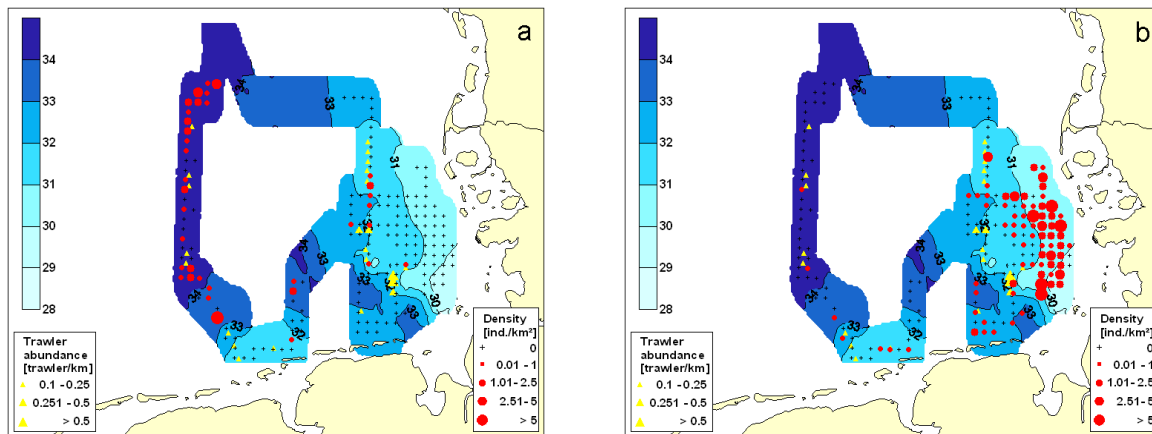


Figure 7.1: Distribution of Northern Fulmar (a) and Common Gull (b) during cruise W in October/November 1993 (see chapter 5) in comparison with sea surface salinity and occurrence of fishing trawlers. Seabird distribution maps were created by calculating densities (sum of individuals / sum of surveyed area) for 3' latitude x 6' longitude grids. Salinity [psu] was mapped by interpolating measurements.

7.3 The link between hydrography and seabird distribution

Hydrography is not the resource seabirds are searching for but rather indicates food availability for the birds indirectly. Or, in other words, as a colleague expressed it at a conference: *'Birds don't eat temperature.'* Hence, the link between hydrography and the distribution of seabirds is their prey. This thesis could show that valuable information on this link can be derived by diet studies. Thus, analysis of the diet composition of Kittiwakes from the breeding colony on Helgoland revealed juvenile Whiting *Merlangius merlangus* to be the main prey (chapter 3). According to the literature, these fish concentrate in frontal areas and are in addition highly abundant in the German Bight in summer. Moreover, fisheries biologists recorded high concentrations of juvenile Whiting in the upper water column in the vicinity of Helgoland. This is in contrast to the general classification of Whiting being a demersal species. Based on the latter assumption, earlier studies on the diet composition of Kittiwakes concluded Whiting to be mainly available for Kittiwakes in the form of fisheries discard. However, results of chapter 3 lead to the conclusion that Whiting in the diet of Kittiwakes at Helgoland does not originate from discards but was preyed upon by Kittiwakes in the frontal areas of the German Bight. This conclusion is based on a number of studies and findings. However, further proof should be achieved by directly sampling food availability for seabirds in the study area. In this context, studies on seabird diet composition should be combined with sampling

of prey available to seabirds at different hydrographic structures, in particular at fronts. However, these aims are difficult to fulfil as the highly dynamic fronts are not easy to locate in the field. Moreover, they are short-lived and predictable only to a low degree. Studies should thus concentrate on regions with known high occurrence of fronts which in the same time are known as concentration areas of seabirds. A suitable study site would therefore be the sea area around Helgoland.

7.4 Seasonality of habitat choice

Seasonality of habitat choice comprises both differences in the quality and the strength of habitat bonds. Within this thesis, no obvious contrasts in habitat preferences were found between winter and late summer (chapter 5). However, preferences of Common Gulls for the Continental Coast water mass and of Black-legged Kittiwakes for the Central North Sea water mass were stronger in winter. On the other hand, Northern Fulmars and Common Guillemots showed strongest associations to the Central North Sea water mass in summer. The relatively higher abundance of Fulmars, Guillemots and Common Gulls in the Continental Coast water mass during winter were related to a presumably better food availability of this habitat in winter. Although Kittiwakes did not show a preference for a specific water mass in summer, they were strongly associated with hydrographic fronts during both summer surveys and hence showed strong habitat bonds (chapter 2).

Seasonal differences in activity revealed higher levels of activity for Common Guillemots, Black-legged Kittiwakes and Lesser Black-backed Gulls during summer (chapter 6). In the case of Guillemots, these were attributed to a higher amount of travelling time caused by the need to commute between foraging areas and the colony. Higher activity levels of the two gull species on the other hand were above all referred to a higher amount of active foraging behaviour in the course of meeting higher demands during the breeding season. All other seasons were characterised by higher amounts of resting behaviour. Hence, one might expect birds to show a stronger bond to preferred foraging areas during summer as resting birds are assumed to show weaker associations with prey patches. This result is well in accordance with the finding that the distribution of Kittiwakes correlated significantly with the occurrence of hydrographic fronts in summer. Frontal areas are characterised by high occurrence of biomass due to passive aggregation and enhanced primary production. A high abundance of organisms at different levels of the food chain thus presents favourable feeding conditions for predators such as fish and consequently attracts also piscivorous seabirds like the Kittiwake. In chapter 3, the main prey species of Kittiwakes in the German Bight was shown to be Whiting, a fish species which concentrates in frontal areas. Consequently, frontal areas are major foraging grounds for Kittiwakes in the study area.

No significant association to hydrographic structures, neither water masses nor fronts, was revealed for the Lesser Black-backed Gull in this thesis. Analyses of activity however

indicated an important role of an anthropogenic food source, i.e. fisheries discards (see also chapter 4). The level of association with fishing vessel was highest during summer, thus confirming the assumption of a stronger bond to foraging habitats during this season.

Both summer cruises analysed in chapter 5 fall into the ‘autumn’ period as classified for Guillemots (see Table 6.2, page 95). Guillemots are almost exclusively encountered swimming during this season (chapter 6), as they are moulting and guarding their not-yet fledged chicks at sea. Due to their heavily restricted mobility, Guillemots can be expected to stay within profitable feeding grounds during their flightless period. Consequently, a strong habitat bond is highly probable during this period and was indeed found in chapter 5.

7.5 Influence of competition on seabird distribution patterns and regulation of seabird populations

Although habitat choice is assumed to be mainly controlled by the availability of specific resources (Bairlein 1996), it is also influenced by the presence of other individuals. Conspecifics and other members of the marine fauna can e.g. attract seabirds or even enhance their foraging success (e.g. Götmark et al. 1986, Camphuysen and Webb 1999). On the other hand, other individuals might act as predators or competitors and may thus influence seabird distribution negatively (e.g. Camphuysen 2002). Ashmole (1963) suggested that breeding seabirds deplete prey stocks in the vicinity of the colony. An increase in colony size would therefore lead to stronger intraspecific competition and an extension of depleted areas, resulting in longer foraging trips (Ashmole 1963). A positive correlation between colony size and foraging trip duration was recently revealed for Northern Gannets nesting in Britain and Ireland (Lewis et al. 2001).

An extension of the foraging area due to intraspecific competition was also indicated by different results of this thesis. Thus, the period of maximum distance from colony of breeding Black-legged Kittiwakes coincided with the peak of total numbers at sea, when observed throughout the day (chapter 4). Moreover, flight activity of adult Kittiwakes and Lesser Black-backed Gulls during the breeding season increased significantly over a period which was also characterised by substantial increases in breeding numbers of both species (chapter 6). Hence, intraspecific competition might have caused an extension of depleted areas around the breeding site forcing birds to forage at increasing distances from the colony. A reduction of natural prey stocks might also be reflected by the fact that proportions of Lesser Black-backed Gulls scavenging at fishing vessels increased over the same period (chapter 6).

Differences in the distribution of Kittiwakes between different times of day however can not be referred to actual prey depletion but might reflect reductions in food availability through avoidance behaviour of disturbed prey (Lewis et al. 2001).

These results and the findings that adult birds show a significantly higher at-sea activity during the breeding season (chapter 6) support the assumption of seabird populations being regulated by density-dependent food supply during the breeding period (Ashmole 1963). Lower levels of Kittiwake activity during winter (chapter 6) on the other hand contradict Lack's hypothesis of a regulation of seabird populations through density-dependent mortality outside the breeding season (Lack 1966). Thus, in spite of higher thermoregulatory costs and a presumably lower food availability in winter, birds allocate lower proportions of the day to active foraging behaviour. Taking shorter periods of daylight during winter into account, overall foraging time presumably is comparatively low. These findings lead to the conclusion that density-dependent effects do not play a major role outside the breeding season.

7.6 Status of the Black-legged Kittiwake in the German Bight and its role as a bioindicator

In the North Sea, breeding numbers of Black-legged Kittiwakes have declined by more than 50% since 1990 (Frederiksen et al. 2004, Heubeck 2004, ICES-WGSE 2006). These severe declines were in particular experienced in the northern breeding colonies that represent the main concentration areas of Kittiwakes in the North Sea. The reasons for this negative population trend are still not explained in detail. However, declines are connected to a low breeding success which is likely to result from low food availability and low food quality (Frederiksen et al. 2004, Wanless et al. 2005, ICES-WGSE 2006, Wanless et al. 2007).

In contrast to the situation in the northern North Sea, the breeding colony in the south-eastern North Sea at Helgoland did not suffer declines. Instead, breeding numbers continued to increase strongly and in the end doubled in size since 1990. Only the last years have shown a period of stagnation (chapter 3). This positive trend is presumably connected to favourable feeding conditions in the German Bight. In this thesis, it could be shown that Kittiwakes of the breeding colony at Helgoland feed mainly on juvenile Whiting (chapter 3). This result parallels earlier studies on the diet of Kittiwakes at Helgoland from the 1980s and 1990s (Vauk-Hentzelt and Bachmann 1983, Prüter 1989, Maul 1994). Juvenile Whiting, which concentrate in the German Bight in summer, presumably do occur at the sea surface in frontal areas (following Flöter 2005 and information on fisheries research catches, D. Stepputtis, pers. comm.). Within this thesis, a significant influence of hydrographic fronts on the distribution of Kittiwakes in summer was revealed by several different analyses (chapters 2 and 4). These results underline the high importance of frontal areas in the German Bight for foraging Kittiwakes. This link to short-lived or dynamic small scale hydrographic structures is believed to result in high temporal variability of at-sea distribution patterns of Kittiwakes. Short-term variation

in Kittiwake distribution was indeed revealed by repeated aerial surveys conducted in the course of this thesis (chapter 4).

The population trend of Whiting in the North Sea is not known but a decreasing trend is indicated for spawning stock biomass as well as stocks of juvenile fish (ICES-WGNSSK 2006, S. Ehrich, pers. comm.). This apparent decline however was mainly recorded in the northern North Sea while the stock in the southern North Sea presumably increased (ICES-WGNSSK 2006). Positive population trends in the southern North Sea are also shown by other pelagic fish species. E.g., a new spawning stock of Anchovy *Engraulis encrasicolus* has recently been discovered in the German Bight (ICES-SGRESK 2006). Moreover, several seabird species in the southern and south-eastern North Sea, in particular terns (Sternidae, E. Stienen and A. Dähnhardt, pers. comm.), experienced extraordinarily high breeding success in 2007 due to high abundance of Herring *Clupea harengus*. Thus, current foraging conditions for seabirds and other piscivorous predators presumably are favourable in the southern North Sea, in particular in comparison to the situation in the northern North Sea. This assumption is underlined by extraordinarily high numbers of seabirds and marine mammals recorded in recent years in the southern part of the North Sea (Camphuysen 2006, Hammond and Macleod 2006).

Top-predators such as seabirds have repeatedly been suggested as indicators of marine prey stocks, thus providing information on marine ecosystem status (Montevecchi 1993, Monaghan 1996, Wanless et al. 2007). Seabirds are highly suitable for this role as they are very conspicuous and often accessible in large colonies. Moreover, due to their restricted foraging area during the breeding season, their breeding performance, foraging behaviour and above all diet composition reflects physical and trophic conditions within a defined sea area (Wanless et al. 2007).

The Black-legged Kittiwake represents a particularly suitable bioindicator (Monaghan 1996, Furness and Tasker 2000, Wanless et al. 2007). Being predominantly piscivorous, it is at the top of the marine food chain. Moreover, it is more vulnerable to reductions in food availability than other seabird species as it is restricted to prey concentrations at the sea surface due to its surface-feeding foraging technique (Monaghan 1996, Furness and Tasker 2000). Thus, future studies of breeding numbers, breeding performance, foraging behaviour and diet composition of Kittiwakes at Helgoland could provide the potential to evaluate the situation of marine prey stocks in the German Bight and to identify major ecosystem changes.

Bibliography

- Aagaard, A., C. G. Warman, and M. H. Depledge. 1995. Tidal and seasonal changes in the temporal and spatial distribution of foraging *Carcinus maenas* in the weakly tidal littoral zone of Kerteminde Fjord, Denmark. *Mar. Ecol. Prog. Ser.* **122**:165–172.
- Aarup, T. 2002. Transparency of the North Sea and Baltic Sea - a Secchi depth data mining study. *Oceanologia* **44**:323–337.
- Aebischer, N. J., and J. C. Coulson. 1990. Survival of the Kittiwake in relation to sex, year, breeding experience and position in the colony. *J. Anim. Ecol.* **59**:1063–1071.
- Ainley, D. G., 1977. Feeding methods of seabirds: a comparison of polar and tropical communities. Pages 669–685 *in* G. A. Llano, editor. *Adaptions within Antarctic Ecosystems*. Smithsonian Inst., Washington.
- Ainley, D. G. 1980. Birds as marine organisms: a review. *Calif. Coop. Ocean. Fish. Invest. Rep.* **21**:48–53.
- Ainley, D. G., L. B. Spear, S. G. Allen, and C. A. Ribic. 1996. Temporal and spatial patterns in the diet of the Common Murre in California waters. *Condor* **98**:691–705.
- Ainley, D. G., L. B. Spear, C. T. Tynan, J. A. Barth, T. J. Cowles, and S. D. Pierce. 2005. Factors affecting occurrence patterns of seabirds in the northern California current, spring and summer 2000. *Deep-Sea Res. II* **52**:123–143.
- Alonso, J. A., and J. C. Alonso. 1993. Age-related differences in time budgets and parental care in wintering Common Cranes. *Auk* **110**:78–88.
- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* **49**:227–267.
- Anonymous. 2002. Surfer 8. Contouring and 3D surface mapping for scientists and engineers. Golden Software, Colorado.
- Arnott, S. A., and G. D. Ruxton. 2002. Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. *Mar. Ecol. Prog. Ser.* **238**:199–210.
- Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* **103b**:458–473.

- Ashmole, N. P., 1971. Seabird ecology and the marine environment. Pages 223–286 in D. S. Farner and J. R. King, editors. Avian biology, volume 1. Academic Press, London.
- Backhaus, K., B. Erichson, W. Plinke, and R. Weiber. 1996. Multivariate Analysemethoden. Springer, Berlin.
- Bairlein, F. 1996. Ökologie der Vögel. Gustav Fischer, Stuttgart.
- Ballance, L. T., R. L. Pitman, and P. C. Fiedler. 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. Prog. Oceanogr. **69**:360–390.
- Barrett, R. T., and O. J. Runde. 1980. Growth and survival of nestling Kittiwakes *Rissa tridactyla* in Norway. Ornis Scand. **11**:228–235.
- Bates, D., and D. Sarkar. 2007. Reference manual lme4: Linear mixed-effects models using S4 classes. <http://mirrors.dotsrc.org/cran/> .
- Beaugrand, G. 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. Prog. Oceanogr. **60**:245–262.
- Becker, B. H., S. R. Beissinger, and H. R. Carter. 1997a. At-sea density monitoring of Marbled Murrelets in central California: methodological considerations. Condor **99**:743–155.
- Becker, G. A., A. F. G. Fiúza, and I. D. James. 1983. Water mass analysis in the German Bight during MARSEN, phase I. J. Geophys. Res. **88**:9865–9870.
- Becker, G. A., and G. Prahm-Rodewald. 1980. Fronten im Meer. Salzgehaltsfronten in der Deutschen Bucht. Seewart **41**:12–21.
- Becker, P. H., T. Troschke, A. Behnke, and M. Wagener. 1997b. Flüge Küken der Flußseeschwalbe *Sterna hirundo* verhungern während Hitzeperioden. J. Ornithol. **138**:171–182.
- Benvenuti, S., L. Dall’Antonia, and P. Lyngs. 2001. Foraging behaviour and time allocation of chick-rearing Razorbills *Alca torda* at Græsholmen, central Baltic Sea. Ibis **143**:402–412.
- Bezzel, E., and R. Prinzinger. 1990. Ornithologie. 2 edition. Ulmer, Stuttgart.
- BirdLife International, 2007. BirdLife’s online World Bird Database: the site for bird conservation. Version 2.1. Cambridge, UK: BirdLife International. Available: <http://www.birdlife.org>.
- Birt, V. L., T. P. Birt, D. Goulet, D. K. Cairns, and W. A. Montevecchi. 1987. Ashmole’s halo: direct evidence for prey depletion by a seabird. Mar. Ecol. Prog. Ser. **40**:205–208.

- Blake, B. F., T. J. Dixon, P. H. Jones, and M. L. Tasker. 1985. Seasonal changes in the feeding ecology of Guillemots (*Uria aalge*) off north and east Scotland. *Estuar. Coast. Shelf Sci.* **20**:559–568.
- Briggs, K. T., W. B. Tyler, D. B. Lewis, and D. R. Carlson. 1987. Bird communities at sea off California: 1975 to 1983. *Stud. Avian Biol.* **11**:1–74.
- Brodie, P. F., D. D. Sameoto, and R. W. Sheldon. 1978. Population densities of euphausiids off Nova Scotia as indicated by net samples, whale stomach contents, and sonar. *Limnol. Oceanogr.* **23**:1264–1267.
- Broekhuizen, N., and E. McKenzie. 1995. Patterns of abundance for *Calanus* and smaller copepods in the North Sea: time series decomposition of two CPR data sets. *Mar. Ecol. Prog. Ser.* **118**:103–120.
- Brown, R. G. B. 1970. Fulmar distribution: a Canadian perspective. *Ibis* **112**:44–51.
- Brown, R. G. B., 1980. Seabirds as marine animals. Pages 1–39 *in* J. Burger, B. Olla, and H. E. Winn, editors. *Marine birds*. Plenum Press, New York.
- Brown, R. G. B., 1988. Zooplankton patchiness and seabird distributions. Pages 1001–1009 *in* H. Ouellet, editor. *Acta XIII Int. Ornithol. Congr.* 1.
- Brugger, K. E. 1992. Differential digestibilities of Channel Catfish, Bluegill, and Gizzard Shad: *in vitro* standards for gastric digestion by seabirds. *Colon. Waterbirds* **15**:257–260.
- BSH. 1994. Klima und Wetter der Nordsee. Bundesamt für Seeschifffahrt und Hydrographie, Hamburg und Rostock, Sonderdruck Nr. **2182**:73–288.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling. Estimating abundance of biological populations. Chapman & Hall, London.
- Burger, J., 1987. Foraging efficiency in gulls: a congeneric comparison of age differences in efficiency and age of maturity. Pages 83–90 *in* J. L. Hand, W. E. Southern, and K. Vermeer, editors. *Ecology and behavior of gulls*. *Stud. Avian Biol.* 10.
- Burt, E. H. 1974. Success of two feeding methods of the Black-legged Kittiwake. *Auk* **91**:827–829.
- BWPi. 2004. The birds of the western Palearctic interactive. DVD Birdguides, Shrewsbury.
- Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. *Biol. Oceanogr.* **5**:261–271.
- Cairns, D. K., K. A. Bredin, and W. A. Montevecchi. 1987. Activity budgets and foraging ranges of breeding Common Murres. *Auk* **104**:218–224.

- Camphuysen, C. J. 1996. De verspreiding van zeevogels in de Noordzee: naar een beter begrip van patronen en verbanden. *Sula* **10**:41–88.
- Camphuysen, C. J. 1998. Diurnal activity patterns and nocturnal group formation of wintering Common Murres in the central North Sea. *Colon. Waterbirds* **21**:406–413.
- Camphuysen, C. J. 2001. Feeding behaviour and foraging interactions of seabirds and marine mammals in the NW North Sea, summer 2001. IMPRESS Report 2001-002. Netherlands Institute for Sea Research, Den Burg, Texel.
- Camphuysen, C. J. 2002. Post-fledging dispersal of Common Guillemots *Uria aalge* guarding chicks in the North Sea: the effect of predator presence and prey availability at sea. *Ardea* **90**:103–119.
- Camphuysen, C. J., editor. 2005. Understanding marine foodweb processes: an ecosystem approach to sustainable sandeel fisheries in the North Sea. IMPRESS Final Report, Royal Netherlands Institute for Sea Research, Texel.
- Camphuysen, C. J., 2006. Seabirds and marine mammals in the Southern Bight, 1960-2005: major distributional shifts as a result of ... poor conditions elsewhere? *in* The Seabird Group 9th International Conference "Seabird populations under pressure", Aberdeen, Scotland.
- Camphuysen, C. J., B. Calvo, J. Durinck, K. Ensor, A. Follestad, R. W. Furness, S. Garthe, G. Leaper, H. Skov, M. L. Tasker, and C. J. N. Winter. 1995. Consumption of discards by seabirds in the North Sea. Final report EC DG XIV research contract BIOECO/93/10. NIOZ Rapport 1995 - 5. Netherlands Institute for Sea Research, Texel.
- Camphuysen, C. J., and S. Garthe. 1997. An evaluation of the distribution and scavenging habits of Northern Fulmars (*Fulmarus glacialis*) in the North Sea. *ICES J. Mar. Sci.* **54**:654–683.
- Camphuysen, C. J., and S. Garthe. 2004. Recording foraging seabirds at sea. Standardised recording and coding of foraging behaviour and multi-species foraging associations. *Atlantic Seabirds* **6**:1–32.
- Camphuysen, C. J., and A. Webb. 1999. Multi-species feeding associations in North Sea seabirds: jointly exploiting a patchy environment. *Ardea* **87**:177–198.
- Catry, P., R. A. Phillips, B. Phalan, J. R. D. Silk, and J. P. Croxall. 2004. Foraging strategies of Grey-headed Albtrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. *Mar. Ecol. Prog. Ser.* **280**:261–273.
- Claireaux, G., D. M. Webber, S. R. Kerr, and R. G. Boutilier. 1995. Physiology and behaviour of free-swimming Atlantic Cod (*Gadus morhua*) facing fluctuating temperature conditions. *J. Exp. Biol.* **198**:49–60.

- Clark, R. A., and C. L. J. Frid. 2001. Long-term changes in the North Sea ecosystem. *Environ. Rev./Dossiers environ.* **9**:131–187.
- Coulson, J. C., and E. White. 1958. Observations on the breeding of the Kittiwake. *Bird Study* **5**:74–83.
- Coulson, J. C., and E. White. 1959. The post-fledging mortality of the Kittiwake. *Bird Study* **6**:97–102.
- Croxall, J. P., J. R. D. Silk, R. A. Phillips, V. Afanasyev, and D. R. Briggs. 2005. Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science* **307**:249–250.
- Dankers, N., H. Kühl, and W. J. Wolff, 1983*a*. Invertebrates of the Wadden Sea. Final report of the section ‘Invertebrate Zoology’ of the Wadden Sea Working Group. Report 4. Pages 1–221 *in* W. J. Wolff, editor. *Ecology of the Wadden Sea*, volume 1. A.A.Balkema, Rotterdam.
- Dankers, N., W. J. Wolff, and J. J. Zijlstra, 1983*b*. Fishes and fisheries of the Wadden Sea. Pages 1–157 *in* W. J. Wolff, editor. *Ecology of the Wadden Sea*, volume 2. A.A. Balkema, Rotterdam.
- Daunt, F., V. Afanasyev, J. R. D. Silk, and S. Wanless. 2006. Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behav. Ecol. Sociobiol.* **59**:381–388.
- Daunt, F., S. Benvenuti, M. P. Harris, L. Dall’Antonia, D. A. Elston, and S. Wanless. 2002. Foraging strategies of the Black-legged Kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. *Mar. Ecol. Prog. Ser.* **245**:239–247.
- Decker, M. B., and G. L. J. Hunt. 1996. Foraging by murre (*Uria* spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. *Mar. Ecol. Prog. Ser.* **139**:1–10.
- Del Norte-Campos, A. G. C., and A. Temming. 1994. Daily activity, feeding and rations in gobies and Brown Shrimp in the Wadden Sea. *Mar. Ecol. Prog. Ser.* **115**:41–53.
- Desrochers, A. 1992. Age and foraging success in European Blackbirds: variation between and within individuals. *Anim. Behav.* **43**:885–894.
- Diederichs, A., G. Nehls, and I. K. Pedersen. 2002. Flugzeugzählungen zur großflächigen Erfassung von Seevögeln und marinen Säugern als Grundlage für Umweltverträglichkeitsstudien im Offshorebereich. *Seevögel* **23**:38–46.
- Dierschke, V., S. Garthe, and N. Markones. 2004. Aktionsradien Helgoländer Dreizehenmöwen *Rissa tridactyla* und Trottellummen *Uria aalge* während der Aufzuchtphase. *Vogelwelt* **125**:11–19.
- Dippner, J. W. 1993. A frontal-resolving model for the German Bight. *Cont. Shelf Res.* **13**:49–66.

- Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**:225–252.
- Drost, R. 1938. Die Dreizehenmöwe ist wieder deutscher Brutvogel. *Orn. Mber.* **46**:118.
- Dunn, E. K. 1973. Changes in fishing ability of terns associated with windspeed and sea surface conditions. *Nature* **244**:520–521.
- Elliot, M., and K. L. Hemingway. 2002. *Fishes in estuaries*. Blackwell Science Ltd., Oxford.
- Ellis, H. I., and G. W. Gabrielsen, 2002. Energetics of free-ranging seabirds. Pages 359–407 *in* E. A. Schreiber and J. Burger, editors. *Biology of marine birds*. CRC Press, Boca Raton.
- Elphick, C. S., and G. L. J. Hunt. 1993. Variations in the distributions of marine birds with water mass in the northern Bering Sea. *Condor* **95**:33–44.
- Esselink, P., and L. Zwarts. 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*. *Mar. Ecol. Prog. Ser.* **56**:243–254.
- Faraway, J. J. 2006. *Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models*. Chapman & Hall, London.
- Finney, S. K., S. Wanless, and M. P. Harris. 1999. The effect of weather conditions on the feeding behaviour of a diving bird, the Common Guillemot *Uria aalge*. *J. Avian Biol.* **30**:23–30.
- Fleet, D. 1984. Changes in numbers of breeding Kittiwakes in Helgoland. *Ringing a. migration* **5**:32–34.
- Floodgate, G. D., G. E. Fogg, D. A. Jones, K. Lochte, and C. M. Turley. 1981. Microbial and zooplankton activity at a front in Liverpool bay. *Nature* **290**:133–136.
- Flöter, J., 2005. *An investigation of key processes affecting trophic interactions in the North Sea fish assemblage and their significance for multi species fisheries assessment*. Ph.D. thesis, University of Hamburg.
- Franks, P. J. S. 1992. Sink or swim: accumulation of biomass at fronts. *Mar. Ecol. Prog. Ser.* **82**:1–12.
- Fransz, H. G., J. M. Colebrook, J. C. Gamble, and M. Krause. 1991. The zooplankton of the North Sea. *Neth. J. Sea Res.* **27**:1–52.
- Frederiksen, M., S. Wanless, M. P. Harris, P. Rothery, and L. J. Wilson. 2004. The role of industrial fisheries and oceanographic change in the decline of North Sea Black-legged Kittiwakes. *J. Appl. Ecol.* **41**:1129–1139.
- Furness, B. L., R. C. Laugksch, and D. C. Duffy. 1984. Cephalopod beaks and studies of seabird diets. *Auk* **101**:619–620.

- Furness, R. W., and D. M. Bryant. 1996. Effect of wind on field metabolic rates of breeding Northern Fulmars. *Ecology* **77**:1181–1188.
- Furness, R. W., and P. Monaghan. 1987. *Seabird ecology*. Blackie, Glasgow and London.
- Furness, R. W., and M. L. Tasker. 2000. Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Mar. Ecol. Prog. Ser.* **202**:253–264.
- Garthe, S., 1996. Distribution and abundance of North Sea seabirds and their feeding ecology in relation to fisheries and hydrography. Ph.D. thesis, Christian-Albrechts-University, Kiel.
- Garthe, S. 1997. Influence of hydrography, fishing activity, and colony location on summer seabird distribution in the south-eastern North Sea. *ICES J. Mar. Sci.* **54**:566–577.
- Garthe, S., 1999. The influence of fishing activities on the distribution and feeding ecology of seabirds at sea. Pages 706–716 *in* N. J. Adams and R. H. Slotow, editors. 22 Int. Ornithol. Congr. BirdLife, South Africa, Johannesburg, Durban.
- Garthe, S., K. Alicki, O. Hüppop, and B. Sprotte. 1995. Die Verbreitung und Häufigkeit ausgewählter See- und Küstenvogelarten während der Brutzeit in der südöstlichen Nordsee. *J. Ornithol.* **136**:253–266.
- Garthe, S., S. Benvenuti, and W. A. Montevecchi. 2003a. Temporal patterns of foraging activities of Northern Gannets *Morus bassanus* in the north-west Atlantic. *Can. J. Zool.* **81**:453–461.
- Garthe, S., C. J. Camphuysen, and R. W. Furness. 1996. Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. *Mar. Ecol. Prog. Ser.* **136**:1–11.
- Garthe, S., V. Dierschke, T. Weichler, and P. Schwemmer, 2004. Teilprojekt 5 - Rastvogelvorkommen und Offshore-Windkraftnutzung: Analyse des Konfliktpotenzials für die deutsche Nord- und Ostsee. Pages 195–333 *in* Kellermann, A. et al., editor. *Marine Warmblüter in Nord- und Ostsee: Grundlagen zur Bewertung von Windkraftanlagen im Offshore-Bereich*. Endbericht.
- Garthe, S., B.-O. Flore, B. Hälterlein, O. Hüppop, U. Kubetzki, and P. Südbeck. 2000. Brutbestandsentwicklung der Möwen (Laridae) an der deutschen Nordseeküste in der zweiten Hälfte des 20. Jahrhunderts. *Vogelwelt* **121**:1–13.
- Garthe, S., and O. Hüppop. 1996. Das "Seabirds-at-sea"-Programm. *Vogelwelt* **117**:303–305.
- Garthe, S., and O. Hüppop. 2000. Aktuelle Entwicklungen beim Seabirds-at-Sea-Programm in Deutschland. *Vogelwelt* **121**:301–305.

- Garthe, S., O. Hüppop, and T. Weichler. 2002. Anleitung zur Erfassung von Seevögeln auf See von Schiffen. *Seevogel* **23**:47–55.
- Garthe, S., T. Krüger, U. Kubetzki, and T. Weichler. 2003*b*. Monitoring von Seevögeln auf See: Gegenwärtiger Stand und Perspektiven. *Berichte des Landesamtes für Umweltschutz Sachsen-Anhalt. Sonderheft* **1/2003**:62–64.
- Garthe, S., and P. Schwemmer. 2005. Seabirds at Sea - Untersuchungen in den deutschen Meeresgebieten. *Vogelwelt* **126**:67–74.
- Garthe, S., N. Sonntag, P. Schwemmer, and V. Dierschke. 2007. Estimation of seabird numbers in the German North Sea throughout the annual cycle and their biogeographic importance. *Vogelwelt* **128**:*in press*.
- Gerdes, D. 1985. Zusammensetzung und Verteilung von Zooplankton sowie Chlorophyll- und Sestonergehalte in verschiedenen Wassermassen der Deutschen Bucht in den Jahren 1982/83. *Veröff. Inst. Meeresforsch. Bremerhaven* **20**:119–139.
- Gibson, R. N., 2003. Go with the flow: tidal migration in marine animals. Pages 153–161 *in* M. B. Jones, E. O. Ingólfsson, E. Ólafsson, G. V. Helgason, K. Gunnarsson, and J. Svavarsson, editors. *Migrations and dispersal of marine organisms. Hydrobiologia* **503**.
- Glutz von Blotzheim, U. N., and K. M. Bauer. 1999. *Handbuch der Vögel Mitteleuropas, Band 8 Charadriiformes*. 2 edition. AULA-Verlag, Wiesbaden.
- Goldstein, D. L. 1990. Energetics of activity and free living in birds. *Stud. Avian Biol.* **13**:423–426.
- Golet, G. H., and D. B. Irons. 1999. Raising young reduces body condition and fat stores in Black-legged Kittiwakes. *Oecologia* **120**:530–538.
- Golet, G. H., D. B. Irons, and J. A. Estes. 1998. Survival costs of chick-rearing in Black-legged Kittiwakes. *J. Anim. Ecol.* **67**:827–841.
- Grunsky-Schöneberg, B. 1998. Brutbiologie und Nahrungsökologie der Trottellumme (*Uria aalge* Pont.) auf Helgoland. *Ökol. Vögel* **20**:217–274.
- Götmark, F., D. W. Winkler, and M. Andersson. 1986. Flock-feeding on fish schools increases individual success in gulls. *Nature* **319**:589–591.
- Guse, N. 2005. Diet of a piscivorous top predator in the Baltic Sea - the Red-throated Diver (*Gavia stellata*) in the Pomeranian Bight. Diploma thesis, Christian-Albrechts-University, Kiel.
- Haccou, P., and E. Meelis. 1994. *Statistical analyses of behavioural data*. Oxford University Press, Oxford.

- Hamer, K. C., R. A. Phillips, J. K. Hill, S. Wanless, and A. G. Wood. 2001. Contrasting foraging strategies of Gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Mar. Ecol. Prog. Ser.* **224**:283–290.
- Hammond, P. S., and K. Macleod. 2006. Scans II – Report on progress. Document for ASCOBANS meeting of parties, Egmond aan Zee, September 2006.
- Haney, J. C., and A. R. Solow. 1992. Analyzing quantitative relationships between seabirds and marine resource patches. *Curr. Ornithol.* **9**:105–161.
- Hansen, V., 1979. Holoplankton. Pages 329–356 in A. Nørrevang and J. Lundø, editors. *Danmarks Natur*, volume 3. Politiken, Copenhagen.
- Hardege, J. D., H. D. Bartels-Hardege, E. Zeeck, and F. T. Grimm. 1990. Induction of swarming of *Nereis succinea*. *Mar. Biol.* **104**:291–295.
- Harrison, N. W., A. Webb, and G. M. Leaper. 1994. Patterns in seabird distribution west of Scotland. *Aquat. Conserv. Mar. Freshwater Ecosyst.* **4**:21–30.
- Hartmann-Schröder, G. 1996. Annelida, Borstenwürmer, Polychaeta. Gustav Fischer Verlag, Jena.
- Hastie, T., and R. Tibshirani. 1990. *Generalised Additive Models*. Chapman & Hall, London.
- Haury, L. R., J. A. McGowan, and P. H. Wiebe, 1978. Patterns and processes in the time-space scales of plankton distributions. Pages 277–327 in J. H. Steele, editor. *Spatial pattern in plankton communities*. Plenum Press, New York.
- Hays, G. C., 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migration. Pages 163–170 in M. B. Jones, E. O. Ingólfsson, E. Ólafsson, G. V. Helgason, K. Gunnarsson, and J. Svavarsson, editors. *Migrations and dispersal of marine organisms*. *Hydrobiologia* **503**.
- Hesse, K.-J., D. Gerdes, and K. Schaumann. 1989*a*. A winter study of plankton distribution across a coastal salinity front in the German Bight. *Meeresforschung* **32**:177–191.
- Hesse, K.-J., Z. L. Liu, and K. Schaumann. 1989*b*. Phytoplankton and fronts in the German Bight. *Scient. Mar.* **53**:187–196.
- Heubeck, M., 2004. Black-legged Kittiwake *Rissa tridactyla*. Pages 277–290 in P. I. Mitchell, S. F. Newton, N. Ratcliffe, and T. E. Dunn, editors. *Seabird populations of Britain and Ireland*. T. & A.D. Poyser, London.
- Hilton, G. M., R. W. Furness, and D. C. Houston. 2000. A comparative study of digestion in North Atlantic seabirds. *J. Avian Biol.* **31**:36–46.
- Hoefler, C. J. 2000. Marine bird attraction to thermal fronts in the California current system. *Condor* **102**:423–427.

- Hüppop, O. 1997. Langzeit-Veränderungen der Brutbestände Helgoländer See- und Küstenvögel. *Seevögel* **18**:38–44.
- Härkönen, T. 1986. Guide to the otoliths of the bony fishes of the Northeast Atlantic. Danbiu Aps, Hellerup.
- Humphreys, E. M., S. Wanless, and D. M. Bryant. 2007. Elevated metabolic costs while resting on water in a surface feeder: the Black-legged Kittiwake *Rissa tridactyla*. *Ibis* **149**:106–111.
- Hunt, G. L. J. 1990. The pelagic distribution of marine birds in a heterogeneous environment. *Polar Res.* **8**:43–54.
- Hunt, G. L. J. 1997. Physics, zooplankton, and the distribution of Least Auklets in the Bering Sea - a review. *ICES J. Mar. Sci.* **54**:600–607.
- Hunt, G. L. J., and D. C. Schneider, 1987. Scale-dependent processes in the physical and biological environment of marine birds. Pages 7–41 *in* J. P. Croxall, editor. *Seabirds - feeding ecology and role in marine ecosystems*. Cambridge University Press, New York.
- Hunt von Herbing, I. 2002. Effects of temperature on larval fish swimming performance: the importance of physics to physiology. *J. Fish Biol.* **61**:865–876.
- ICES-SGRESP. 2006. Report of the study group on regional scale ecology of small pelagic fish. ICES CM 2006/LRC:05.
- ICES-SGSIMUW. 2005. Report of the study group on stock identity and management units of Whiting. ICES CM 2005/G:03.
- ICES-WGNSSK. 2006. Report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak. ACFM:35.
- ICES-WGSE. 2006. Report of the working group on seabird ecology. ICES CM 2006/LRC:08, Ref. ACE, ACME.
- Irons, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* **79**:647–655.
- Jodice, P. G. R., D. D. Roby, R. M. Suryan, D. B. Irons, A. M. Kaufman, K. R. Turco, and G. H. Visser. 2003. Variation in energy expenditure among Black-legged Kittiwakes: effects of activity-specific metabolic rates and activity budgets. *Physiol. Biochem. Zool.* **76**:375–388.
- Joiris, C. 1978. Seabirds recorded in the northern North Sea in July: the ecological implications of their distribution. *Gerfaut* **68**:419–440.
- Joiris, C. 1983. Winter distribution of seabirds in the North Sea: an oceanological interpretation. *Gerfaut* **73**:107–122.

- Kahlert, J., M. Desholm, I. Clausager, and I. K. Petersen. 2000. Environmental impact assessment of an offshore wind farm at Rødsand. Technical report on birds. Report from NERI.
- Kellermann, A., K. Eskildsen, and B. Frank, 2006. The MINOS project: ecological assessments of possible impacts of offshore wind energy projects. Pages 239–248 *in* H. von Nordheim, D. Boedeker, and J. C. Krause, editors. Progress in marine conservation in Europe. Springer, Berlin Heidelberg.
- Knijn, R. J., T. W. Boon, H. J. L. Heessen, and J. R. G. Hislop. 1993. Atlas of North Sea Fishes. ICES, Copenhagen, Denmark.
- Koffijberg, K., L. Dijkzen, B. Hälterlein, K. Laursen, P. Potel, and P. Südbeck. 2006. Breeding birds in the Wadden Sea in 2001 - Results of the total survey in 2001 and trends in numbers between 1991-2001. Wadden Sea Ecosystem No. **22**. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Joint Monitoring Group of Breeding Birds in the Wadden Sea. Wilhelmshaven, Germany.
- Krause, G., G. Budeus, K. Gerdes, K. Schaumann, and K. Hesse, 1986. Frontal systems in the German Bight and their physical and biological effects. Pages 119–140 *in* J. C. J. Nihoul, editor. Marine interfaces ecohydrodynamics. Elsevier, Amsterdam.
- Krause, M., and P. Martens. 1990. Distribution patterns of mesozooplankton biomass in the North Sea. Helgoländer Meeresunters. **44**:295–327.
- Körner, D., and G. Weichart. 1992. Nutrients in the German Bight: concentrations and trends. ICES Mar. Sci. Symp. **195**:159–176.
- Köth, T. 1985. Zur Altersklassifizierung nestjunger Dreizehenmöwen (*Rissa tridactyla*) auf Helgoland. Seevögel **6**:141–144.
- Kubetzki, U., and S. Garthe. 2003. Distribution, diet and habitat selection by four sympatrically breeding gull species in the southeastern North Sea. Mar. Biol. **143**:199–207.
- Laake, J. L., S. T. Buckland, D. R. Anderson, and K. P. Burnham. 1993. DiISTANCE user's guide v2.0. Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University, Fort Collins, CO.
- Lack, D. 1966. Population studies of birds. Oxford University Press, Oxford.
- Lacroix, D. L., S. Boyd, D. Esler, M. Kirk, T. Lewis, and S. Lipovsky. 2005. Surf Scoters *Melanitta perspicillata* aggregate in association with ephemerally abundant polychaetes. Mar. Ornithol. **33**:61–63.
- Leopold, M. F. 1993. Het Friese Front: hydrografie, geologie en biologie, met nadruk op de zeevogels. Sula **7**:5–18.

- Leopold, M. F., and C. J. G. Van Damme. 2003. Great Cormorants *Phalacrocorax carbo* and polychaetes: can worms be a major prey of a piscivorous seabird? *Mar. Ornithol.* **31**:83–87.
- Leopold, M. F., C. J. G. Van Damme, C. J. M. Philippart, and C. J. N. Winter. 2001. Otoliths of North Sea fish: interactive guide of identification of fish from the SE North Sea, Wadden Sea and adjacent fresh waters by means of otoliths and other hard parts. CD-Rom, ETI, Amsterdam.
- Leopold, M. F., C. J. G. Van Damme, and H. W. Van Der Veer. 1998. Diet of Cormorants and the impact of Cormorant predation on juvenile flatfish in the Dutch Wadden Sea. *J. Sea Res.* **40**:93–107.
- Leopold, M. F., P. W. Van Leeuwen, H. Horn, and C. J. Camphuysen. 2000. Grote Ijsduiker *Gavia immer* eet kleine visjes: een verdronken vogel geeft geheimen prijs. *Limosa* **73**:135–143.
- Lewis, S., T. N. Sherratt, K. C. Hamer, and S. Wanless. 2001. Evidence of intra-specific competition for food in a pelagic seabird. *Nature* **412**:816–819.
- Lloyd, C., M. L. Tasker, and K. Partridge. 1991. The status of seabirds in Britain and Ireland. T. & A.D. Poyser, London.
- Loewe, P., G. Becker, U. Brockmann, A. Frohse, K. Herklotz, H. Klein, and A. Schulz. 2003. Nordsee und Deutsche Bucht 2002 - Ozeanographischer Zustandsbericht. Berichte des Bundesamtes für Seeschifffahrt und Hydrographie Nr. 33/2003.
- Manikowski, S. 1971. The influence of meteorological factors on the behaviour of seabirds. *Acta Zool. Cracov.* **20**:581–667.
- Maul, A. M. 1994. Ernährungsweisen und Brutbiologie der Dreizehenmöwe *Rissa tridactyla* (Linnaeus, 1758) auf Helgoland. Diploma thesis, Karl-Franzens-University, Graz.
- Maunder, J. E., and W. Threlfall. 1972. The breeding biology of the Black-legged Kittiwake in Newfoundland. *Auk* **89**:789–816.
- Mavor, R. A., M. Parsons, M. Heubeck, and S. Schmitt. 2005. Seabird numbers and breeding success in Britain and Ireland, 2004. Joint Nature Conservation Committee, Peterborough, UK.
- McCullagh, P., and J. A. Nelder. 1989. Generalized Linear Models. Chapman & Hall, London.
- McGregor, P. K., 1992. Quantifying responses to playback: one, many, or composite multivariate measures? Pages 79–96 *in* P. K. McGregor, editor. Playback and studies of animal communication. Plenum Press, New York, London.

- Mönkkönen, M., and J. Aspi. 1997. Sampling error in measuring temporal density variability in animal populations and communities. *Ann. Zool. Fennici* **34**:47–57.
- Monaghan, P. 1996. Relevance of the behaviour of seabirds to the conservation of marine environments. *Oikos* **77**:227–237.
- Montevecchi, W. A., 1993. Birds as indicators of change in marine prey stocks. Pages 217–266 in R. W. Furness and J. J. D. Greenwood, editors. *Birds as monitors of environmental change*. Chapman & Hall, London.
- Morgan, C. A., A. De Robertis, and R. W. Zabel. 2005. Columbia River plume fronts. I. Hydrography, zooplankton distribution, and community composition. *Mar. Ecol. Prog. Ser.* **299**:19–31.
- Munk, P., P. O. Larsson, D. Danielsen, and E. Moksness. 1995. Larval and small juvenile Cod *Gadus morhua* concentrated in the highly productive areas of a shelf break front. *Mar. Ecol. Prog. Ser.* **125**:21–30.
- Muus, B. J., and J. G. Nielsen. 1999. *Die Meeresfische Europas in Nordsee, Ostsee und Atlantik*. Franckh-Kosmos, Stuttgart.
- Nettleship, D. N., and A. J. Gaston. 1978. Patterns of pelagic distribution of seabirds in western Lancaster Sound and Barrow Strait, Northwest Territories, in August and September 1976. Canadian Wildlife Service, Ottawa, Occasional paper **39**.
- Orians, G. H., and N. E. Pearson, 1979. On the theory of central place foraging. Pages 155–177 in D. J. Horn, R. Mitchell, and G. R. Stair, editors. *Analysis of ecological systems*. Ohio State University Press, Columbus, Ohio.
- Otto, L., J. T. F. Zimmerman, G. K. Furnes, M. Mork, R. Saetre, and G. Becker. 1990. Physical oceanography of the North Sea. *Neth. J. Sea Res.* **26**:163–238.
- Ouwehand, J., M. F. Leopold, and C. J. Camphuysen. 2004. A comparative study of the diet of Guillemots *Uria aalge* and Razorbills *Alca torda* killed during the Tricolor oil incident in the south-eastern North Sea in January 2003. *Atlantic Seabirds* **6**:147–164.
- Pearson, T. H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. *J. Anim. Ecol.* **37**:521–552.
- Pennycuik, C. J. 1987. Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: ornithodolite observations. *J. Exp. Biol.* **128**:335–347.
- Pennycuik, C. J. 1997. Actual and ‘optimum’ flight speeds: field data reassessed. *J. Exp. Biol.* **200**:2355–2361.
- Petersen, S., E. Ryan, and D. Grémillet. 2006. Is food availability limiting African Penguins *Spheniscus demersus* at Boulders? A comparison of foraging effort at mainland and island colonies. *Ibis* **148**:14–26.

- Petersen, W., M. Petschatnikov, H. Wehde, and F. Schroeder. 2005. FerryBox: Real-time monitoring of water quality by ferryboats. *Environ. res. eng. manage.* **3**:12–17.
- Phillips, R. A., M. K. Petersen, K. Lilliendahl, J. Solmundsson, K. C. Hamer, C. J. Camphuysen, and B. Zonfrillo. 1999. Diet of the Northern Fulmar *Fulmarus glacialis*: reliance on commercial fisheries? *Mar. Biol.* **135**:159–170.
- Pickard, G. L., and W. J. Emery. 1990. *Descriptive physical oceanography: an introduction*. Pergamon Press, Oxford.
- Pingree, R. D., P. M. Holligan, and G. T. Mardell. 1978. The effects of vertical stability on phytoplankton distributions in the summer on the northwest European Shelf. *Deep-Sea Res.* **25**:1011–1028.
- Poremba, K., U. Tillmann, and K.-J. Hesse. 1999. Distribution patterns of bacterioplankton and chlorophyll-a in the German Wadden Sea. *Helgol. Mar. Res.* **53**:28–35.
- Prüter, J., 1986. Untersuchungen zum Bestandsaufbau und zur Ökologie der Möwen (Laridae) im Seegebiet der Deutschen Bucht. Ph.D. thesis, University of Hannover.
- Prüter, J. 1989. Phänologie und Ernährungsökologie der Dreizehenmöwen (*Rissa tridactyla*)-Brutpopulation auf Helgoland. *Ökol. Vögel* **11**:189–200.
- Puttick, G. M., 1984. Foraging and activity patterns in wintering shorebirds. Pages 203–231 in J. Burger and B. L. Olla, editors. *Behavior of marine animals*, volume 6. *Shorebirds: migration and foraging behavior*. Plenum Press, New York.
- Ricklefs, R. E. 1984. Some considerations on the reproductive energetics of pelagic seabirds. *Stud. Avian Biol.* **8**:84–94.
- Ropert-Coudert, Y., D. Grémillet, A. Kato, P. G. Ryan, Y. Naito, and Y. Le Maho. 2004. A fine-scale time budget of Cape Gannets provides insights into the foraging strategies of coastal seabirds. *Anim. Behav.* **67**:985–992.
- Ropert-Coudert, Y., and R. Wilson. 2004. Subjectivity in bio-logging science: do logged data mislead? *Mem. Natl Inst. Polar Res., Spec. Issue* **58**:23–33.
- Ropert-Coudert, Y., and R. Wilson. 2005. Trends and perspectives in animal-attached remote sensing. *Front. Ecol. Environ.* **3**:437–444.
- Rothery, P., M. P. Harris, S. Wanless, and D. N. Shaw. 2002. Colony size, adult survival rates, productivity and population projections of Black-legged Kittiwakes *Rissa tridactyla* on Fair Isle. *Atlantic Seabirds* **4**:17–28.
- Salewski, V., and B. Bruderer. 2007. The evolution of bird migration - a synthesis. *Naturwiss.* **94**:268–279.
- Sandvik, H., K. E. Erikstad, R. T. Barrett, and N. G. Yoccoz. 2005. The effect of climate on adult survival in five species of North Atlantic seabirds. *J. Anim. Ecol.* **74**:817–831.

- Schneider, D., N. M. Harrison, and G. L. J. Hunt. 1987. Variation in the occurrence of marine birds at fronts in the Bering Sea. *Estuar. Coast. Shelf Sci.* **25**:135–141.
- Scholander, P. F., R. Hock, V. Walters, and L. Irving. 1950. Adaptation to cold in Arctic and tropical mammals and birds in relation to body temperature. Insulation and basal metabolic rate. *Biol. Bull.* **99**:259–271.
- Schwemmer, P., and S. Garthe. 2005. At-sea distribution and behaviour of a surface-feeding seabird, the Lesser Black-backed Gull *Larus fuscus*, and its association with different prey. *Mar. Ecol. Prog. Ser.* **285**:245–258.
- Schwemmer, P., and S. Garthe. 2006. Spatial patterns in at-sea behaviour during spring migration by Little Gulls (*Larus minutus*) in the southeastern North Sea. *J. Ornithol.* **147**:354–366.
- Schwemmer, P., and S. Garthe, 2008. Regular habitat switch as an important feeding strategy of an opportunistic seabird species at the interface between land and sea. *Estuar. Coast. Shelf Sci.*, *in press*.
- Shaffer, S. A., Y. Tremblay, H. Weimerskirch, D. Scott, D. R. Thompson, P. M. Sagar, H. Moller, G. A. Taylor, D. G. Foley, B. A. Block, and D. P. Costa. 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proc. Natl Acad. Sci. US* **103**:12799–12802.
- Shealer, D. A., 2002. Foraging behavior and food of seabirds. Pages 137–177 *in* E. A. Schreiber and J. Burger, editors. *Biology of marine birds*. CRC Press, Boca Raton.
- Skov, H., and J. Durinck. 1998. Constancy of frontal aggregations of seabirds at the shelf break in the Skagerrak. *J. Sea Res.* **39**:305–311.
- Skov, H., and J. Durinck. 2000. Seabird distribution in relation to hydrography in the Skagerrak. *Cont. Shelf Res.* **20**:169–187.
- Skov, H., and J. Durinck. 2001. Seabird attraction to fishing vessels is a local process. *Mar. Ecol. Prog. Ser.* **214**:289–298.
- Skov, H., and E. Prins. 2001. Impact of estuarine fronts on the dispersal of piscivorous birds in the German Bight. *Mar. Ecol. Prog. Ser.* **214**:279–287.
- Speckman, S. G., A. M. Springer, J. F. Piatt, and D. L. Thomas. 2000. Temporal variability in abundance of Marbled Murrelets at sea in southeast Alaska. *Waterbirds* **23**:364–377.
- Stommel, H. 1963. Varieties of oceanographic experience. *Science* **139**:572–576.
- Stone, C. J., A. Webb, C. Barton, N. Ratcliffe, T. C. Reed, M. L. Tasker, C. J. Camphuysen, and M. W. Pienkowski. 1995. An atlas of seabird distribution in North-West European waters. Joint Nature Conservation Committee, Peterborough.

- Tasker, M. L., and R. W. Furness, 1996. Estimation of food consumption by seabirds in the North Sea. Pages 6–42 in G. L. J. Hunt and R. W. Furness, editors. Seabird/fish interactions, with particular reference to seabirds in the North Sea. ICES Coop. Res. Rep. **216**.
- Tasker, M. L., P. Hope Jones, T. Dixon, and B. F. Blake. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk* **101**:567–577.
- Thiel, R., A. Sepúlveda, R. Kafemann, and W. Nellen. 1995. Environmental factors as forces structuring the fish community of the Elbe estuary. *J. Fish Biol.* **46**:47–69.
- Tremblay, Y., Y. Cherel, M. Oremus, T. Tveraa, and O. Chastel. 2003. Unconventional ventral attachment of time-depth recorders as a new method for investigating time budget and diving behaviour of seabirds. *J. Exp. Biol.* **206**:1929–1940.
- Uspenski, S. M. 1956. The bird bazaars of Novaya Zemlya. Translated by Canadian Wildlife Service, Ottawa, 1958.
- Valenzuela, G., J. Alheit, S. H. Coombs, and R. Knust. 1991. Spawning patterns of Sprat and survival chances of Sprat larvae in relation to frontal systems in the German Bight. ICES Doc. CM 1991/L:45.
- Van Franeker, J. A. 1983. Inwendig onderzoek aan zeevogels. (Dissection of seabirds). *Nieuwsbrief NSO* **4**:144–167.
- Van Franeker, J. A. 2004. Save the North Sea Fulmar-Litter-EcoQO manual part 1: collection and dissection procedures. Alterra-raport 672. Wageningen, Alterra.
- Van Franeker, J. A., and P. J. Bell. 1988. Plastic ingestion by petrels breeding in Antarctica. *Mar. Poll. Bull.* **19**:672–674.
- Vauk-Hentzelt, E., and L. Bachmann. 1983. Zur Ernährung nestjunger Dreizehenmöwen (*Rissa tridactyla*) aus der Kolonie des Helgoländer Lummenfelsens. *Seevögel* **4**:42–45.
- Vermeer, K., I. Szabo, and P. Greismann. 1987. The relationship of plankton-feeding Bonaparte's and Mew Gulls and tidal upwelling at Active Pass, British Columbia. *J. Plankton Res.* **9**:483–501.
- Vorberg, R., and P. Breckling. 1999. Atlas der Fische im schleswig-holsteinischen Wattenmeer. Schriftenreihe des Nationalparks Schleswig-Holsteinisches Wattenmeer 10.
- Voss, M., E. Hartwig, and G. Vauk. 1987. Untersuchungen zum Nahrungsverbrauch der Dreizehenmöwe (*Rissa tridactyla*) auf Helgoland an handaufgezogenen Jungtieren. *Seevögel* **8**:5–13.
- Wanless, S., M. Frederiksen, F. Daunt, B. E. Scott, and M. P. Harris. 2007. Black-legged Kittiwakes as indicators of environmental change in the North Sea: evidence from long-term studies. *Prog. Oceanogr.* **72**:30–38.

- Wanless, S., M. P. Harris, and J. A. Morris. 1988. The effect of radio transmitters on the behavior of Common Murres and Razorbills during chick rearing. *Condor* **90**:816–823.
- Wanless, S., M. P. Harris, P. Redman, and J. R. Speakman. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar. Ecol. Prog. Ser.* **294**:1–8.
- Watson, G. J., M. E. Williams, and M. G. Bentley. 2000. Can synchronous spawning be predicted from environmental parameters? A case study of the Lugworm *Arenicola marina*. *Mar. Biol.* **136**:1003–1017.
- Watt, J., G. J. Pierce, and P. R. Boyle. 1997. Guide to the identification of North Sea fish using premaxillae and vertebrae. ICES Coop. Res. Rep. **220**.
- Webb, A., and J. Durinck, 1992. Counting birds from ship. Pages 24–37 in J. Komdeur, J. Bertelsen, and G. Cracknell, editors. Manual for aeroplane and ship surveys of waterfowl and seabirds. IWRB Spec. Pub. 19.
- Wegner, G., 2007. "Die Nordsee ist so warm wie noch nie!" - Stimmen derartige Nachrichten? http://www.bfa-fish.de/nn_820254/DE/aktuelles/aktuelles/2007/2007__06__08__Nordsee.html.
- Weijerman, M., H. Lindeboom, and A. F. Zuur. 2005. Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Mar. Ecol. Prog. Ser.* **298**:21–39.
- Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? *Deep-Sea Res. II* **54**:211–223.
- Weimerskirch, H., M. Salamolard, F. Sarrazin, and P. Jouventin. 1993. Foraging strategy of Wandering Albatrosses through the breeding season: a study using satellite telemetry. *Auk* **110**:325–342.
- Wilson, B., R. J. Reid, K. Grellier, P. M. Thompson, and P. S. Hammond. 2004. Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management for Bottlenose Dolphins. *Anim. Conserv.* **7**:331–338.
- Wiltshire, K. H., and B. F. J. Manly. 2004. The warming trend at Helgoland Roads, North Sea: phytoplankton response. *Helgol. Mar. Res.* **58**:269–273.
- Wood, S. N. 2000. Modelling and smoothing parameter estimation with multiple quadratic penalties. *J. R. Statist. Soc. B* **62**:413–428.
- Wood, S. N. 2006. *Generalized Additive Models. An introduction with R.* Chapman & Hall, London.
- Woodcock, A. H. 1940. Observations of Herring Gull soaring. *Auk* **57**:219–224.

Description of the individual scientific contributions to the multiple-author papers

The chapters 2-6 included in this thesis were written as manuscripts with multiple authorship. In the following, I will give details on my contribution to the individual papers.

Manuscript 1 (chapter 2, page 13): **Influence of ephemeral fronts on seabird distribution in the south-eastern North Sea**

Authors: Nele Markones¹, Stefan Garthe¹, Ommo Hüppop², Roger Mundry^{1,3}

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Stefan Garthe and Nele Markones developed the idea for the study. Field work was conducted by Stefan Garthe, Ommo Hüppop and co-workers. Data analysis was conducted by Nele Markones and Roger Mundry. Nele Markones and Stefan Garthe discussed the results. Nele Markones wrote the manuscript, reviewed by Stefan Garthe, Ommo Hüppop and Roger Mundry.

Manuscript 2 (chapter 3, page 27): **A menu of winners? - Diet composition of Black-legged Kittiwakes *Rissa tridactyla* in the breeding colony at Helgoland, south-eastern North Sea**

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Stefan Garthe, Nele Markones and Nils Guse developed the idea for the study. Collection of samples and assessment of breeding numbers of Kittiwakes was coordinated by Ommo Hüppop. Dissections were conducted by Nils Guse, Nele Markones and colleagues. Samples were analysed by Nele Markones with assistance of Nils Guse. Data analysis was conducted by Nele Markones with assistance of Sven Adler. Nele Markones, Nils Guse and Stefan Garthe discussed the results. Nele Markones wrote the manuscript, reviewed by Nils Guse, Stefan Garthe and Ommo Hüppop.

Manuscript 3 (chapter 4, page 49): **Small scale temporal variability of seabird distribution patterns in the south-eastern North Sea**

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Nele Markones and Stefan Garthe developed the ideas for the studies. Field work was mainly conducted by Nele Markones with contributions from Volker Dierschke and colleagues. Data analysis was conducted by Nele Markones and Sven Adler. Nele Markones and Stefan Garthe discussed the results. Nele Markones wrote the manuscript, reviewed by Stefan Garthe, Volker Dierschke and Franciscus Colijn.

Manuscript 4 (chapter 5, page 71): **Seasonality of seabird habitat choice in the German Bight (North Sea)**

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Manuscript 5 (chapter 6, page 89): **Seasonal differences in at-sea activity of seabirds underline high energetic demands during the chick-rearing period**

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¹Besonders fürs Bekanntmachen mit L^AT_EX!

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Erklärung

Hiermit erkläre ich, dass die vorliegende Dissertation selbständig von mir angefertigt wurde und in Inhalt und Form meine eigene Arbeit ist. Es wurden - abgesehen von der wissenschaftlichen Beratung durch meinen Betreuer - keine anderen als die angegebenen Hilfsmittel und Quellen verwendet. Die Arbeit wurde unter Einhaltung guter wissenschaftlicher Praxis entwickelt.

Diese Arbeit wurde weder ganz noch zum Teil schon einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein erster Promotionsversuch.

Die Promotion soll im Fach Biologische Meereskunde erfolgen. Für die Prüfung wird die Form der Disputation gewählt. Der Zulassung von Zuhörern bei der mündlichen Prüfung wird nicht widersprochen.

Kiel, den

Nele Markones