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Habitat use of the coastal zone of the German North Sea by surface-feeding seabirds

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Contents

Summary	1
Zusammenfassung	3
General Introduction	5
Thesis Outline	11
 Chapters	
I Regular habitat switch as an important feeding strategy of an opportunistic seabird species	13
Submitted	
 II At-sea distribution and behaviour of a surface-feeding seabird, the lesser black-backed gull (<i>Larus fuscus</i>), and its association with different prey	37
Published in <i>Marine Ecology Progress Series</i> 285: 245-258 (2005)	
 III Spatial patterns in at-sea behaviour during spring migration by little gulls (<i>Larus minutus</i>) in the south-eastern North Sea	55
Published in <i>Journal of Ornithology</i> 147: 354-366 (2006)	
 IV Area utilisation of gulls in a coastal farmland landscape: Habitat mosaic supports niche segregation of opportunistic species.....	71
Submitted	
 V Influence of water flow velocity and water depth on distribution and foraging patterns of a surface-feeding seabird in the German Wadden Sea	91
Prepared for submission	
 General Discussion	111
Danksagung (Acknowledgements)	121
References	123
Curriculum Vitae	139
Erklärung	141

Summary

In seabird ecology much attention has been paid to explore the breeding biology of different species, whereas studies on the use of foraging habitats are far more scarce. However, it is necessary to reveal temporal and spatial patterns of foraging habitat choice to understand mechanisms of coexistence among closely related species, to shed light on the ecological function and quality of different habitat types for seabirds and to judge the overall role of seabirds in food web dynamics. Surface-feeding seabirds are expected to be particularly closely related to the spatial and temporal patterns of their main prey species as a consequence of their foraging technique which allows them to exploit only the uppermost part of the water column. The German North Sea coast is inhabited by various surface-feeding species. It provides a particularly complex habitat mosaic dominated by three major landscape types (i.e. the pelagic offshore zone, the Wadden Sea area and the coastal mainland). Using an integrative approach, this study aims to unravel important temporal and spatial patterns of habitat use by several surface-feeding seabirds (i.e. five gull and one tern species) in the coastal zone of the German North Sea by combining direct observations on the distribution with behavioural and dietary analyses. Furthermore, this approach uses seabirds as bioindicators to unravel the quality and ecological function of different habitat types of the coastal zone as well as historical changes of food web dynamics against the background of anthropogenic activities.

As one of the most opportunistic species the black-headed gull (*Larus ridibundus*) showed a daily and seasonal routine of regular habitat switches between the major landscape types of the coastal zone as a consequence of varying prey availability and energy demands of growing chicks. A comparison with historical data clearly indicated a reduced utilisation of the marine foraging habitat and an increasing importance of terrestrial sites presumably related to major changes of foraging site quality.

The predominantly pelagic lesser black-backed gull (*L. fuscus*) showed distinct spatial and temporal associations with its apparently most important natural prey, swimming crabs (*Liocarcinus spec.*). Moreover, at least during the post-breeding period, it was possible to detect a significant relationship between at-sea distribution and areas of intensive fishery that provide discards and offal as additional food. Historical changes of habitat utilisation as well as changes in food choice of this species indicated major alterations of food web dynamics of the pelagic offshore zone.

The little gull (*L. minutus*) uses the German pelagic offshore zone as a staging site during its migration to and from its breeding grounds. Behavioural data on at-sea distribution clearly showed the existence of sites that were used primarily for foraging while others were used mainly for resting or as a migration corridor. The major foraging

sites could be characterized by hydrographic phenomena that provided enhanced prey availability and prey quality.

The coastal mainland holds a variety of different agricultural habitat types at a comparatively small spatial scale. It was possible to detect major differences in the utilisation of the terrestrial habitat mosaic among the four gull species black-headed, lesser black-backed, herring (*L. argentatus*) and common gull (*L. canus*). Notably black-headed gulls were highly associated with direct anthropogenic activities and with sites of intensive farming, while in contrast mainly common gulls depended on carefully managed pastures. The results demonstrate the high importance of the availability of the small scale habitat mosaic and of different intensities of anthropogenic activities for foraging niche segregation of the four closely related species.

The predominantly piscivorous Arctic tern (*Sterna paradisaea*) was found to mainly forage within the tidal streams of the Wadden Sea. It could be shown that both water depth and the physical effect of tides (i.e. high water flow velocities) played a decisive role for the choice of foraging habitats. Highest foraging intensities were encountered within sites of low water depth and high water currents which indicates that prey availability might be significantly increased by turbulences caused by tidal flow. Furthermore, the location of breeding colonies could be related to the location of tide-induced optimal foraging sites. These findings indicate the important role of physical factors to influence the ecology of surface-feeding seabirds.

In conclusion, this thesis revealed important temporal and spatial patterns of habitat use by surface-feeding seabirds (and its underlying causes) within the whole coastal zone. The integrative approach to merge observations of habitat use with analysis of behaviour and prey taken by seabirds provides an excellent opportunity to evaluate the ecological function and quality of different habitat types for seabirds as well as to monitor historical changes of habitat use and prey intake. This can be considered as a major step forward towards the identification of sensible sites for conservational management purposes within the whole coastal zone.

Zusammenfassung

Die Seevogelökologie widmete sich bereits intensiv der Untersuchung der Brutbiologie verschiedener Arten, wohingegen die Nutzung von Nahrungshabitaten weitaus weniger gut untersucht ist. Das Aufdecken raum-zeitlicher Muster in der Wahl von Nahrungshabitaten ist jedoch besonders wichtig, um Mechanismen der Koexistenz zwischen nah verwandten Arten zu verstehen, um Licht auf die ökologische Funktion und Qualität verschiedener Habitattypen für Seevögel zu werfen und um die Rolle von Seevögeln in der Nahrungsnetzodynamik zu verstehen. Enge raum-zeitliche Beziehungen zu den wichtigsten Beuteorganismen lassen sich besonders bei an der Oberfläche fressenden Seevögeln vermuten, da ihre Fresstechnik ihnen nur erlaubt, den obersten Teil der Wassersäule zu nutzen. Verschiedene Arten von Oberflächenfressern kommen auch an der deutschen Nordseeküste vor. Diese ist durch ein besonders komplexes Habitatmosaik gekennzeichnet, welches hauptsächlich durch drei Landschaftstypen geprägt wird (der Seebereich, das Wattenmeer und das küstennahe Binnenland). Die vorliegende Studie bedient sich eines integrativen Ansatzes, um wichtige raum-zeitliche Muster der Habitatnutzung von fünf Möwen- und einer Seeschwalbenart in der Küstenzone der deutschen Nordsee aufzudecken. Die zugrunde liegende Methode verschneidet direkte Beobachtungen von Verbreitungsmustern mit Verhaltens- und Nahrungsanalysen. Des Weiteren werden Seevögel als Bioindikatoren genutzt, um die Qualität und die ökologische Funktion verschiedener Habitattypen der Küstenzone sowie historische Veränderungen der Nahrungsnetzodynamik vor dem Hintergrund anthropogener Aktivitäten aufzudecken.

Als eine der opportunistischsten Arten zeigte die Lachmöwe (*Larus ridibundus*) ein regelmäßiges Muster eines täglichen und eines saisonalen Habitatwechsel zwischen den drei Landschaftstypen der Küstenzone. Dies war vor allem auf unterschiedliche Nahrungsverfügbarkeit und auf energetische Bedürfnisse der wachsenden Küken zurückzuführen. Ein Vergleich mit historischen Daten zeigte eine herabgesetzte Nutzung des marinen Habitates und eine gestiegene Bedeutung terrestrischer Gebiete, wahrscheinlich bedingt durch grundlegende Veränderungen in der Habitatqualität.

Die hauptsächlich pelagisch lebende Heringsmöwe (*L. fuscus*) zeigte auf See eine hohe räumliche und zeitliche Assoziation mit ihrer scheinbar wichtigsten natürlichen Beuteart, der Schwimmkrabbe (*Liocarcinus spec.*). Weiterhin war es zumindest für die Nachbrutzeit möglich, einen signifikanten Zusammenhang zwischen der Verbreitung auf See und Gebieten intensiver Fischerei aufzudecken, welche zusätzliche Nahrung in Form von Beifang bereitstellt. Historische Änderungen der Habitatnutzung sowie Veränderungen in der Nahrungswahl dieser Art deuteten auf einen grundlegenden Wandel in der Dynamik des marinen Nahrungsnetzes hin.

Die Zwergmöwe (*L. minutus*) nutzt das deutsche Seegebiet als Etappe während des Zuges zu und von ihren Brutkolonien. Kombinierte Verhaltens- und Verbreitungsdaten auf See konnten die Existenz von Nahrungsgebieten aufdecken, während andere Gebiete zum Rasten und als Zugkorridor genutzt wurden. Die Hauptnahrungsgebiete waren durch hydrographische Phänomene charakterisiert, welche erhöhte Nahrungsverfügbarkeit und –qualität hervorriefen.

Das küstennahe Binnenland verfügt über eine Vielzahl von vergleichsweise kleinräumigen Habitattypen. Es war möglich, übergeordnete Unterschiede im Raumnutzungsverhalten des terrestrischen Habitatmosaiks zwischen den vier Möwenarten Lach-, Herings-, Silber-, (*L. argentatus*) und Sturmmöwe (*L. canus*) aufzudecken. Besonders Lachmöwen waren stark mit direkten anthropogenen Aktivitäten assoziiert bzw. mit Habitaten hoher Bewirtschaftungsintensität, wohingegen vor allem Sturmmöwen von extensiv genutztem Grünland abhingen. Diese Ergebnisse demonstrieren die hohe Bedeutung des kleinräumigen Habitatangebotes und der verschieden stark ausgeprägten anthropogenen Aktivitäten für die Nischenabgrenzung der vier nah verwandten Möwenarten.

Die Fressgebiete der überwiegend piscivoren Küstenseeschwalbe (*Sterna paradisaea*) lagen überwiegend in den Prielen des Wattenmeeres. Es war möglich zu zeigen, dass sowohl die Wassertiefe als auch der mechanische Effekt der Tide (in Form von hohen Strömungsgeschwindigkeiten) eine entscheidende Rolle für die Habitatwahl spielten. Die höchsten Nahrungsaufnahmeraten wurden in Bereichen flachen Wassers und hoher Wasserströmungen angetroffen. Dies deutet darauf hin, dass eine deutliche Erhöhung der Beutemengen durch Verwirbelungen der Tide stattfand. Darüber hinaus konnte die Lage von Brutkolonien mit der Lage der durch die Tide begünstigten Nahrungsgebiete in Verbindung gebracht werden. Dies zeigt deutlich, wie stark physikalische Prozesse die Ökologie oberflächenfressender Seevögel beeinflussen können.

Zusammenfassend hat diese Studie wichtige raum-zeitliche Muster der Habitatnutzung (und deren zugrunde liegende Faktoren) von Oberflächenfressern in der Küstenzone aufdecken können. Der hier angewandte integrative Ansatz, direkte Beobachtungen der Habitatnutzung mit Analysen von Verhalten und Nahrungswahl von Seevögeln zu verschmelzen, bietet eine wichtige Möglichkeit die ökologische Funktion und Qualität verschiedener Habitattypen für Seevögel aufzudecken und darüber hinaus historische Veränderungen der Habitatnutzung und der genutzten Beuteorganismen herauszustellen. Dies bedeutet einen wichtigen Schritt zur Identifizierung besonders sensibler Gebiete und kann eine wichtige Grundlage für Regelungen des Naturschutzes in der gesamten Küstenzone darstellen.

General Introduction

Characteristics of surface-feeding seabirds

Basic traits in the life history of seabirds are a long life, deferred maturity, a small number of offspring, high parental care and high survival rates of adults (Ashmole 1971; Schreiber & Burger 2002). These characteristics – typical attributes of K-strategists – have been discussed as evolutionary adaptations and important buffer mechanisms against rapid changes in the marine environment (Hamer et al. 2002). One of the most important pressures shaping such adaptations is the often unpredictable and patchy availability of food. The development of special feeding methods is an important trait to exploit different food resources and to separate ecological niches from other species. Among different taxa of seabirds, a convergent development of feeding techniques has taken place (Ashmole 1971; Dunnet et al. 1990; Fig. 1). After pursuit diving, surface-feeding is the most common foraging behaviour of seabirds, which is adopted by a variety of species utilising food from all kind of trophic levels, from plankton (e.g. fulmars) to carcasses of marine predators (e.g. albatrosses, gulls; Shealer 2002). However, in contrast to diving species, surface-feeders are limited to exploit the uppermost (“two-dimensional”) part of the water column. Thus, they have to rely on biological, physical or anthropogenic processes that make prey available at the water surface. Because of this restraint, surface-feeders have been described to reflect prey availability in the marine environment (as far as within reach of these species) very reliably, as they are often forced to utilise a variety of available prey types more unselectively compared to other species (Ashmole 1971; Monaghan 1996). Moreover, due to the same fact, surface-feeders were found to show distinct temporal and spatial interactions with their prey species, such as diurnal vertical migration patterns to the water surface (Sjöberg 1989). Feeding habitat choice and timing are thus most important particularly for surface-feeding seabirds in order to match temporal and spatial patterns of their prey (see Monaghan 1996).

The superior aim of the present study was to investigate temporal patterns of habitat use by surface-feeding seabirds in the German North Sea coast and to relate these patterns to prey availability. Moreover, this study uses seabirds as bioindicators that can provide important information on temporal and spatial patterns of their prey and even may allow to elucidate the quality and ecological function of different habitats (i.e. for instance to reveal the existence of sites used for feeding resting or migration). Finally, this study evaluates possible mechanisms among closely related species to avoid interspecific competition and to allow coexistence in the same area. Lastly, possible scenarios of changes in the coastal food web (both induced by natural processes and dependent on anthropogenic activities) are discussed.

All species investigated within the scope of this study either breed at the German North Sea coast or utilise the coastal zone during their migration to and from their breeding sites further north. In particular, five gull and one tern species were chosen, i.e. little gull (*Larus minutus*), black-headed gull (*L. ridibundus*), common gull (*L. canus*), herring gull (*L. argentatus*), lesser black-backed gull (*L. fuscus*) and Arctic tern (*Sterna paradisaea*). These species have in common a more or less similarly high affinity to the coastal zone of the German North Sea coast and only occur in comparatively low numbers very far away from the shore (at least during the breeding period). The special feeding techniques of these surface-feeders are also very similar, i.e. shallow plunging, dipping, surface-seizing, surface pecking, kleptoparasitising, aerial pursuit (Ashmole 1971; Camphuysen & Garthe 2004; see red circles in Fig. 1). A detailed overview about the intention to choose these species is given in the chapter “Thesis outline” (see below). In the following sections an introduction of the basic approach of the present study as well as necessary background information on the study site are given.

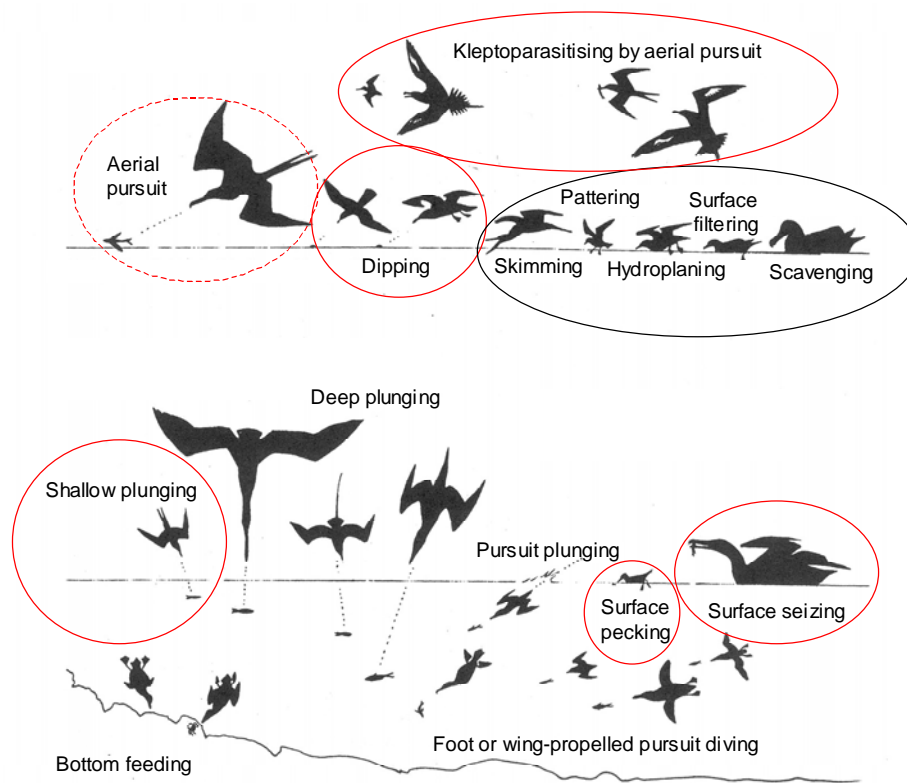


Fig. 1: Various feeding techniques used by seabirds. Surface-feeding techniques are encircled (red circles): Techniques applied by species investigated in this study; black circles: Techniques applied by other species; dashed circle: In this study aerial pursuit was only observed for insects). Taken from Shealer (2002) and slightly modified.

An integrative approach to unravel habitat use and its underlying causes

There are various factors that influence the distribution patterns and habitat choice of seabirds in a coastal zone (see also review in Dunnet et al. 1990), as for instance: (1) During breeding time central-place foraging seabirds are bound to their breeding colonies, and only few species are adapted to perform long-distance foraging flights

during this period of time (Shealer 2002). Thus, foraging ranges can significantly limit the distribution of most seabird species. (2) Inter- and intraspecific competition close to the breeding colonies have been described to lead to density-dependent effects as a consequence of prey depletion (Ashmole 1963; Birt et al. 1987; Lewis et al. 2001). (3) The most decisive factor affecting distribution and habitat choice, however is certainly the availability of prey itself, which is likely to vary between different sites, seasons and years as well as even on a daily basis (Sjöberg 1985; Piersma et al. 1988; Sjöberg 1989; Phillips et al. 1997; Lyons et al. 2005). Particularly surface-feeding seabirds have to cope with this and can be expected to exhibit spatial and temporal patterns in order to match their prey species.

Distribution patterns of surface-feeding seabirds in the pelagic zone of the North Sea have already been described with respect to some of the issues mentioned above (Becker et al. 1993; Camphuysen 1995; Garthe 1997; Kubetzki & Garthe 2003). However, besides the marine area, the German North Sea coast holds two more landscape types that provide important foraging opportunities for (opportunistic) surface-feeding seabird species, i.e. the tidal flats and streams of the Wadden Sea as well as the coastal mainland (for a detailed description of the study site see below). So far, studies dealing with habitat selection of surface-feeding seabirds have commonly focussed on either coastal landscape type (e.g. Jones 1985; Dervedde 1994; Kubetzki & Garthe 2003; Gloe 2006). The high structural complexity and dynamic nature of the coastal zone as a whole, however, may provide important foraging opportunities for surface-feeding species. Furthermore, studies on temporal and spatial relationships between seabirds and their available prey are still scarce. The major aim of the present study is to reveal temporal and spatial patterns of habitat use by applying an integrative approach that considers the whole coastal zone:

Habitat use of seabirds will be primarily linked to prey availability in different foraging habitats. To describe habitat use, the distribution of seabirds within different parts (and at different scales) of the coastal zone was recorded. Moreover, recordings of behaviour of seabirds were carried out. This enables to draw conclusions whether certain habitat types are used mainly for feeding, resting, migration or other purposes and thus provides an indication of the ecological function and quality of the site. In addition to this “direct” approach the simultaneous analysis of prey taken by seabirds and the measurement of prey availability in the field (“indirect”) can provide important supplementary information on habitat use and quality as well as ecological function (see Fig. 2 for a schematic, simplified flowchart). The approach to evaluate the ecological function and habitat quality via the use of foraging habitats, behaviour and the food taken within these habitats (bioindication) is described in more detail in the following chapter.

The here presented integrative approach to analyse distribution and behaviour of seabirds within different foraging habitats of the whole coastal zone and to link these findings to analyses on prey availability and prey taken by seabirds is the overall scheme used in this study to unravel the causes for habitat utilisation. Using surface-feeding

seabirds as an exemplary group, this approach provides a major step towards the classification of the ecological importance of different coastal regions, which may highly usefully be applied for management schemes in the context of conservation purposes.

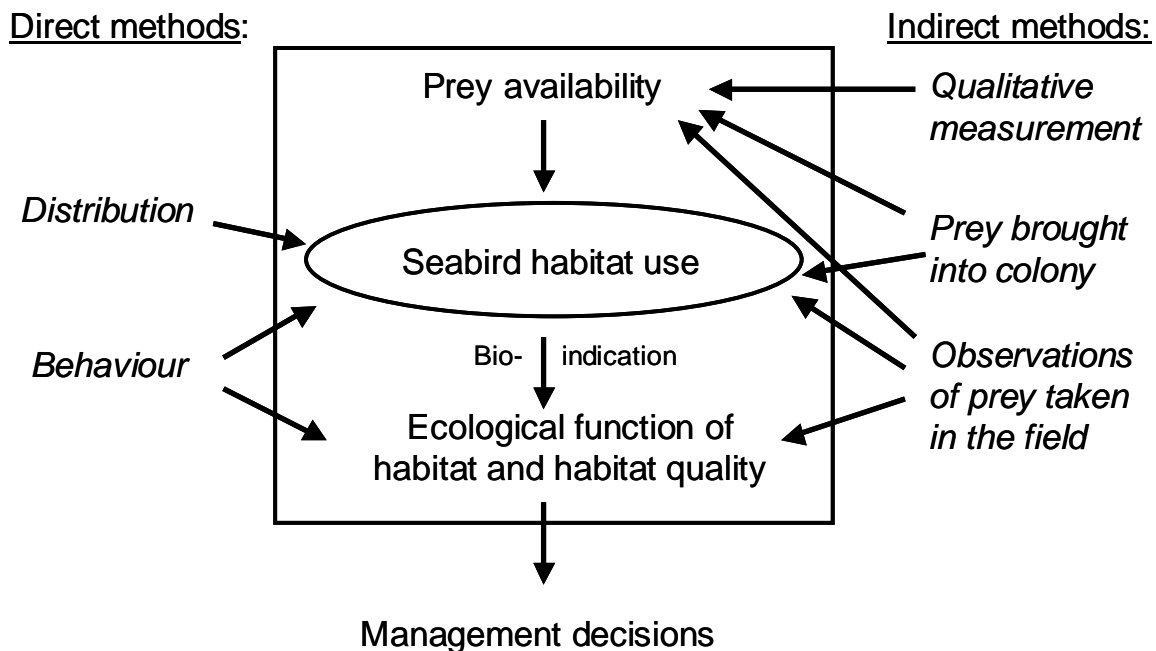


Fig. 2: Schematic, simplified flowchart of the integrative approach applied in this study to reveal habitat use by seabirds in the coastal zone of the German North Sea. The parameters investigated within the scope of this study are shown in the rectangle. Methods used are indicated in italics. The main aim of the study was to investigate the habitat use of seabirds within the whole coastal zone, which was assumed to be primarily linked to prey availability. Temporal and spatial patterns of habitat use provide important information on the quality and ecological function of different sites as well as on parts of the coastal food web (bioindicator approach), which furthermore can be used as an important tool for conservation measures (that are beyond the scope of this study). Habitat use, habitat quality and ecological functions of habitats were investigated (1) via direct observations of distribution and behaviour of birds as well as (2) by applying analysis of food used by seabirds (indirect methods).

Seabirds as bioindicators

Many authors have tried to use seabirds as indicators of the status of the marine environment (see review in Furness & Camphuysen 1997). Breeding success, breeding pair numbers, adult condition and reproductive parameters of seabirds have been analysed in order to gain information on feeding conditions and changes in prey populations (Cairns 1987; Montevecchi 1993). Monaghan (1996) pointed out that the best parameter, which is most sensitive against changes in prey stocks and prey availability, is the foraging behaviour of seabirds – a relationship which was also used for the present study (Fig. 2). The main focus was not set on the monitoring of whole prey populations (which anyway would not be too reliable using opportunistic species), but to use habitat utilisation and behaviour as indications of foraging site quality that reflect prey abundance and availability qualitatively. Although monophagous species are known to indicate changes in food availability more accurately (Cairns 1987; Monaghan 1996), opportunistic species will enable to draw conclusions on the quality of a variety of

foraging habitats of the coastal zone at different temporal and spatial scales. Additionally, opportunistic seabirds are expected to switch foraging habitats in accordance with the best prey availability / quality of prey. Additionally, they are particularly well-suited to reflect interactions of major parts of the food web, as they forage at various trophic levels.

Characteristics of the coastal zone of the south-eastern North Sea and trends of breeding pair numbers of surface-feeding seabirds

In general, investigating patterns in spatial distribution and habitat use of seabirds is basically a matter of scale. For instance, in the marine area, at a large spatial scale mainly physical processes such as ocean currents or gyres will influence water masses and thus explain habitat choice. On the other hand, at a smaller scale mainly biological processes (as for instance local prey availability, competition and many more) will significantly influence area utilisation by seabirds (Schneider & Duffy 1985; Hunt & Schneider 1987). However, also some small scale processes can be induced by physical phenomena, such as tide-related upwellings or freshwater plumes in an estuarine region that might cause local patches of enhanced prey availability for seabirds (Zamon 2003). In this study the focus was set mainly on a coastal region. Thus, small scale processes might be expected to play the most decisive role for habitat use.

Coastal sites are particularly important for seabirds as they provide both breeding grounds as well as important feeding opportunities. Typical attributes of coastal regions are shallow waters, nutrient richness and consequently high biological productivity as well as the important function to serve as nurseries for fish and other marine organisms (e.g. Kaiser et al. 2005). These characteristics make coastal zones optimal foraging habitats for seabirds. The German North Sea coast (for detailed study area see figures in the respective chapters of this thesis) is a particularly complex and highly structured coastal zone which provides three major landscape types as foraging habitats (i.e. (1) the pelagic offshore zone, (2) the Wadden Sea area with its vast tidal flats and streams and (3) the terrestrial nearshore zone), each of it consisting of a heterorganic complex of micro-habitats.

(1) The pelagic zone is characterised by distinct hydrographic phenomena such as upwellings (Becker et al. 1983; Krause et al. 1986) and river plume fronts caused by convergence of freshwater originating from the large river systems and the high saline North Sea water (e.g. Becker & Prahm-Rodewald 1980; Krause & Reuter 1988). These hydrographic phenomena can be of major importance to enhance prey availability for seabirds (e.g. Krause et al. 1986).

(2) The Wadden Sea provides a particularly rich habitat supply, as foraging individuals can use both the vast tidal flats and the tidal channels. The tidal flats of the Wadden Sea carry a high biomass of invertebrate species that are an eminent food source for many different bird species (e.g. Beukema et al. 1993; Stock et al. 1996;

Petersen & Exo 1999). Additionally, surface-feeding seabirds are able to exploit also the water bodies of tidal streams of the Wadden Sea. Vorberg & Breckling (1999) stated the high importance of this habitat type as nursery of fish, which indicates its significance as foraging habitat for seabirds. The same holds true for the estuaries of the German coastal zone (Thiel et al. 1995; Thiel & Potter 2001). Finally, the physical effect of tides can enhance the availability of prey within the pelagic zone of the Wadden Sea (Frank & Becker 1992; Frick & Becker 1995).

(3) The terrestrial coastal zone of the German North Sea coast is mainly an agricultural landscape that provides a highly structured habitat mosaic. Both, permanent grassland as well as sites used for cultivation are available. The mosaic of different farmland types as foraging and breeding habitats has already been shown to play a major role for many coastal bird species in the nearshore zone of Germany and elsewhere (e.g. Atkinson et al. 2002; Gloe 2006).

Whereas the facts described above more or less exclusively reflect natural foraging site parameters, the German coastal zone is of course strongly affected by anthropogenic activities. Both in the offshore zone and in the Wadden Sea, intensive fishery is taking place. The impact of different types of fishery on seabirds is manifold, and there are a lot of studies on this issue (e.g. Garthe & Hüppop 1994; Garthe et al. 1996; Walter & Becker 1997; Tasker et al. 2000). Besides fishery, the coastal mainland of Germany is intensively used for agriculture. Most interestingly, there are a lot fewer studies on the effects of agriculture on coastal birds (Vernon 1972; Atkinson et al. 2002) than there are on interactions with fisheries. The strong intensification of agricultural methods has led to an increasing impact on various species of birds utilizing such

habitats (Chamberlain et al. 2000; Vickery et al. 2001).

Enhanced anthropogenic activities in the coastal zone on the one hand side as well as conservation measures in breeding habitats on the other, might have led to comparatively high breeding pair numbers of some of the surface-feeding seabird species investigated (especially black-headed gull and lesser black-backed gull; Fig. 3). As the present study deals with closely

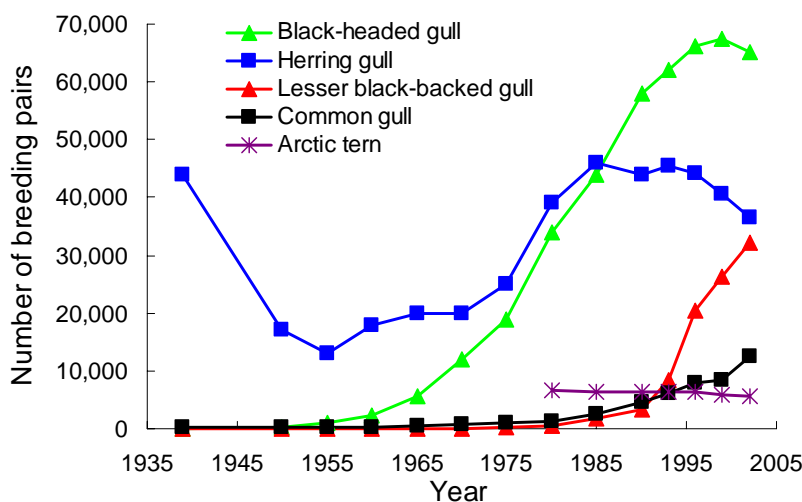


Fig. 3: Development of breeding pair numbers of the surface-feeding seabird species investigated that breed at the German North Sea coast and in the upper section of the Elbe river. Mean breeding pair numbers for periods of three, five or ten years are calculated. Source: Garthe et al. (2000); Hälterlein et al. (2000); Südbeck & Hälterlein (2001); Hälterlein unpubl. data. No reliable breeding pair numbers of Arctic terns are available before 1980. The trend of Arctic terns should be interpreted carefully due to uncertainties in recording methods.

related species coexisting in the same area, one additional aim is to elucidate mechanisms of niche segregation on the basis of differences in habitat use, temporal patterns and resource partitioning. These findings are discussed against the background of the role of anthropogenic activities and the development of breeding pair numbers along the German North Sea coast.

Thesis outline

This thesis is divided into five independent chapters. In accordance with the integrative approach applied in this study (see above) each chapter generally addresses the following issues:

- (1) Analyses of distribution patterns and behaviour of the species in the whole coastal region or in their core areas at different temporal and spatial scales.
- (2) An evaluation of the prey used.
- (3) An assessment of the ecological quality and function of different coastal regions for the respective species.
- (4) Analyses of mechanisms that enable coexistence of closely related species in the same area.
- (5) Some chapters aim to identify historical changes of foraging habitat use and / or changes in prey species taken and thus to gain insight into basic changes of the marine food web.
- (6) For some chapters scenarios of possible future changes of prey availability induced by natural phenomena and / or anthropogenic activities are developed.

The following outline indicates the respective contributions of the dedicated chapters to these overall questions. Moreover, each chapter addresses different main topics by focussing on different species and landscape types of the coastal zone:

Chapter I

In the first chapter I investigated the utilisation of the three landscape types of the coastal zone (i.e. the coastal mainland, Wadden Sea area and pelagic offshore zone) by black-headed gulls. According to the low foraging radius of this species, I expected site-dependent differences of habitat use by individuals of different colonies. Moreover, I assumed a temporal pattern of habitat switch according to prey availability in each of the three landscape types. Finally, changes in habitat use of this species over the last years were assumed to enable drawing conclusions on (historical) changes of quality of different habitat types of the German coastal zone.

Chapter II

The second chapter focuses on the widely distributed lesser black-backed gull which is known as a mainly pelagic species (e.g. Camphuysen 1995; Kubetzki & Garthe 2003).

The aim of this chapter was to elucidate the function of certain (large scale) offshore areas for this species. I expected distinct spatial and temporal associations of this gull with both, its major natural prey type, swimming crabs (*Liocarcinus* spec.) and with fishery activities. Moreover, historical shifts in the general at-sea distribution of lesser black-backed gulls were assumed to be related to changes in prey availability indicating important changes in the marine food web.

Chapter III

The third chapter deals with habitat use by little gulls, the only species investigated which is not breeding at the German North Sea coast. Little gulls use different parts of the pelagic coastal zone of the south-eastern North Sea during their migration to and from their breeding colonies. In general, migrating species depend on highly favourable conditions at their staging sites in order to maintain their fitness and condition needed for a successful reproduction (e.g. Evans et al. 1991; Ebbinge & Spaans 1995). Thus, their habitat use and behaviour should reliably mirror the quality of foraging habitats. I assumed that distribution and foraging behaviour of this pelagic species would be closely associated with distinct offshore regions as a consequence of small scale differences in prey availability.

Chapter IV

The overall role of the coastal mainland for gulls is elucidated in the fourth chapter, using an approach based on a high temporal and spatial resolution. In detail, I assumed that the habitat mosaic of the agricultural landscape would play an essential role for niche segregation of the four gull species. I expected temporal, spatial and behavioural differences in habitat utilisation as well as resource partitioning between the species in order to enable coexistence within the coastal mainland. Moreover, anthropogenic activities leading to dynamic changes within the habitat mosaic as well as other environmental parameters were expected to play a crucial role for niche segregation.

Chapter V

The last chapter focuses on the role of the Wadden Sea as the foraging habitat for Arctic terns. It highlights the important role of physical processes to steer habitat choice of surface-feeding seabirds by influencing prey availability. Compared to the gull species treated within the previous chapters, terns rely on pelagic foraging habitats and frequently use the tidal streams of the Wadden Sea and the adjacent offshore zones. Foraging behaviour and habitat use were expected to be related to both water depth and the tidal cycle, as turbulences and local upwellings caused by high water currents should enhance prey availability. Thus, I assumed that the most important foraging areas of Arctic terns would be located within shallow areas of highest water flow velocity. Moreover, it was expected that the location of the optimal foraging sites would also allow to predict the location of breeding colonies.

CHAPTER I

Regular habitat switch as an important feeding strategy of an opportunistic seabird species

Abstract

Surface-feeding seabirds may show density-dependent effects during the breeding period as a consequence of prey depletion caused by intra- and interspecific competition in the foraging habitat. Gulls are such central-place foragers that feed intensively at the water surface. However, in contrast to purely pelagic avian predators, opportunistic gull species in the coastal zone may benefit from foraging in a variety of habitats (i.e. the marine offshore area, tidal flats and also the nearshore mainland). Thus, prey depletion or reduced availability in either habitat should be avoided by switching between foraging habitats. In this study, we investigated the distribution and feeding ecology of one of the most opportunistic seabird species, the black-headed gull (*Larus ridibundus*), in various habitat types of the German part of the North Sea coast. We expected distinct temporal patterns of habitat switch during times of reduced prey availability. We carried out ship-based and aerial surveys as well as dietary analyses of different colonies, seasons and years. To our knowledge, this is the first integrative approach to investigate habitat use and foraging ecology of an important avian top predator within the complex mosaic of the coastal zone of the southern North Sea. The distribution of the black-headed gull within the available large scale habitats varied strongly between different times of the year. Furthermore, we revealed significant differences in the diet of birds from different colonies and a significant switch from terrestrial to marine feeding sites both on a daily basis (related to tidal cycle) and over the whole breeding season. Most likely, the latter switch is the result of lower prey abundance / depletion in the terrestrial habitats during summer and an increasing quality (in terms of prey availability and energy intake) of the marine area. The high dietary plasticity and flexible feeding strategy, switching between terrestrial and marine prey is certainly one of the success parameters of *L. ridibundus*. Especially during times of lower prey abundance, it is likely to be a key element for superior competitive performance in contrast to other predators of the coastal zone.

Introduction

Coastal zones often provide highly important habitat structures for seabirds. Pure pelagic seabird species with a comparatively small foraging niche (ranging both nearshore and offshore) were found to deplete their feeding stock during the breeding period, leading to intraspecific competition (Ashmole 1963; Birt et al. 1987; Lewis et al. 2001). For surface-feeding seabirds prey depletion might be even more crucial, as their feeding technique only allows them to exploit a small part of the water column (Ashmole 1963; Monaghan 1996). Gulls (Laridae) are such central-place-foraging, surface-feeding seabirds. However, as opportunistic feeders (in contrast to pure pelagic species) they might utilise all available habitat types of the coastal zone for foraging including the terrestrial nearshore habitat, tidal flats and the pelagic offshore zone. The black-headed gull (*Larus ridibundus*) is one of the most generalist gull species at the German North Sea coast. Former studies separately described either its utilisation of the marine habitat (e.g. Curtis et al. 1985; Gorke 1990; Kubetzki & Garthe 2003) or of the terrestrial nearshore area (Jones 1985; Gloe 2006). To our knowledge, Vernon (1970a) and Mudge & Ferns (1982) present the only approach to quantify habitat use of this species in the coastal zone of the UK as a whole. We consider such an integrative approach as highly useful to analyse the feeding ecology of an opportunistic avian predator. Switching between a variety of available foraging habitats might be an essential part of its feeding strategy. An integrative approach to analyse such a switch considering different temporal scales has not been applied so far.

We expected that the complex coastal habitat mosaic of the German North Sea coast (consisting of tidal flats, open-sea water areas as well as pastures and arable land) might provide excellent opportunities to switch feeding habitats according to food availability and environmental constraints. The ability to switch food and foraging habitats were found to be beneficial for different species of gulls (e.g. Spaans 1971; Annett & Pierotti 1989). Thus, we assumed that the high structural variability of the coastal zone and the permanent availability of suitable foraging sites might account for possible prey depletion in certain habitats and reduce intraspecific competition. Furthermore, particularly surface-feeding seabirds are most sensible to alterations in food supply and should reflect the status of their resources very well (Monaghan 1996). We used the black-headed gull as a bioindicator to elucidate temporal patterns of habitat quality (in terms of feeding site quality) of different parts of the coastal system during different times of the year. In detail, we derived the three following hypotheses:

(1) Since the flight radius of black-headed gulls breeding at the North Sea coast was found to be comparatively low (i.e. ca. 5 km; Gorke 1990), we assumed that colony location would reflect prey supply in the vicinity of the colony and that prey components should thus differ between different colonies, especially when these are located at different distances from the major habitat types (for detailed expected differences between colonies see below). (2) Superabundant prey should be used most intensively in order to reduce searching time, leading to a switch of foraging habitats according to

prey availability / prey depletion and thus differences in gull nutrition in space and time (i.e. between colonies, seasons and years). (3) The hatching of chicks has been found to trigger diet switches (Annett & Pierotti 1989), and additionally, energy demands of chicks increase with age (Spaans 1971; Hartwig & Hüppop 1982). Thus, we expected dietary responses in adults leading to distinct differences in nutrition between incubation and chick-rearing period which might be again accompanied by a switch of foraging habitats.

We carried out aerial and ship-based surveys to reveal distribution patterns and habitat use of black-headed gulls in the coastal zone throughout the annual cycle. Furthermore, we analysed pellets of three different colonies during incubation and chick-rearing for two years. In order to assess short time, tide-related habitat switch and the importance of tidal flats / offshore zone vs. the mainland, flight activity patterns were observed in a gull colony.

Black-headed gulls exhibited considerable increases in breeding pair numbers along the German North Sea coast since the second half of the 20th century until very recent (Garthe et al. 2000; Koffijberg et al. 2006; Fig. 3). However, breeding pair numbers in the Danish and Dutch part of the North Sea showed a consistent decline since a few years (Heldbjerg 2001; Koffijberg et al. 2006). Moreover, the strong increase of breeding pair numbers in the coastal zone of Germany seems to have come to a halt (unpubl. data). Reviewing historical studies on foraging ecology of black-headed gulls, possible implications of the quality of different coastal foraging habitats are discussed against the background of future population trends of this species in the German coastal zone. Finally, a brief comparison of its foraging strategy with related species is given.

Material and Methods

Study area

The study was carried out at the North Sea coast and the adjacent mainland of Schleswig-Holstein, northern Germany (east of 8°; west of 9° 30' and south of 55°; Fig. 4). The coastal mainland and most of the islands are characterized by a mix of intensive agriculture and pastoral farming. The coastal seas consist of tidal flats and shallow tidal streams belonging to the "Nationalpark Wadden Sea". Further offshore, the water depth increases slowly and tidal flats are followed by the offshore zone (Fig. 4).

Distribution over the annual cycle

Aerial surveys in the mainland

Distribution of black-headed gulls in the coastal mainland was recorded using aerial surveys. Flights were carried out during winter (November to February), spring (March to April), incubation (1 May to 15 June), chick-rearing (16 June to 31 July) and autumn (August to October) of the years 2005 and 2006 (for observation effort see Table 1). Basically, we applied the common aerial census technique for recording seabirds at sea

(Diederichs et al. 2002). Gulls were recorded within a single counting transect of $T = 240$ m width flying at an altitude (Alt) of 150 m. Width of the transect was calculated with inclinometers measuring two angles against the horizon ($25^\circ =$ distant boarder of the transect, $60^\circ =$ closer boarder of the transect; for further details see Diederichs et al. 2002):

$$T = \text{Alt} * (\tan(90^\circ - 25^\circ) - \tan(90^\circ - 60^\circ)) \approx 240 \text{ m}$$

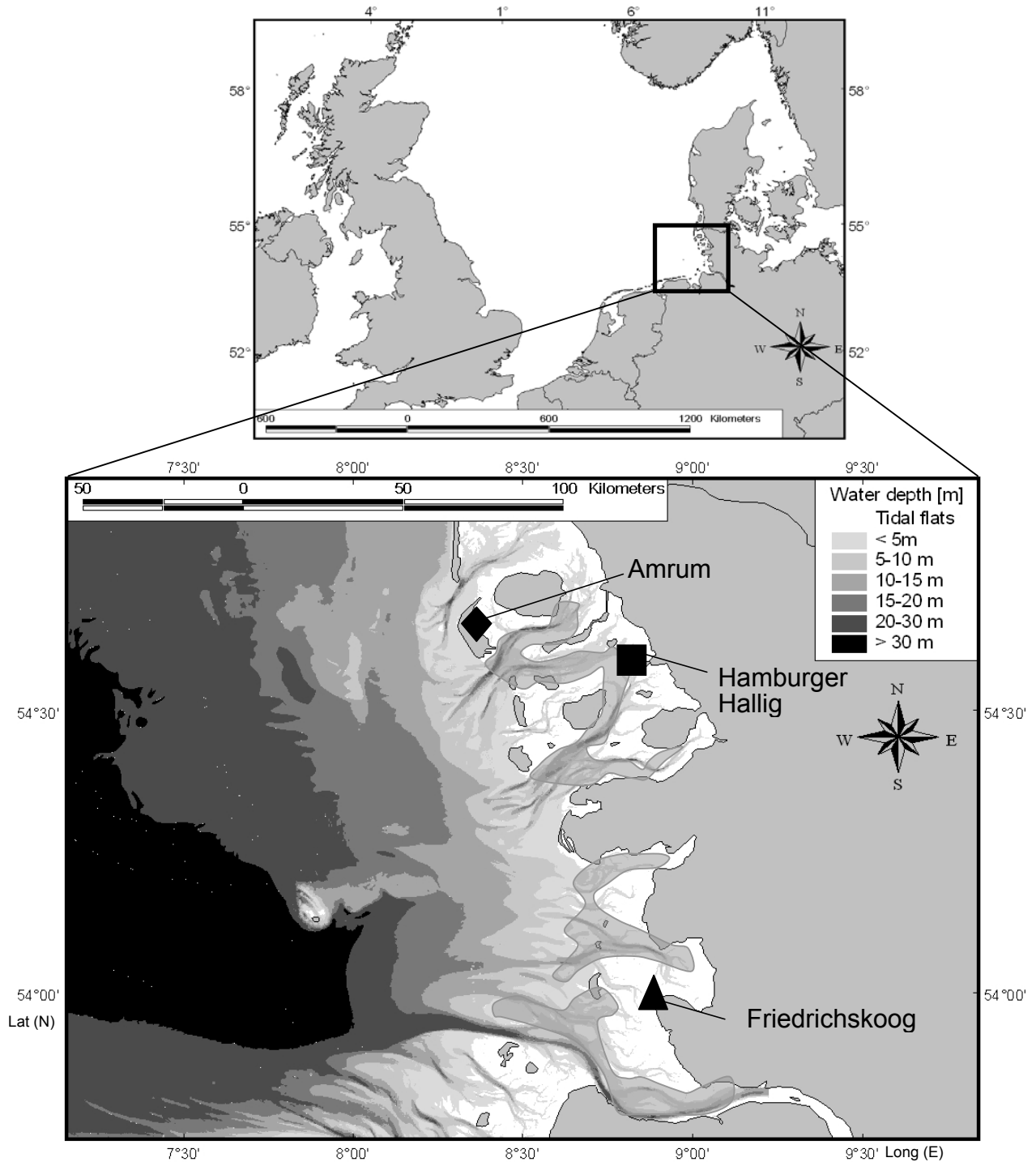


Fig. 4: Location and details of the study area, with the location of the three black-headed gull colonies sampled for pellets (triangle: Colony of Friedrichskoog, 1,200 breeding pairs; square: Colony of Hamburger Hallig, 600 breeding pairs; diamond: Colony of Amrum, 80 breeding pairs; source: Hälterlein unpubl. data; shaded areas: Tidal flats scanned for black-headed gulls during ship surveys).

Gull numbers and distance travelled (using GPS) as well as area surveyed (i.e. distance travelled * T) were recorded at intervals of one second. Mean gull densities were computed for a grid of 1.5° latitude x 2.5° longitude by dividing the total gull numbers within each grid cell by the total area surveyed within each grid cell.

Table 1: Observer effort [km] of aerial surveys on mainland (years 2005-2006) and ship surveys on the open water (years 1996-2006) and nearby tidal flats (years 2005-2006).

	Plane (mainland)	Ship (open water)	Ship (tidal flats)
Spring	2,091	8,390	554
Incubation	1,143	12,439	1,017
Chick-rearing	1,148	19,297	233
Autumn	2,281	21,421	834
Winter	2,711	7,078	246

Ship-based surveys

Distribution of black-headed gulls sitting on or flying across open water (i.e. the offshore region and the tidal streams in the Wadden Sea area) were recorded for the same seasons as in the mainland during the years 1996 – 2006 (German Seabirds at Sea database, version 5.07; as of October 2006; for observation effort see

Table 1). We used ship-based surveys applying the transect method described by Tasker et al. (1984) and Garthe et al. (2002), following the same principle as stated for aerial surveys, despite that a transect of 300 m width was measured using callipers (Heinemann 1981) and recording interval was 1 min. All birds located on the water surface within the transect were counted. In order to avoid bias of flying individuals due to the comparably slow ship speed, we applied the 'snapshot' method; i.e. arbitrarily counting only those birds which flew into or across the transect at each full minute to avoid counting any individual more than once (Tasker et al. 1984).

Black-headed gulls foraging or resting on tidal flats were recorded during the years 2005 and 2006 (for observation effort see Table 1). Only the parts of tidal areas that could be scanned easily from board of the vessel were observed (see hatched areas in Fig. 4). Since no transect method was applied, we did not correct sightings for observer effort and simply recorded individual numbers. Thus, distribution patterns of black-headed gulls on tidal flats should only be interpreted qualitatively.

Diet analysis

A total of 648 pellets of black-headed gulls was collected in three different colonies: (1) Friedrichskoog (FKoog; 8° 49' 12 E and 54° 18' 00 N; 1,200 breeding pairs); (2) Hamburger Hallig (HHHallig; 8° 48' 36 E and 54° 36' 36 N; 600 breeding pairs); (3) Amrum (8° 28' 48 E and 54° 40' 48 N; 80 breeding pairs). According to colony location, low foraging radii of black-headed gulls (Gorke 1990) and the principle of energy maximization (i.e. choosing foraging habitats close to the colony; Brandl & Gorke 1988), the first colony was expected to consist of black-headed gulls which forage mainly on the mainland and only moderately in the Wadden Sea, while the second colony should

provide better foraging opportunities in the Wadden Sea. The third colony was assumed to allow for both, offshore and Wadden Sea based foraging, but hardly for terrestrial foraging as the mainland is at a fair distance. Colonies were sampled once during incubation (i.e. 1 May to 15 June) and once during the chick-rearing period (i.e. 16 June to 31 July) of both years 2005 and 2006. The colony of Amrum could not be sampled during the chick-rearing period in 2006, as the chicks had died due to flooding and the adults had left the colony. Number of pellets collected varied between colonies, seasons and years depending on number of breeding pairs and weather conditions, as rain might destroy pellets (see Table 2 for number of samples in each colony, season and year).

The analysis of pellets was conducted following the method described by Duffy & Jackson (1986): We determined the frequency of occurrence of each detectable food item by assessing its presence or absence in each pellet. No quantification of any food category was carried out, as hard shelled food remains or prey which is not easily digestible would have led to a strong bias (Duffy and Jackson 1986). In order to detect also small food remains (e.g. setae of poly- or oligochaetes), each pellet was scanned intensively using a 8 x 23 binocular. Food items found were determined to the lowest possible taxon. Remains of invertebrates and terrestrial mammals were determined following Stresemann (1992) and Schaefer (1994), while fishes were identified by otoliths, bones and scales following Harkönen (1986) and Leopold et al. (2001). For statistical analyses (see below), we grouped prey items into 11 categories according to foraging habitat and taxonomic considerations (see Table 4).

To document switch of feeding habitats, the food remains were classified as terrestrial (including freshwater) or marine according to their apparent origin. We were able to assign each food remain to either habitat category (for statistics see below). Classification was only doubtful in case of stickleback (*Gasterosteus aculeatus*) as this species occurs both in marine and freshwater. However, according to Vorberg & Breckling (1999) sticklebacks disappear nearly completely from the Wadden Sea / offshore region during May to July and migrate up small rivers in large numbers towards the mainland. Thus, this species was classified as taken in terrestrial habitats.

Statistics on diet analysis

We carried out Canonical Correspondence Analysis (CCA; Leps & Smilauer 2003) on the basis of the 11 prey categories for each combination of colony, season and year to reveal spatial and temporal differences and possible habitat switch. Furthermore, we conducted Monte-Carlo permutation tests (Efron 1992; Legendre & Legendre 1998) using colony, season and year as predictor variables. We conducted 9,999 unrestricted permutations with forward selection. This procedure allows to test different sample sizes independent of the sample distribution. Tests were performed on two different levels: (1) On the basis of all prey categories, (2) with the 11 prey categories (see Table 4). In order to focus on origin of food, we determined whether the prey components in pellets originated from marine, terrestrial or both habitats (see above). To test for differences

between colonies, within years and seasons, a Linear Mixed Effect Model (LME) based on Restricted Maximum Likelihood (REML) was applied (Venables & Ripley 2002). We defined colony as fixed effect factor and season nested in year as random factor. To test for significant effects of the random factor we applied a Linear Model (LM) which was tested against the LME using ANOVA.

Permutation tests and CCA were performed with CANOCO 4.5, while all other tests were conducted with the open source software package of R 2.4.1 (www.r-project.org) using the library MASS and NLME (Venables & Ripley 2002; Pinheiro & Bates 2000). All indicated p-values are two-tailed.

Flight activity in relation to tide and time of day

To assess short-term habitat switch and the importance of the coastal mainland vs. the nearby tidal flats / offshore area, flight activity patterns were observed in the colony of FKoog (see Fig. 4) on 6 days in early June and 4 days in mid July 2005. Individuals were counted during daylight hours when flying across two lines of 1 km length set arbitrarily along the colony edge. One line was set perpendicular to the mainland, the other line perpendicular to the tidal flats / offshore area. Counts were conducted within 5 min intervals alternating both lines and covering different stages of the tidal cycle and time of day. 68 double 5 min counts were carried out during June and 42 during July. Flight activity of birds leaving and returning (to) the colony, respectively, was calculated and related to tide and time of day [UTC].

As many seabirds related to tidal flats are expected to forage mainly during low tide (e.g. Gorke 1990; Garthe et al. 1999), flight activity in relation to tide was analysed by fitting a square function. Most birds reveal activity patterns with two peaks per day (Aschoff 1966), which was also reported for gulls (Schwemmer & Garthe 2005). Thus, flight activity in relation to time of day was analysed by fitting a 4th order polynomial function. The statistical significance of a resulting model was tested using the F-test described in Zar (1999). Coefficients of polynomial functions and corresponding significance tests were derived using a self-written software (R Mundry) applying a permutation test (10,000 permutations).

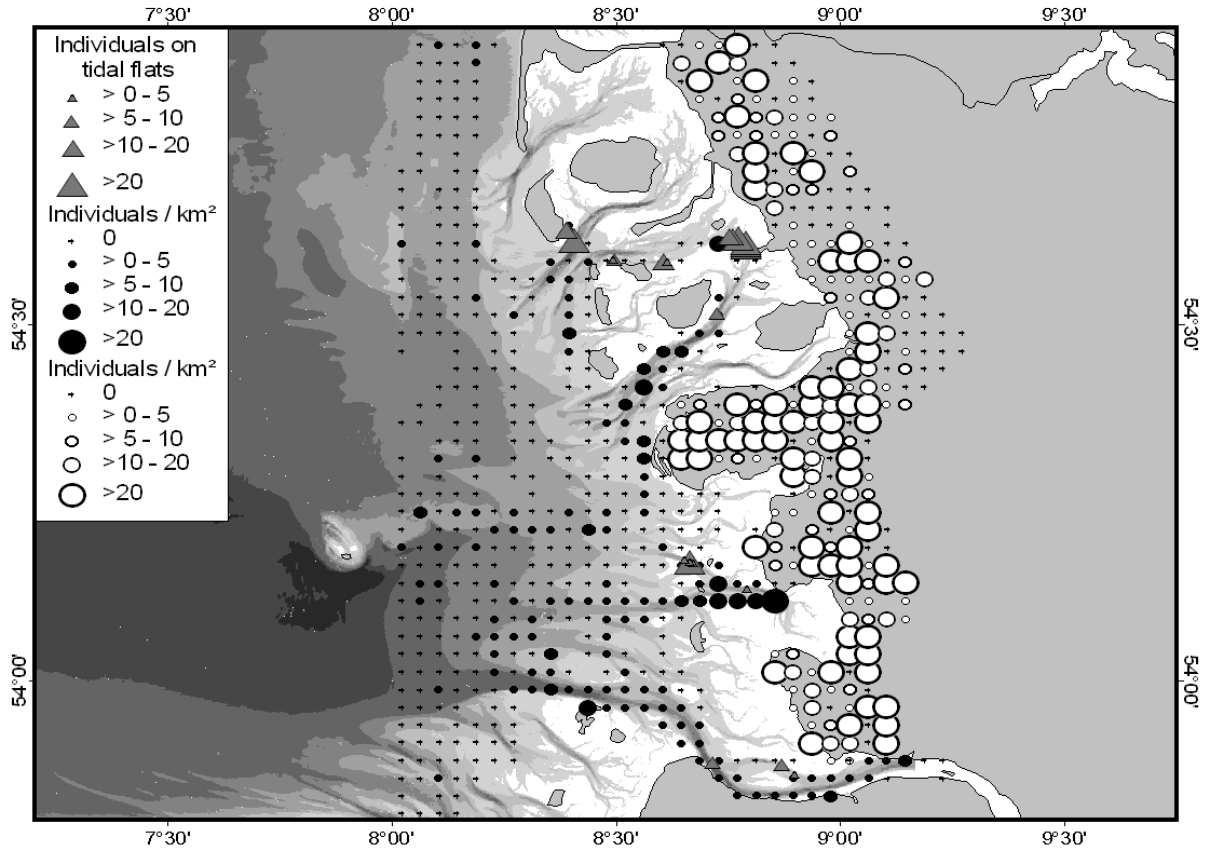
Results

Distribution

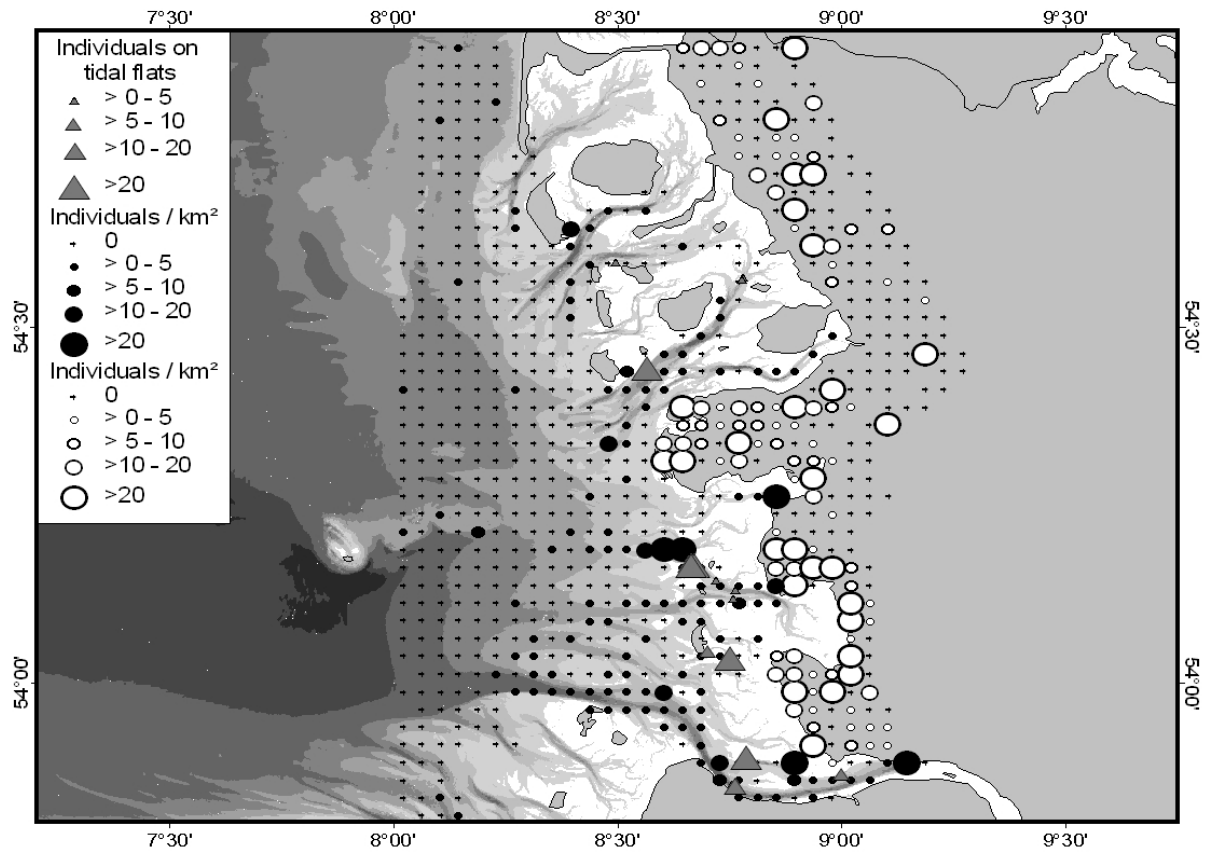
Densities of black-headed gulls in the mainland peaked during spring migration, while the marine area revealed moderate numbers (Fig. 5a). With the beginning of the breeding season, total numbers in the whole study area decreased: On the mainland, densities were higher during incubation than during chick-rearing, while numbers in the marine area changed complementarily (Fig. 5b-c). On the mainland, distribution patterns were sharply focused on the border to the marine area, particularly in the southern part of the

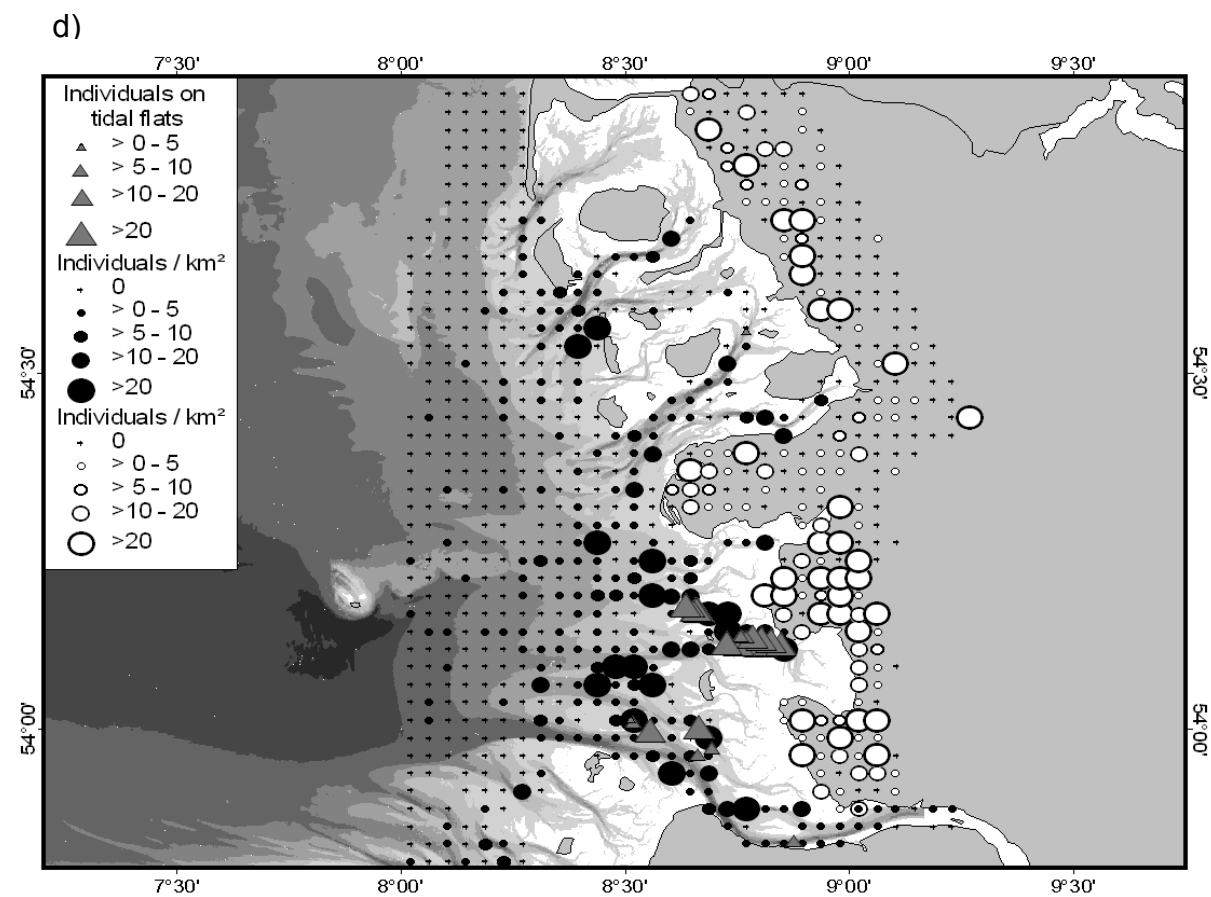
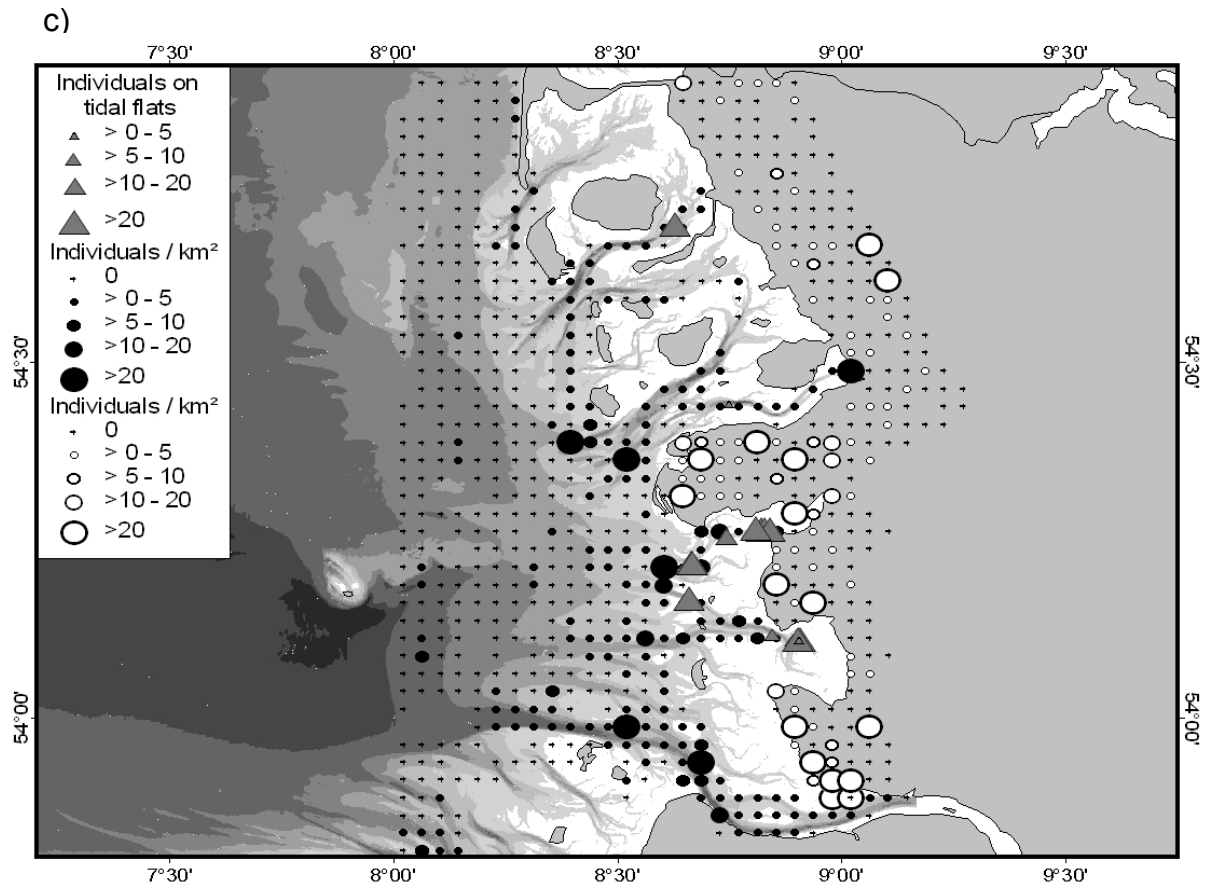
study area and during the whole breeding season, indicating a fast access (to) and possible turnover with the marine area.

a)



b)





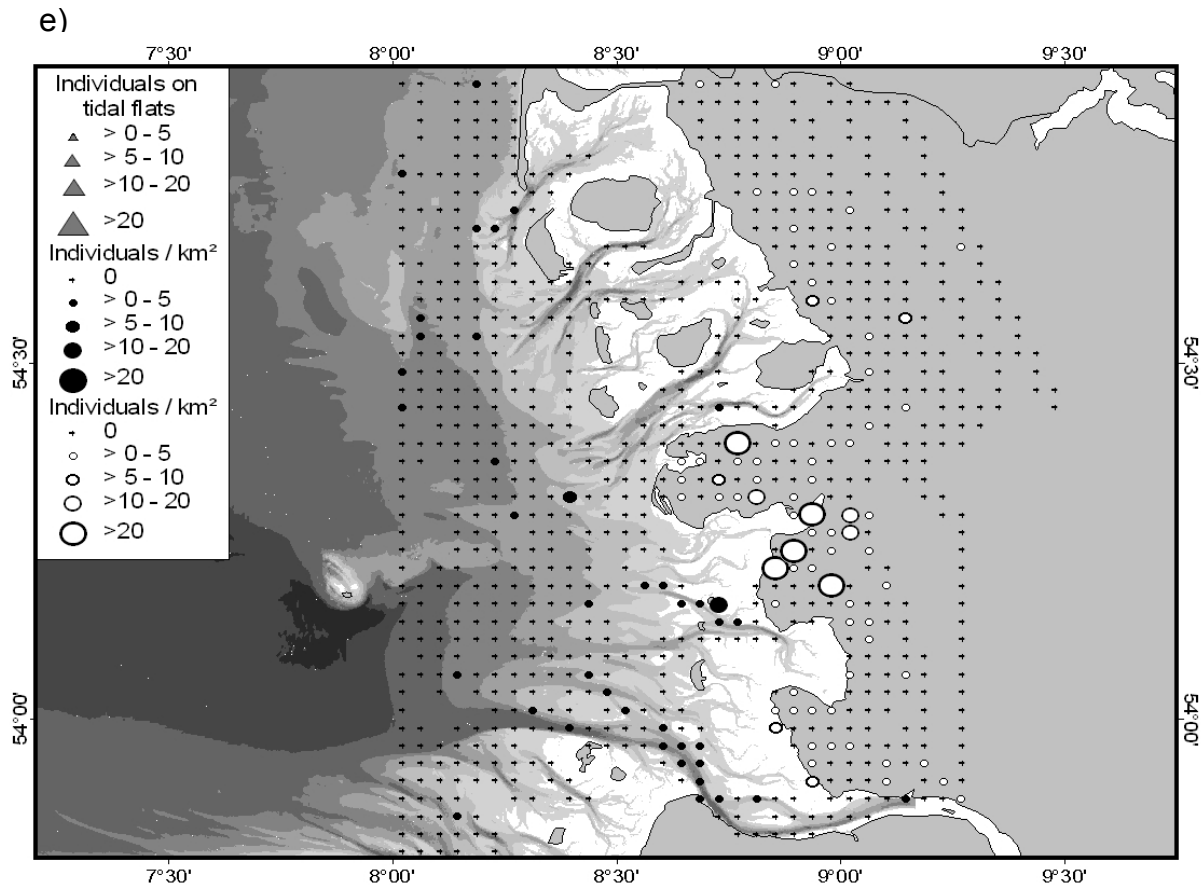


Fig. 5: Distribution patterns of black-headed gulls along the western German North Sea coast and coastal mainland during a) spring migration, b) incubation period, c) chick-rearing period, d) autumn migration, e) winter.

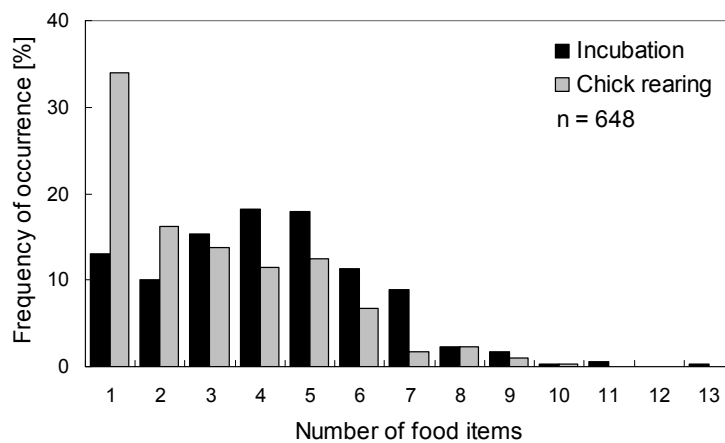
With the beginning of the autumn migration, total densities in both the marine area and the mainland increased again, displaying an obvious concentration of individuals in the southern part of the study area (Fig. 5d). During autumn, total numbers in the marine area reached peak values, whereas during winter total numbers of black-headed gulls reached a minimum along the whole coast and particularly within the marine area (Fig. 5e).

Diet

A total of 117 different food components were found in black-headed gull pellets. Mean number of all food items per pellet was 3.64 (± 2.17), the maximum number found was 13. During incubation, the composition of pellets at all three colonies was more diverse compared to the chick stage (Table 2; Fig. 6). Generally, in all colonies the most important terrestrial prey items were earthworms (Lumbricidae), followed by beetles (particularly Carabidae and Elateridae), while the most frequent marine prey were North Sea shrimps (*Crangon crangon*) and shore crabs (*Carcinus maenas*) (Table 3).

Table 2: Mean number \pm standard deviation of food items per pellet and number of pellets sampled (in brackets) for each combination of colony, season and year.

	2005	2005	2006	2006
	Incubation	Chick stage	Incubation	Chick stage
Fkoog	3.41 \pm 1.66 (63)	1.89 \pm 1.26 (79)	4.07 \pm 2.71 (61)	1.67 \pm 1.15 (21)
HHHallig	4.61 \pm 1.76 (70)	3.62 \pm 1.82 (86)	4.47 \pm 2.62 (90)	3.83 \pm 2.39 (90)
Amrum	4.26 \pm 1.88 (43)	2.05 \pm 1.16 (21)	3.89 \pm 2.05 (24)	-

**Fig. 6:** Frequency of occurrence [%] of pellets with different numbers of food items (black bars: incubation; grey bars: chick stage).

Considering all food items (Table 3), permutation tests revealed significant differences between colonies ($F = 8.96$), seasons ($F = 11.21$) and years ($F = 7.22$; $p < 0.001$, respectively). This was mainly caused by preference of certain prey items during different years or seasons within each colony, indicating the use of prey species that were

superabundant: For instance Diplopoda in Fkoog during incubation in 2006 as well as the pine weevil (*Hylobius abietis*) or leatherjackets (*Tipula paludosa*) in Amrum during incubation in 2005 (Table 3).

Occurrence of the 11 categories of food types in pellets showed significant differences between colonies ($F = 19.92$; $p < 0.001$), seasons ($F = 23.51$, $p < 0.001$) and years ($F = 4.71$; $p < 0.005$; Table 4). Insects / terrestrial arthropods as well as earthworms and plant material showed the highest presence values in all colonies and years, whereas crustaceans from the tidal flats (and partly polychaetes and molluscs) were important mainly for the colony of Fkoog particularly during chick-rearing (Table 4).

Table 3: Frequency of occurrence [%] of food items in black-headed gull pellets originating from three colonies collected during incubation (1 May – 15 June) and chick-rearing (16 June – 31 July) in 2005 and 2006.

Food item	Friedrichskoog				Hamburger Hallig				Amrum		
	Incubation	Chick rearing	Incubation	Chick rearing	Incubation	Chick rearing	Incubation	Chick rearing	Incubation	Chick rearing	Incubation
	2005 n = 63	2005 n = 79	2006 n = 61	2006 n = 21	2005 n = 70	2005 n = 86	2006 n = 90	2006 n = 90	2005 n = 43	2005 n = 21	2006 n = 24
MOLLUSCA											
terrestrial snails	-	-	1.6	-	-	-	2.2	2.2	-	-	4.2
<i>Hydrobia ulvae</i>	12.7	2.5	16.4	4.8	8.6	5.8	10.0	6.7	7.0	9.5	4.2
<i>Littorina littorea</i>	-	-	-	-	-	1.2	-	1.1	-	-	-
<i>Retusa obtusa</i>	-	-	-	-	-	-	-	1.1	-	-	-
Bivalvia unident.	4.8	2.5	4.9	4.8	10.0	-	8.9	6.7	-	4.8	-
<i>Cerastoderma edule</i>	-	5.6	18.3	9.5	4.3	1.2	4.4	13.3	4.7	14.3	12.5
<i>Macoma baltica</i>	1.6	2.5	4.9	4.8	2.9	-	3.3	3.3	-	-	-
<i>Mya arenaria</i>	-	-	6.6	-	-	-	-	1.1	-	-	4.2
<i>Mytilus edulis</i>	-	-	1.6	-	-	-	2.2	-	-	-	4.2
ANNELIDA											
<i>Lanice conchilega</i>	-	2.5	-	-	-	-	-	1.1	-	-	4.2
<i>Arenicola marina</i>	-	2.5	1.6	4.8	1.4	-	2.2	4.4	-	-	20.8
<i>Hediste spec.</i>	22.2	2.3	8.2	9.5	1.4	5.8	3.3	13.3	4.7	9.5	-
<i>Lumbricus spec.</i>	63.5	13.9	47.5	4.8	92.9	64.0	51.1	46.7	20.9	4.8	37.5
ARTHROPODA											
Araneida unident.	1.6	-	-	-	-	1.2	-	1.1	-	-	-
Lycosidae unident.	-	-	-	-	-	-	-	1.1	-	-	4.2
Crustacea unident.	6.3	1.3	9.8	-	-	1.2	5.6	5.6	-	4.8	20.8
<i>Balanus spec.</i>	-	-	-	-	2.9	-	-	2.2	-	-	-
<i>Crangon crangon</i>	4.8	44.3	18.3	19.5	-	14.0	2.2	12.2	-	14.3	8.3
Brachyura unident.	-	1.3	-	19.5	1.4	1.2	-	4.4	7.0	-	-
<i>Carcinus maenas</i>	22.2	24.6	13.1	33.3	-	4.7	5.6	3.3	2.3	9.5	4.2
<i>Eriocheir sinensis</i>	1.6	1.3	-	-	-	-	-	-	-	-	-
<i>Liocarcinus spec.</i>	3.2	1.3	3.3	4.8	-	2.3	1.1	2.2	-	4.8	4.2
Philosciidae unident.	3.2	-	-	-	-	-	1.1	-	-	-	-
<i>Idotea balthica</i>	-	2.5	1.6	-	-	-	-	-	-	-	4.2
<i>Corophium volutator</i>	-	8.9	3.3	-	-	1.2	-	6.7	-	-	4.2
<i>Orchestia spec.</i>	-	-	-	-	-	-	-	1.1	-	-	-
Diplopoda unident.	9.5	-	34.4	-	4.3	1.2	2.2	5.6	2.3	-	4.2
Chilopoda unident.	-	-	-	-	-	1.2	2.2	-	-	-	-
Insecta unident.	-	1.3	3.3	-	4.3	2.3	1.1	-	2.3	-	25.0
Ordonata unident.	-	-	-	4.8	1.4	-	-	-	-	-	-
<i>Forficula spec.</i>	1.6	1.3	4.9	-	4.3	2.3	1.1	2.2	4.7	-	8.3
Heteroptera unident.	-	-	-	-	-	-	1.1	1.1	-	-	-
Corixidae unident.	-	-	-	-	-	-	1.1	-	-	-	-
<i>Ilyocoris cimicoides</i>	-	-	-	-	-	1.2	-	-	2.3	-	-
Auchenorrhyncha unident.	-	-	-	-	-	-	1.1	-	-	-	-

Table 3: continued...

Food item	Friedrichskoog				Hamburger Hallig				Amrum		
	Incubation	Chick rearing	Incubation	Chick rearing	Incubation	Chick rearing	Incubation	Chick rearing	Incubation	Chick rearing	Incubation
	2005	2005	2006	2006	2005	2005	2006	2006	2005	2005	2006
Coleoptera unident.	7.9	2.5	16.4	4.8	14.3	1.5	30.0	16.7	16.3	9.5	29.2
Elateridae unident.	-	-	11.5	-	21.4	1.5	25.6	6.7	16.3	-	8.3
Elateridae larvae unident.	-	-	6.6	-	1.4	-	3.3	-	-	-	-
<i>Agriotes lineatus</i>	-	-	-	-	-	-	11.1	-	9.3	-	-
<i>Byrrhus</i> spec.	-	-	-	-	-	-	-	-	2.3	-	-
Carabidae unident.	41.3	5.6	32.8	-	60.0	57.0	43.3	35.6	55.8	4.8	20.8
Carabidae larvae unident.	-	-	8.2	-	-	-	3.3	-	-	-	8.3
<i>Carabus violaceus</i>	1.6	-	1.6	-	10.0	4.7	2.2	2.2	2.3	-	-
<i>Carabus granulatus</i>	3.2	-	4.9	-	12.9	9.3	12.2	14.4	7.0	-	4.2
<i>Brosicus cephalotes</i>	-	-	-	-	7.1	-	-	-	-	-	-
Dytiscidae unident.	-	-	-	-	-	-	2.2	-	-	-	-
Silphidae unident.	3.2	1.3	-	-	4.3	9.3	1.1	8.9	-	-	-
<i>Liodes</i> spec.	1.6	-	-	-	-	-	-	-	-	-	-
Staphylinidae unident.	-	-	-	-	1.4	-	6.7	3.3	-	-	4.2
<i>Philonthus</i> spec.	-	-	-	-	-	-	1.1	-	-	-	-
<i>Bledius arenarius</i>	-	-	-	-	-	-	1.1	-	-	-	-
<i>Helophorus</i> spec.	-	-	1.6	-	-	-	3.3	-	-	-	-
Hydrophiloidea unident.	-	-	1.6	-	-	1.2	2.2	-	-	-	-
<i>Sphaeridium</i> spec.	-	-	-	-	-	-	7.8	1.1	-	-	-
Histeridae unident.	-	-	1.6	-	4.3	1.2	7.8	5.6	-	-	-
<i>Geotrupes stercorarius</i>	-	-	6.6	-	10.0	1.2	4.4	-	2.3	-	-
<i>Amphimallon solstitialis</i>	-	1.3	-	-	-	1.2	-	-	-	-	-
<i>Aphodius</i> spec.	-	-	4.9	-	-	-	14.4	2.2	-	-	-
<i>Aphodius distinctus</i>	-	-	1.6	-	-	-	-	-	-	-	-
<i>Cassida</i> spec.	-	-	-	-	-	-	-	-	-	-	4.2
Curculionidae unident.	-	-	6.6	-	5.7	3.5	16.7	8.9	-	-	25.0
<i>Philopodon plagiatus</i>	-	-	-	-	-	-	-	-	9.3	-	4.2
<i>Otiorhynchus</i> spec.	1.6	-	1.6	-	2.9	1.2	1.1	-	2.3	-	-
<i>Hyllobius abietis</i>	-	-	-	-	-	-	1.1	1.1	18.6	4.8	-
<i>Polydrusus cervinus</i>	-	1.3	-	-	-	-	-	1.1	-	-	-
<i>Cleonus piger</i>	-	-	-	-	-	-	1.1	-	-	-	-
Apioninae unident.	-	-	-	-	1.4	-	-	-	2.3	-	-
<i>Phyllobius</i> spec.	-	-	6.6	-	4.3	-	4.4	1.1	-	-	12.5
<i>Sitona</i> spec.	-	-	1.6	-	-	-	1.1	-	-	-	-
<i>Curculio</i> spec.	-	-	-	-	-	-	1.1	-	-	-	-
<i>Barynotus obscurus</i>	-	-	-	-	-	-	1.1	-	-	-	-
Hymenoptera unident.	-	-	-	4.8	-	-	2.2	-	2.3	-	-
Ichneumonidae unident.	-	-	-	-	-	-	-	-	2.3	-	-
Myrmicinae unident.	1.6	-	1.6	-	-	1.2	-	2.2	2.3	-	-
<i>Formica</i> spec.	3.2	-	-	-	-	-	-	1.1	9.3	-	-
<i>Myrmica rubra</i>	-	-	-	-	-	-	-	1.1	-	-	-
Vespidae unident.	-	-	-	-	-	-	-	-	-	-	4.2
Trichoptera larvae unident.	-	-	-	-	-	-	-	-	2.3	-	-
Lepidoptera larvae unident.	-	-	-	-	-	-	-	2.2	-	-	-
<i>Noctua pronuba</i>	-	-	-	-	-	-	-	1.1	-	-	-
Diptera unident.	-	-	-	-	-	-	1.1	-	-	-	-
Brachycera unident.	-	1.3	-	-	1.4	-	1.1	2.2	-	-	-
Brachycera (larvae) unident.	-	-	-	-	-	-	-	-	-	42.9	-
<i>Tipula paludosa</i>	-	1.3	-	-	2.9	5.8	-	1.1	60.5	-	-
<i>Tipula paludosa</i> (Eg)	-	-	-	-	1.4	5.8	2.2	-	58.1	-	-
<i>Tipula</i> spec. (larvae)	3.2	-	-	-	-	-	-	-	-	-	-
Bibionidae unident.	-	-	-	-	-	-	1.1	-	-	-	20.8
Asilidae unident.	-	-	1.6	-	-	-	-	-	-	-	-
Scatophagidae unident.	-	-	1.6	-	-	-	4.4	-	-	-	-

Table 3: continued...

Food item	Friedrichskoog				Hamburger Hallig				Amrum		
	Incubation	Chick rearing	Incubation	Chick rearing	Incubation	Chick rearing	Incubation	Chick rearing	Incubation	Chick rearing	Incubation
	2005	2005	2006	2006	2005	2005	2006	2006	2005	2005	2006
CHORDATA											
Teleostei unident.	-	1.3	1.6	4.8	1.4	1.2	-	8.9	-	-	4.2
Clupeidae unident.	-	-	-	-	1.4	1.2	-	-	2.3	-	-
<i>Clupea harengus</i>	-	-	-	-	1.4	-	-	3.3	-	-	-
<i>Osmerus eperlanus</i>	1.6	1.3	3.3	-	1.4	1.2	-	-	-	-	-
<i>Gasterosteus aculeatus</i>	-	-	-	4.8	-	-	12.2	1.1	-	-	-
<i>Gobius niger</i>	-	-	-	-	-	-	1.1	-	-	-	-
<i>Pomatoschistus spec.</i>	-	1.3	-	-	-	-	6.7	-	2.3	-	-
<i>Pomatoschistus minutus</i>	-	-	-	-	-	-	1.1	1.1	-	-	-
Pleuronectiformes unident.	-	-	-	-	-	-	1.1	-	-	-	-
<i>Arnoglossus laterna</i>	-	-	-	-	-	-	1.1	-	-	-	-
<i>Pleuronectes platessa</i>	-	2.5	-	-	-	-	-	-	-	-	-
Cyprinidae unident.	-	-	-	-	1.4	-	-	-	-	-	-
Aves unident.											
<i>Larus ridibundus</i> (eg)	-	-	3.3	-	1.4	3.5	1.1	5.6	-	4.8	-
<i>Larus ridibundus</i> (chick)	-	1.3	13.1	14.3	1.4	1.2	12.2	5.6	-	-	4.2
Passeriformes unident.	1.6	3.8	-	-	-	-	-	1.1	-	-	-
3.2	-	-	-	-	-	-	-	1.1	-	-	-
Mammalia unident.											
<i>Talpa europaea</i>	3.2	-	-	-	2.9	8.1	2.2	6.7	-	-	-
<i>Sorex araneus</i>	-	-	-	-	-	-	-	1.1	-	-	-
<i>Sorex minutus</i>	-	-	-	-	1.4	-	-	-	-	-	-
Muridae unident.	1.6	2.5	1.6	-	2.9	2.3	-	-	-	-	-
<i>Micromys minutus</i>	1.6	-	-	-	-	1.2	-	-	-	-	-
Arvicolidae unident.	-	-	-	-	-	1.2	-	-	2.3	-	-
<i>Ondatra zibethicus</i>	3.2	-	-	-	-	1.2	-	-	-	-	-
<i>Microtus arvalis</i>	-	-	-	-	-	-	-	-	-	4.8	-
-	-	-	-	-	1.4	4.7	3.3	13.3	-	-	-
PLANT MATERIAL											
Gras	61.9	19.0	49.2	4.8	97.1	68.6	54.4	53.3	44.2	19.5	37.5
Seeds/Wheat	34.9	-	9.8	-	41.4	28.0	14.4	15.6	14.0	19.5	16.7
WASTE											
1.6	2.5	-	4.8	-	3.5	2.2	2.2	20.9	19.5	-	-

Table 4: Frequency of occurrence [%] of 11 prey categories in 648 black-headed gull pellets from three colonies, two seasons and two years (terr. arthrop. = terrestrial arthropods).

	Friedrichskoog				Hamburger Hallig				Amrum		
	2005		2006		2005		2006		2005		2006
	Incubation stage	Chick stage	Incubation stage	Chick stage	Incubation stage	Chick stage	Incubation stage	Chick stage	Incubation stage	Chick stage	Incubation stage
n pellets	63	79	61	21	70	86	90	90	43	21	24
Insects / terr. arthrop.	57	14	67	10	87	72	78	63	100	52	88
Earthworms	63	14	48	5	93	64	51	47	21	5	38
Molluscs	17	10	30	24	21	8	22	21	12	24	21
Polychaetes	22	28	13	14	3	7	4	22	5	10	25
Crustaceans (tidal flats)	30	66	34	52	4	20	12	24	9	29	29
Crustaceans (offshore)	3	4	5	5	-	2	1	2	-	5	4
Fish	2	5	5	10	6	2	17	13	5	-	4
Birds	5	5	16	14	3	5	13	13	-	5	4
Mammals	10	3	2	-	9	16	6	21	2	5	0
Plant material	62	19	52	5	97	70	59	54	49	29	42
Waste	2	3	-	5	-	3	2	2	21	19	-

As revealed by CCA, the 11 food components differed most intensively between the three colonies, moderately between the two seasons and least between the two years (as can be seen by the location of the combinations of colonies, seasons and years in the ordination diagram, Fig. 7). The strongest inter-colony difference was found between FKoog and Amrum, which has been expected.

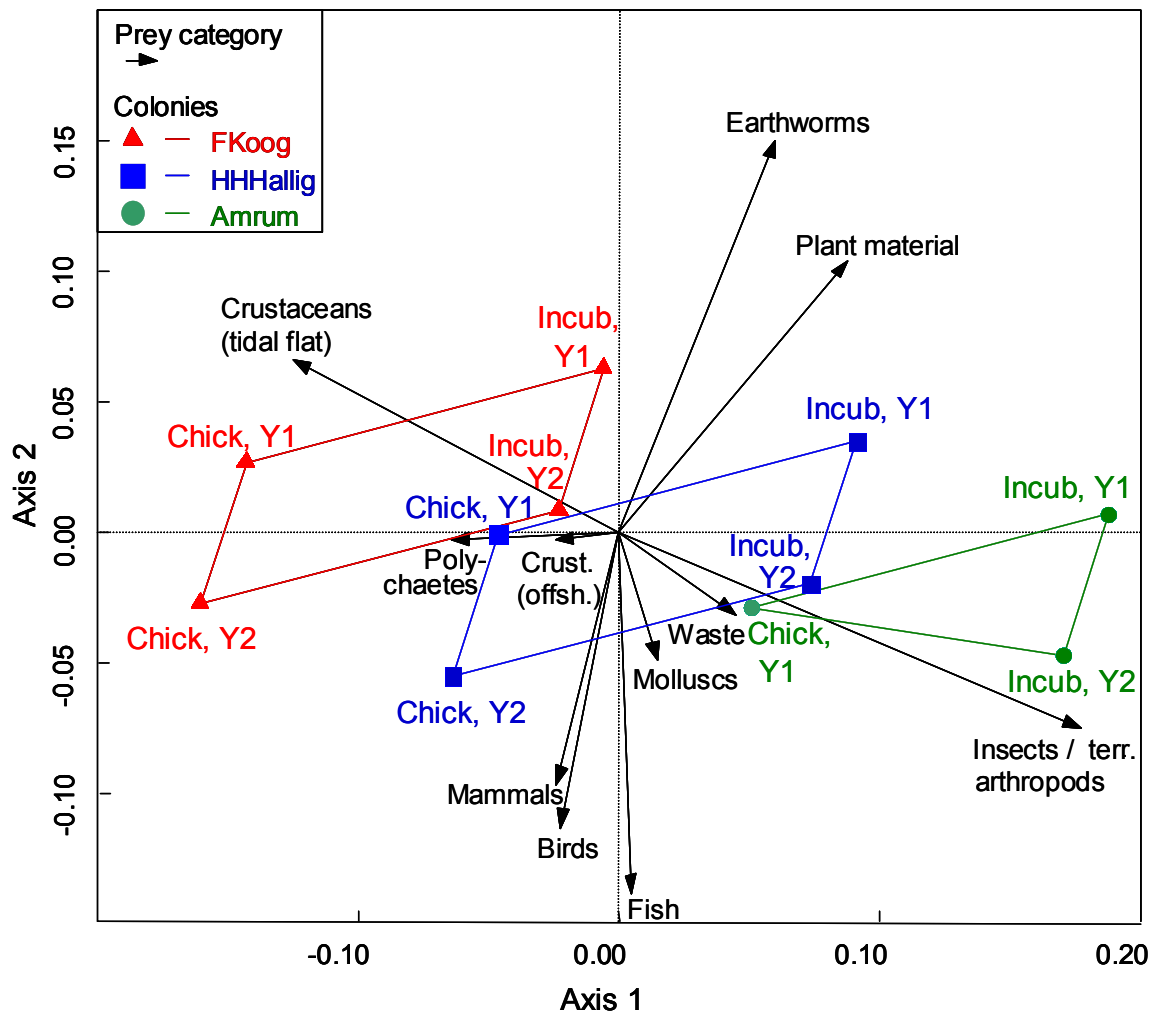


Fig. 7: Canonical Correspondence Analysis of 11 prey categories in pellets sampled in different colonies, seasons and years (Incub = incubation; Chick = chick-rearing; Y1 = year 2005; Y2 = year 2006; terr. arthrop. = terrestrial arthropods; Crust. (offsh.) = crustaceans offshore).

Origin of food and seasonal effects

For most combinations of colonies, seasons and years, food originating from terrestrial habitats dominated in pellets (despite of FKoog during chick-rearing in both years; Table 5). Unlike our assumptions, the colony of FKoog showed the highest proportion of marine prey, while HHHallig and Amrum mainly revealed food components from terrestrial habitats.

There was a consistent seasonal switch in feeding habitats at all three colonies and in both years, with more gulls apparently foraging in marine compared to terrestrial habitats during the chick-rearing vs. the incubation stage (Table 5). This switch was most

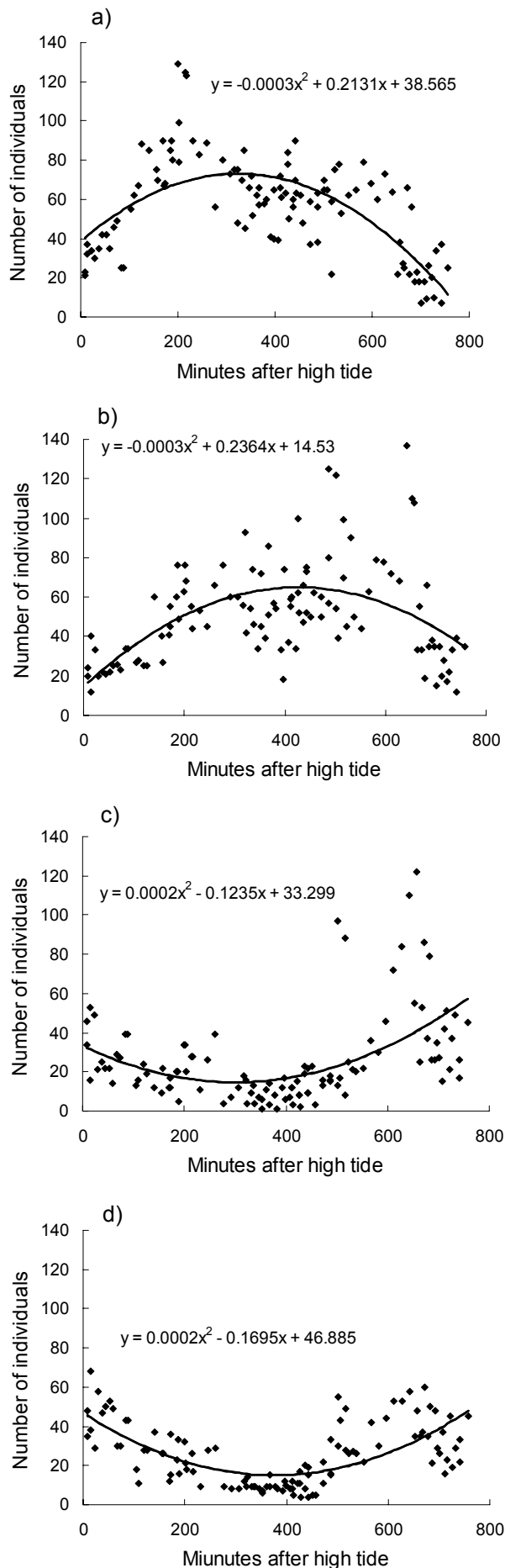
Table 5: Proportion of pellets with food items originating from terrestrial, marine or both habitats.

	2005 Incubation		2005 Chick stage		2006 Incubation		2006 Chick stage	
	terrestrial marine	terrestrial & marine	terrestrial marine	terrestrial & marine	terrestrial marine	terrestrial & marine	terrestrial marine	terrestrial & marine
Fkoog	38%	40%	18%	13%	36%	20%	24%	5%
HHHallig	70%	30%	71%	14%	63%	4%	46%	38%
Amrum	81%	19%	48%	24%	33%	8%	-	-

profound for the colony of Fkoog. Furthermore, the proportion of pellets consisting of both marine and terrestrial prey decreased during the chick-rearing stage (despite of Amrum in 2005 and HHHallig in 2006), indicating a more exclusive use of marine foraging habitats and a lower “mixed” habitat utilisation (Table 5). The LME revealed significant differences in origin of food between colonies (effect of intercept: 2.13; $p < 0.001$; effect of colony: -0.19; $p < 0.001$; variance of random factor: < 0.001 ; variance of residual: 0.85). ANOVA comparing LME and LM detected a significant improvement of the model adding season nested in year as random factor.

Flight activity

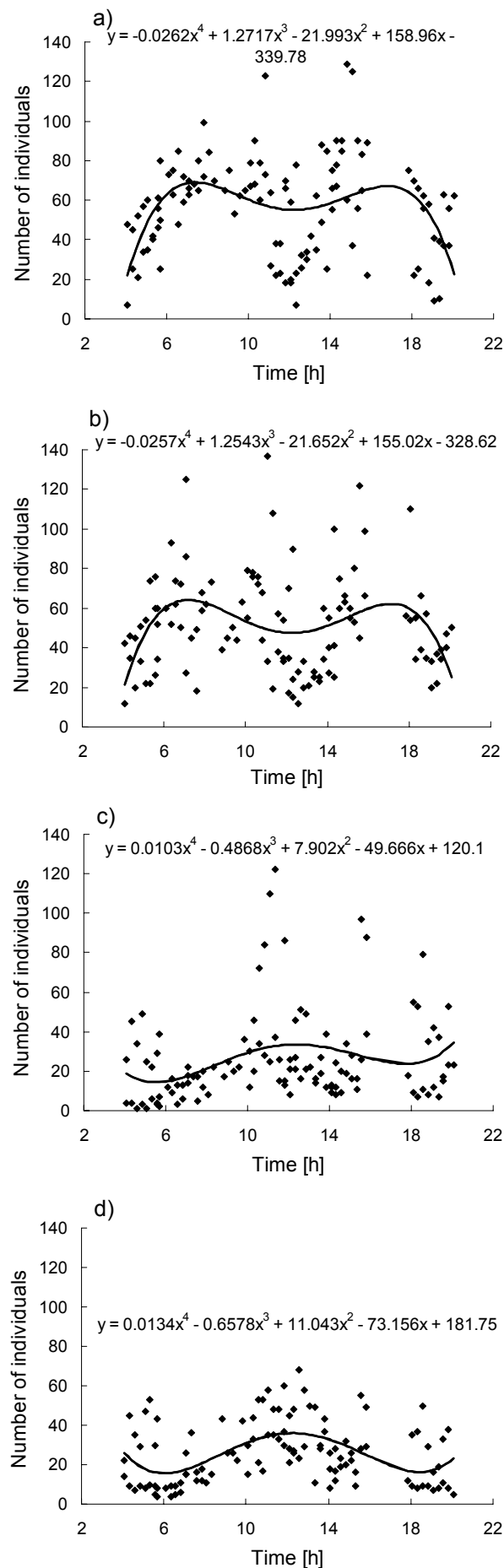
Flight activity of black-headed gulls was clearly related to tide, fitting best a quadratic function (Fig. 8a-d; for statistical values see figure legend). Patterns of gulls that used the tidal flats / offshore area and those that used the mainland were complementary: The former individuals revealed peak numbers during low tide (Fig. 8a-b), whereas the latter showed lowest flight activity during low and highest values during high tide (Fig. 8c-d). Peak numbers of gulls that were leaving the colony heading towards the tidal flats / offshore area and of those coming back in relation to tide differed slightly: Individuals leaving the colony reached highest values shortly before low tide, indicating most frequent foraging during ebb water, while individuals returning to the colony reached highest values shortly after low tide, during early flood (Fig. 8a-b). Generally, total flight activity of gulls using the mainland was significantly lower compared to those using the tidal flats / offshore (Mann-Whitney U-test: $U = 1841.5$; $N_{\text{counts mainland}} = 110$; $N_{\text{counts tidal flats / offshore}} = 110$; $p < 0.001$).



Flight activity in relation to time of day corresponded best with a 4th order polynomial function (Fig. 9a-d, for statistical values see figure legend), although the correlation coefficient in all cases was weaker compared to the correlation between flight activity and tide (see above). Gulls using the tidal flats / offshore area showed two peaks of flight activity, both in the morning and in the evening hours, while flight activity decreased during mid-day. During sunset and sunrise, flight activity was lowest (Fig. 9a-b). Gulls using the mainland showed complementary patterns: Flight activity peaked during mid-day, while it showed lowest values in the morning and evening (Fig. 9c-d). However, the curve fit of flight activity was very weak at least for individuals leaving the colony towards the mainland (Fig. 9c).

Total flight activity of individuals using the mainland differed during the two months of observation, with significantly more individuals using the mainland during June (Mann-Whitney U-test: $U = 801$; $N_{\text{counts June}} = N_{\text{counts July}} = 68$; $p < 0.001$), while total flight activity of individuals using the tidal flats / offshore area increased slightly but not significantly during July.

Fig. 8: a) Flight activity of gulls heading from the colony to tidal flats / offshore area and b) the other way round. c) flight activity of gulls heading from the colony to the mainland and d) the other way round in relation to tide (expressed as minutes after high tide). Curve fit values: a) $R^2 = 0.46$; $F_{2;107} = 91.98$; $p < 0.001$; b) $R^2 = 0.3$; $F_{2;107} = 46.4$; $p < 0.001$; c) $R^2 = 0.26$; $F_{2;107} = 38.33$; $p < 0.001$; d) $R^2 = 0.43$; $F_{2;107} = 81.11$; $p < 0.001$.



Discussion

Seasonal changes of abundance

The seasonal abundance patterns obtained during this study fit well with other studies at the coastal zone of the south-eastern North Sea (Prüter 1982; Platteuw 1987; Gloe 2006; Chapter IV). However, all these authors mention higher numbers during autumn than during spring migration. This contrasts our study which indicates much higher numbers in the whole study area during spring at least for the mainland. As we carried out only two flights during autumn migration, our findings for this period might be biased by non-representative days of lower gull numbers. However, we are still able to show that both migration periods revealed highest numbers in general. Again in accordance with the studies mentioned above, we found lowest abundance values during winter. During that time both terrestrial and marine habitats do not seem to be able to support high numbers of black-headed gulls. A high proportion of the breeding birds of the German North Sea coast and also of migrating individuals winters in the south-eastern part of Great Britain (Horton et al. 1984; MacKinnon & Coulson 1987) or even further south.

Fig. 9: a) Flight activity of gulls heading from the colony to tidal flats / offshore area and b) the other way round. c) flight activity of gulls heading from the colony to the mainland and d) the other way round in relation to time of day [UTC]. Curve fit values: a) $R^2 = 0.17$; $F_{2;105} = 13.9$; $p < 0.001$; b) $R^2 = 0.13$; $F_{2;105} = 12.95$; $p < 0.001$; c) $R^2 = 0.09$; $F_{2;105} = 2.17$; not significant; d) $R^2 = 0.23$; $F_{2;105} = 10.65$; $p < 0.001$.

The utilisation of marine and terrestrial foraging habitats (as revealed by aerial and ship-based surveys) changed obviously between the seasons (Fig. 5). A pronounced habitat switch from the mainland to the offshore area and tidal flats occurred between the incubation and chick-rearing period (Fig. 5b-c). This switch was reflected by a higher proportion of marine food in all three sampled colonies. A more exclusive use of the marine habitat is indicated by a reduced number of pellets with mixed food (i.e. samples with both terrestrial and marine prey) and also by lower numbers of gulls heading towards the mainland compared to the tidal flats / offshore area. Utilisation of marine resources eventually peaked during autumn migration (Fig. 5d). Subsequently, possible reasons for the switch between terrestrial and marine habitats are discussed.

Habitat switching

Our study clearly showed that habitat switches are an important feature in the use of the coastal zone by black-headed gulls. In general, we found two temporal levels of habitat switch: (1) A regular short-term habitat switch according to the tidal cycle (and partly also due to time of day) as revealed by flight activity patterns and (2) a seasonal habitat switch as revealed by a stronger utilisation of marine vs. terrestrial feeding habitats:

Short-term habitat switch and role of the tidal cycle

Regular daily switches of foraging habitats in relation to time of day and stage of the tide have been described before in herring gulls (*Larus argentatus*) (e.g. Verbeek 1977; Sibly & McCleery 1983). For our study it is important to consider that we only recorded abundance patterns of birds and did not document feeding actions. Thus, a certain proportion of gulls in the direct vicinity of the coastline (where a high number of individuals aggregated during the breeding period; Fig. 5b-c) might consist of individuals that used the mainland only for resting. The same uncertainty exists for the high number of individuals heading towards the mainland during high tide. For a mainland colony Brandl & Nelsen (1988) found feeding intervals of black-headed gull chicks of about 45 min equalling 21-28 feeds each day. The time frame of low tide during which the tidal flats can be exploited, however, would be too short to perform such a high number of foraging flights. This indicates that either the offshore zone or terrestrial habitats or both must have been used (in addition to tidal flats) by black-headed gulls for foraging. The high proportion of pellets containing both terrestrial and marine food items supports this. It must be considered, though, that feeding frequency and length of foraging flights might differ between coastal and mainland colonies (Gorke 1990).

The strong correlation between flight activity and tide during the whole breeding period indicates the high importance of the marine area for at least the colony of FKooG. The maximum flight activity of gulls heading towards the marine area was reached before low tide, indicating strongest feeding activity during ebb water. This foraging behaviour has already been described as beneficial for seabirds, as many benthic

organisms are best available on the edge of the retreating water (Crook 1953; Gorke 1990; but see Burger 1976).

Seasonal habitat switching

For seasonal changes in habitat use there appear to be three main reasons: (1) Prey depletion and density-dependent effects causing competition (Ashmole 1963; Gorke & Brandl 1986; Birt et al. 1987; Lewis et al. 2001); (2) energetic or nutritional demands of growing chicks (Spaans 1971; Hartwig & Hüppop 1982; Pierotti & Annett 1990; 1991); (3) changing quality of different foraging habitats as determined by abundance and quality of prey species.

We can assume that either one of these factors or a combination of the three might explain the habitat switch from terrestrial to marine foraging habitats in the late breeding season. In contrast to inland colonies where black-headed gulls have to increase their foraging radius during the breeding season (Gorke & Brandl 1986), black-headed gulls of the North Sea coast showed constant foraging radii (Gorke 1990). Thus, prey depletion caused by the birds themselves should not be considered as a main effect. Switch of food as a consequence of dietary demands of hatched or growing chicks has been described before in gulls (Spaans 1971; Annett & Pierotti 1989). However, prey originating from marine habitats has not generally higher energetic values than terrestrial food. In our study, the strongest increase of abundance values in pellets was found in shore crabs (Table 4). This food type does not have a higher energy value compared to many terrestrial prey species (Cummins & Wuycheck 1971). Spaans (1971) as well as Annett & Pierotti (1989) described a high importance of highly energy-rich fish in gull diets during the chick-rearing period. In contrast, our results do not show a higher proportion of fish or other food of high energy in the diet (except a higher proportion of terrestrial mammals in HHHallig during chick-rearing; Table 4). Potentially, food originating from terrestrial habitats would be sufficient to rear black-headed gull chicks despite of increasing energy demands of growing chicks. Black terns (*Chlidonias niger*) are able to rear their chicks on a diet dominated by insects showing only a slight increase of fish with nestlings age (Gilbert & Servello 2005). However, it is important to consider, that energy content of prey is not the only issue affecting prey choice of seabirds. Pierotti & Annett (1990, 1991) explained the preference for food of lower energetic value by gulls with other nutritional components, such as calcium, which is essential for the development of bones. The increasing utilisation of shore crabs (Table 4) might be a suitable source for calcium.

Thus, we can conclude that the quality of feeding habitats (i.e. sites showing high abundance and quality of prey species) might play the most important role to cause habitat switch. Indeed, there seems to be a general increase in the quality of the marine area as foraging habitat for black-headed gulls from early summer to autumn: (1) Total biomass of the macro-benthos community on tidal flats reaches peak values during the late breeding season / early autumn (Beukema 1974; Curtis et al. 1985; Stolpmann

2004). (2) Individual benthic organisms reach highest qualities for predators during that time as a consequence of mass gain (e.g. Beukema 1974). This would equal a higher energy intake rate per unit foraging time. Oppositely, the quality of the terrestrial feeding habitat seems to decrease during the late breeding period, which is reflected by the lower numbers of black-headed gulls recorded during aerial surveys, lower numbers of gulls flying towards the mainland and a lower proportion of food originating from terrestrial habitats. Most probably the main reasons for decreasing foraging site quality are reduced farming activities (Chapter IV) and high vegetation that reduces access to soil invertebrates (Morris 2000; Butler & Gillings 2004; Devereux et al. 2006).

Inter-colony diet variation

We were able to show distinct dietary differences between the three colonies, however, we could not confirm our hypothesis of intensive area utilisation in the vicinity of the breeding colonies. In contrast, our results revealed the opposite of what was expected: In FKoog we found the highest proportion of food originating from marine habitats of all colonies (although a high proportion of terrestrial food was expected). In addition, we found significantly more individuals heading towards the tidal flats / offshore area than towards the mainland. At HHHallig and Amrum we found highest proportions of terrestrial food (although a higher proportion of marine food was expected). Indeed we had expected the strongest difference between FKoog and Amrum, which our findings stated (Fig. 7 and Table 4). However, we assumed highest proportions of marine prey in Amrum and lowest in FKoog. Our results revealed the opposite. Thus, we may conclude that location of foraging habitats does not seem to influence foraging behaviour at first hand. Moreover, it can be assumed that foraging habitat quality might again play a more crucial role, rather than moderate distances to foraging sites.

The quality of the marine area near FKoog is potentially higher compared to the other two colonies for a number of reasons: (1) This area holds extensive fine grained tidal flats that are particularly rich of invertebrates (Stolpmann 2004). (2) The intensity of Brown Shrimp fishery in this area is higher compared to the other regions (Ehrich et al. 2006; own unpubl. data). The high number of pellets from FKoog with undersized shrimps that probably originate from fishing vessels as discards, support this conclusion. (3) High breeding pair numbers of particularly herring and common gulls, that have the closest foraging niche overlap with black-headed gulls (Kubetzki & Garthe 2003), might cause interspecific competition at least in the marine zone. Such colonies are located closest to Amrum and HHHallig. Thus, the high proportion of terrestrial prey in HHHallig and Amrum might also be caused by intensive foraging on islands and mainland to avoid competition in the marine area. The excellent foraging conditions near FKoog are confirmed by a consistent increase of breeding pair numbers in this colony during recent years, while the colonies of Amrum and HHHallig showed a stagnating trend (Hälterlein unpubl. data). The high-quality foraging conditions in FKoog might account for a potentially longer distances to foraging grounds.

Conclusions

Although we found increasing use of the marine feeding habitats during the late breeding period in all three colonies and both years of sampling, the overall proportion of food originating from the marine area can be considered low when compared to findings of other studies conducted during the last 20 years (Table 6).

Table 6: Historical data taken from studies on black-headed gull food, originating from marine and terrestrial foraging habitats. Values indicate frequency of occurrence of prey items in pellets / faeces [%].

Study	Gorke (1990)	Dernedde (1993)	Kubetzki & Garthe (2003)	Kubetzki & Garthe (2003)
Period	Incubation 1986-1988 ⁽¹⁾	Post breeding 1991 ⁽²⁾	Incubation 1997	Chick rearing 1997
Study area	Island of Norderoog	Island of Sylt	Island of Juist	Island of Juist
Marine prey				
Bivalves	59	17	86	42
Gastropods	< 1	11	20	16
Polychaetes	43	44	28 ⁽⁴⁾	11
Crustaceans	10	18 ⁽³⁾	8	18
Fish	19	43	8	11
Terrestrial prey				
terrestrial arthropods	11	17	13	26
Oligochaetes	?	13	6	8
Birds	< 1	?	0	0
Eggs	< 1	?	2	0
Mammals	< 1	?	1	0
Plant material	40	19	14	45
Refuse	< 1	?	0	3

⁽¹⁾ Mean values of 327 pellets collected during the three years.

⁽²⁾ Mean values of 27 faeces samples from September and October; only selected food components were available.

⁽³⁾ Crustaceans: Mean values of presence of *Crangon crangon*, *Gammarus spec.*, *Carcinus maenas*.

⁽⁴⁾ Polychaetes: Mean values of 83 pellets and 25 faeces.

A few years ago, the proportion of marine-littoral prey in the diet of black-headed gulls was far higher compared to the findings of our study. Of course it is important to note that the reviewed studies were conducted in different sites and might be methodologically inconsistent. However, the general minor use of terrestrial feeding sites in the past years compared to our study is obvious. There are two possible reasons for this: (1) Increased interspecific competition with other gull and shorebird species and (2) a decrease of feeding site quality. Breeding pair counts showed a decrease of herring gulls during the last few years along the whole German North Sea coast (Garthe et al. 2000; Koffijberg et al. 2006). This species mainly exploits tidal flats (e.g. Kubetzki & Garthe 2003).

Additionally, a high number of migrating and breeding shorebird species (mainly mussel eaters) showed considerable declines in the study area as well (Blew et al. 2005a; 2005b; Koffijberg et al. 2006). Eventually, most recent counts also revealed that the increase of breeding pairs of black-headed gulls themselves seems to have stopped (Hälterlein unpubl. data). This suggests that the low utilisation of the marine area compared to previous years might indeed be a consequence of poorer habitat quality.

However, in contrast to individuals breeding inland with no access to the marine area, as well as in contrast to wading birds that are forced to utilise the tidal flats, the black-headed gull of the North Sea coast can switch intensively between foraging habitats during different stages of the tide, time of day, seasons and breeding stages. Other less opportunistic gull species at the German North Sea coast have much smaller foraging niches and consequently mainly use distinct habitat types (Kubetzki & Garthe 2003). *Larus ridibundus*, thus, must be regarded as one of the most competitive species in the whole coastal zone. Its flexible feeding strategy, switching between marine and terrestrial prey is certainly one of its success parameters. For the near future, this will most probably provide a strong basis to sustain breeding pair numbers, despite of possible substantial changes in one of the feeding habitats.

Acknowledgements

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Chapter II

At-sea distribution and behaviour of a surface-feeding seabird, the lesser black-backed gull (*Larus fuscus*), and its association with different prey

Abstract

The lesser black-backed gull (*Larus fuscus*) is a typical surface-feeding seabird with a widespread, patchy distribution in the south-eastern North Sea. During the 1990s, breeding numbers along the German North Sea coast increased exponentially. Analyses of a multiple-year data set revealed changes in the at-sea distribution, that seemed to reflect an increase in the numbers of breeding birds. Detailed recordings of feeding and resting behaviour at sea revealed distinct use of different areas by the lesser black-backed gull. Observations at sea and dietary analysis showed that swimming crabs (*Liocarcinus spec.*) are a major dietary item of this gull species. This natural food source was primarily captured close to the shore; whereas at longer distances from the coast the gulls mainly fed on other natural prey items or discarded fishes from trawlers and avoided competition with other breeding gull species. During July and August 1990 to 1995 (post-breeding period) *L. fuscus* abundance was significantly correlated with fishing effort, while in May and June there was no such correlation. Time of day was the main environmental variable influencing the gulls' flight activity and indicated an association between activity and availability of their major natural prey, swimming crabs. Distinct changes in the patterns of at-sea distribution and foraging behaviour of *L. fuscus* in the south-eastern North Sea reflect anthropogenic and natural influences in their habitats.

Introduction

In many parts of the world, seabirds choose different habitat types at sea and exhibit typical patterns of niche segregation in order to avoid competition (e.g. Hunt 1990; Ainley et al. 1992; Ribic & Ainley 1997; Hunt et al. 1998). These relationships may be even more important for closely related species like gulls (Laridae). In this context, foraging habitat selection is of primary importance (e.g. Hunt & Hunt 1973; Camphuysen 1995; Garthe et al. 1999). The four closely related breeding gull species, black-headed gull (*Larus ridibundus*), common gull (*L. canus*), herring gull (*L. argentatus*) and lesser black-backed gull (*L. fuscus*), live sympatrically along the south-eastern North Sea coast. For the lesser black-backed gull, a particularly pronounced and widespread offshore distribution even during the reproductive period, has been found in recent years (Camphuysen 1995; Kubetzki & Garthe 2003). This species also shows dietary differences from the other breeding gull species, indicating specialised foraging strategies (Kubetzki & Garthe 2003). Both distribution and foraging behaviour must be considered to be related to the strong population growth of this species along the south-eastern North Sea coast (Garthe et al. 1999; 2000; Dierschke & Hüppop 2003; Kubetzki & Garthe 2003).

However, it is still unclear whether the distribution patterns of *Larus fuscus* at sea have changed during the last few years as a result of changes in the marine food supply or because of the exponential growth of the population that has been recorded since the mid-1980s (Garthe et al. 2000; Fig. 3) and that might have forced the lesser black-backed gull to re-distribute in particular areas to avoid competition. It is also not clear whether certain areas at sea are used more intensively than others suggesting the use of particular natural or anthropogenic food sources.

Changes of distribution and habitat utilisation patterns of this gull species have never been analysed using a multiple-year data set, nor have they been examined in relation to its feeding behaviour and diet. Such approach could reveal areas of special importance and with different ecological function to this gull as well as major historical changes in foraging strategies and food web dynamics. In contrast to fishery by-catch and discards which are known to comprise an important supplement to its diet (e.g. Hunt & Hunt 1973; Spaans et al. 1994; Walter & Becker 1994; Camphuysen et al. 1995; Walter & Becker 1994), the role of natural food (i.e. food unconnected with anthropogenic activities) is still unclear. There are several indications that this gull is able to live on pelagic prey species hunted in a natural way (Goethe 1975; Sjöberg 1989; Strann & Vader 1992), but it is still not known what particular role this natural food plays in the gull's diet and in which way it may effect its at-sea distribution with regard to its high population numbers.

In this study, multiple-year data sets on lesser black-backed gull distribution from 1990 to 2002 have been combined with newly developed recording schemes of behavioural patterns at sea using a standardised method (Camphuysen & Garthe 2004). Habitat use and abundance as well as behaviour at sea were related to the abundance

of major prey types in diet samples collected in breeding colonies in the study area. Potential explanations for spatial and temporal patterns are presented that may help to understand the foraging strategies of this abundant surface-feeding seabird in the south-eastern North Sea.

Material and Methods

The distribution and behaviour of *Larus fuscus* at sea were investigated in the German Bight, south-eastern North Sea; the study area was 5° E to 9° E and 55° 30' N to 53° 30' N (Fig. 10). Birds were counted from the top decks of various research vessels in accordance to the method of Tasker et al. (1984) and Garthe et al. (2002). Each bird swimming within a 300 m wide transect (distance from the sides of the vessels, usually travelling at about 10 knots) was counted. Birds flying inside the transect were recorded by the 'snapshot' method; i.e. arbitrarily counting only those birds which flew into or across the transect at every full min to avoid counting any individual more than once (Tasker et al. 1984). As the probability of detecting birds swimming close to the vessel is higher than that of detecting more distant individuals, the density of swimming birds was corrected by multiplying by a correction factor of 1.3 (Garthe 1997 after Buckland et al. 1993).

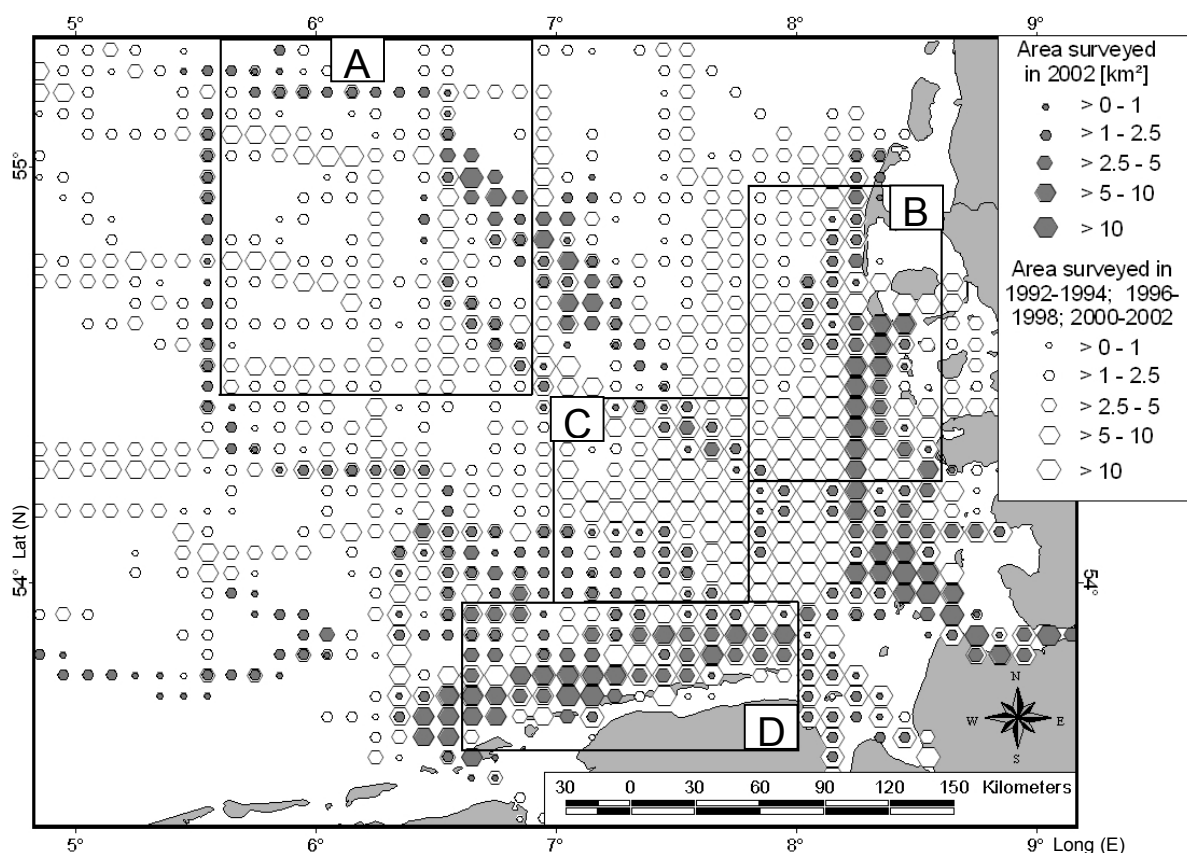


Fig. 10: Study area in the south-eastern North Sea. Open symbols indicate areas surveyed (i.e. observer effort) in 1992–1994, 1996–1998 and 2000–2002; filled symbols indicate areas surveyed for behaviour analyses in 2002 only. Boxes A to D are for statistical comparison between areas. A: Offshore; B: North Frisian; C: Central; D: East Frisian.

Densities were estimated by dividing the sum of all individuals recorded per 3' latitude x 6' longitude grid (grid cell-size equivalent to ca. 36 km²) by the total area surveyed within that grid (i.e. observer effort; open symbols in Fig. 10). The data used for investigating distribution patterns were taken from the German Seabirds at Sea database (Garthe & Hüppop 2000) Version 3.04 (September 2002) for the months May to August of the years 1990-1992, 1994-1996, and 2000-2002. To detect variation in gull distribution between the three time intervals and between different areas of the German Bight, four specific areas (boxes A to D in Fig. 10) with a similar observation effort were compared using χ^2 -tests for goodness of fit. In order to run the test, expected values for gull densities were calculated for each of the four areas.

Behaviour at sea was analysed from May to August 2002 (observer effort indicated by filled symbols in Fig. 10) following the descriptions of Ashmole (1971) and Camphuysen & Garthe (2004). We chose three different classes of behaviour: (1) Searching for natural food (gulls flying with their heads pointing down towards the sea surface or actively hunting or feeding); (2) association with fishing vessel (gulls in vicinity of an operating fishing vessel searching for discards or by-catch or resting after having fed from trawler wastes); (3) resting (gulls resting inactive on the sea surface, sleeping or preening). Different feeding techniques were also recorded as four categories: (1) Dipping (taking up prey in flight while barely touching the sea surface); (2) pecking (sitting on the water while pecking up tiny prey items); (3) shallow plunging (diving for prey); (4) surface seizing (sitting on surface while feeding on large prey which could not be swallowed at once). The three behavioural categories were analysed on a spatial and on a daily time scale applying χ^2 -statistics. For the daily scale, the day was divided into morning, mid-day and evening (3:00-8:59 h, 9:00-14:59 h and 15:00-19:59 h [UTC] respectively). Morning and evening hours were combined in order to obtain comparably large sample sizes. Prey items were recorded as often and as accurately as possible before being ingested by the gulls.

Distance to the coast is a major factor affecting seabird distributions in the German Bight (Garthe 1997), and the three behavioural categories were therefore examined as a function of this factor by calculating the distance of each central point of the 3' latitude x 6' longitude grid cells from the closest point on land (including Wadden Sea islands but excluding island of Helgoland) and comparing with gull densities in the particular grid cell using χ^2 -tests.

The distribution of gulls can be closely related to trawler presence, although this does not seem to have had any significant effect on the distribution of the lesser black-backed gull at the temporal and spatial scales studied so far (e.g. Camphuysen 1995; Garthe 1997). To test for any possible relationship at a large spatial and temporal scale, international fishing-effort data (British, Danish, Dutch, German and Norwegian trawlers) from 1990 to 1995 (Jennings et al. 1999) were compared with *L. fuscus* distribution recorded over the same period. Spearman rank-correlation was used to compare total

fishing effort in 16 ICES-rectangles with the mean densities of lesser black-backed gulls in each rectangle for two different annual periods.

The activity of gulls in a breeding colony can be influenced by various temporal, physical or meteorological factors (e.g. Burger 1976; Garthe et al. 1999). In addition to behaviour recorded at sea, flight-activity patterns were recorded near a lesser black-backed gull colony on the island of Norderney (see Fig. 11) for seven days in June and five days in July 2002. Gulls heading out to sea or returning to the colony and flying across a line of 800 m length set arbitrarily along the colony edge were counted during daylight hours. The flight activity of birds leaving and returning to the colony was calculated and compared to time of day [UTC], tide, wind force, wind direction and abundance of fishing vessels, using a 5-way ANOVA.

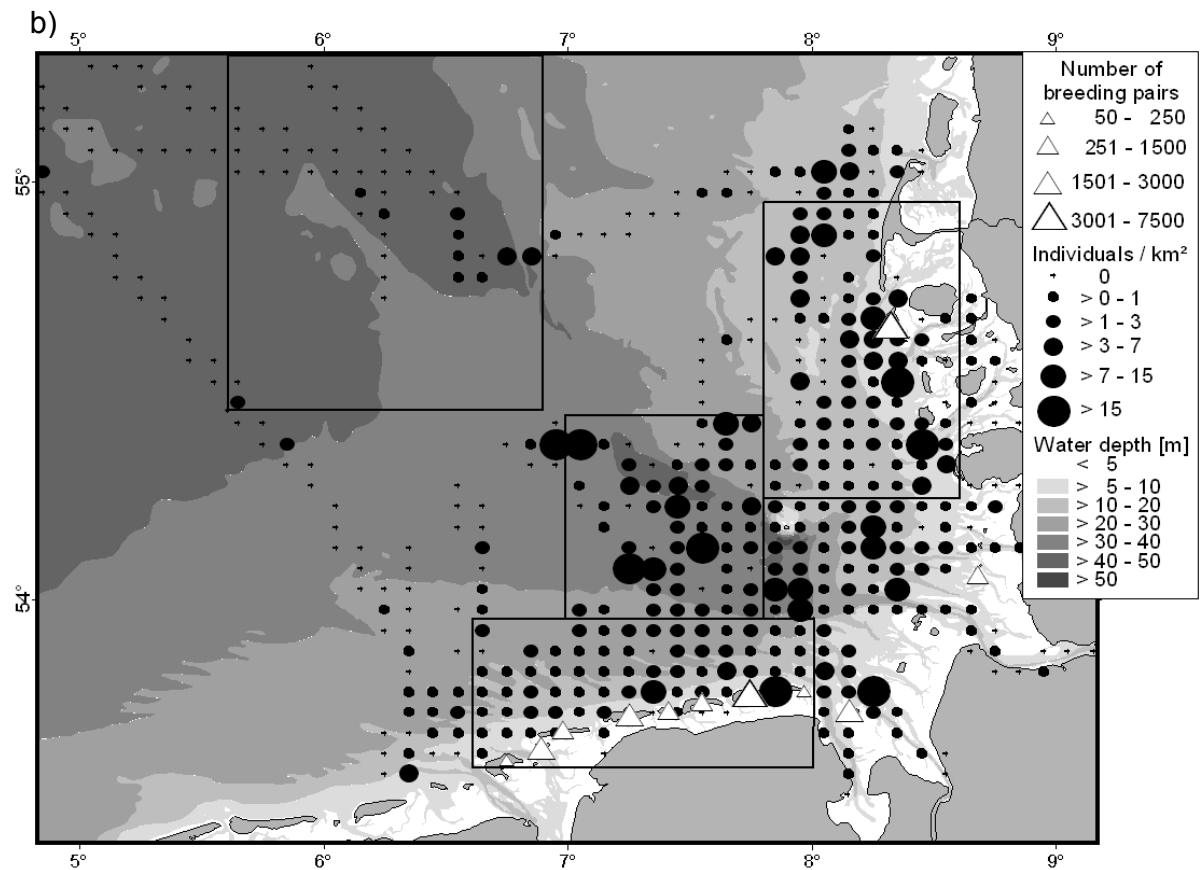
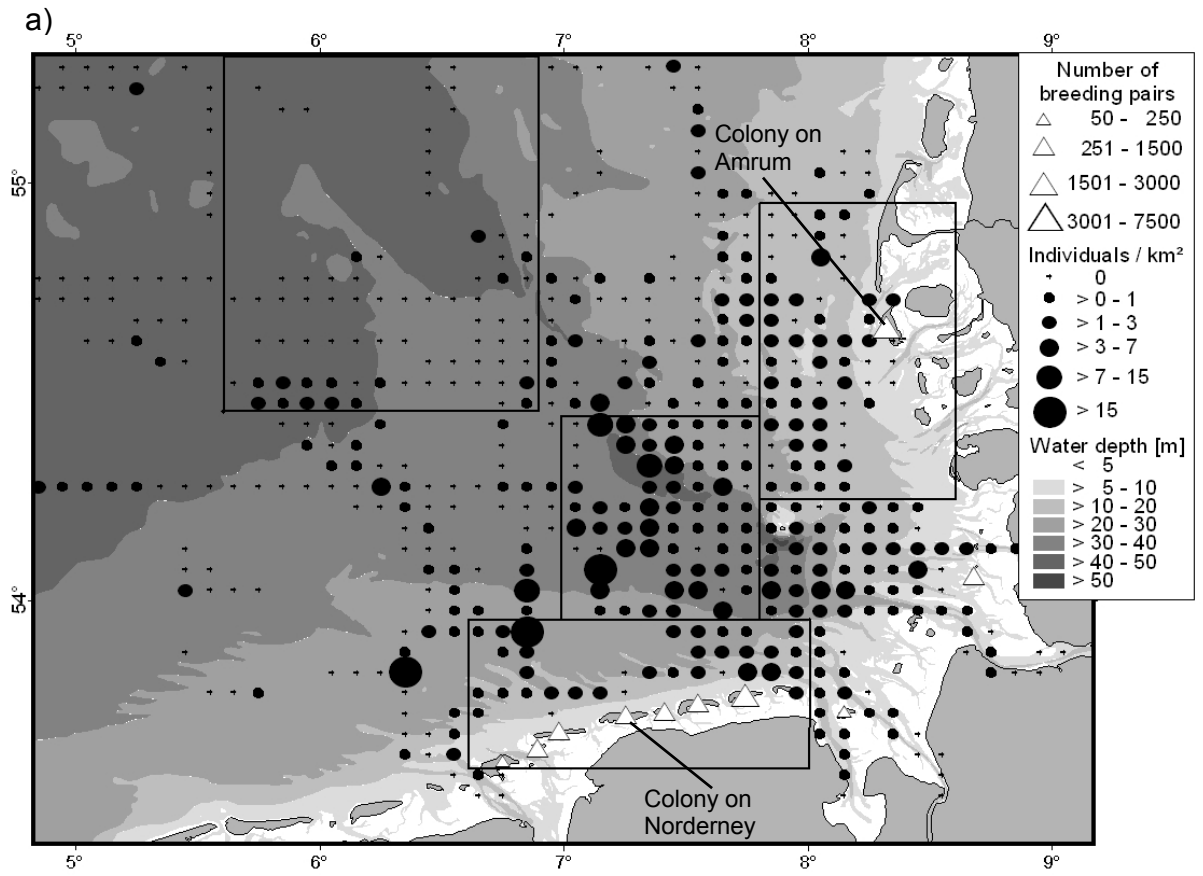
To assess the importance of prey items taken by the gulls at sea, their diet was analysed on the basis of pellets collected during the incubation and the chick-rearing period in the colony on Norderney in 2002 and in the colony on Amrum in 2003 (for location see Fig. 11). Following the method of Duffy & Jackson (1986), the frequency of occurrence of each food category was determined. Duffy & Jackson (1986) pointed out biases in the use of this method, in that hard components may be overestimated and soft items such as small fishes are likely to be underestimated. However, as the present study mainly focuses on trends in the diet of major prey categories and compares these to those in other dietary studies of the lesser black-backed gull, results using this method should be valid. More detailed analyses for the same or nearby colonies using similar methods have recently been published (Garthe et al. 1999; Kubetzki & Garthe 2003).

Results

Distribution at sea

The lesser black-backed gull showed a widespread distribution and appeared in high numbers in both coastal waters and offshore areas up to more than 100 km distance from the coast in all years (Fig. 11). Densities differed significantly between two of the four areas over the three time periods (box A: $\chi^2 = 233.86$, $df = 6$, $p < 0.001$; box B: $\chi^2 = 93.78$, $df = 6$, $p < 0.001$), whereas there was no significant difference for the boxes C and D (χ^2 -test for goodness-of-fit).

The sites of highest densities changed from 1992 to 2002: Until 1998, maximum numbers were recorded in the centre of the study area, while in 2000 to 2002 numbers near the North Frisian coast increased. This resulted in significantly different densities between the four boxes for all three time periods (1992 to 1994: $\chi^2 = 381.93$; 1996 to 1998: $\chi^2 = 298.59$; 2000 to 2002: $\chi^2 = 500.78$; $df = 6$, $p < 0.001$, respectively).



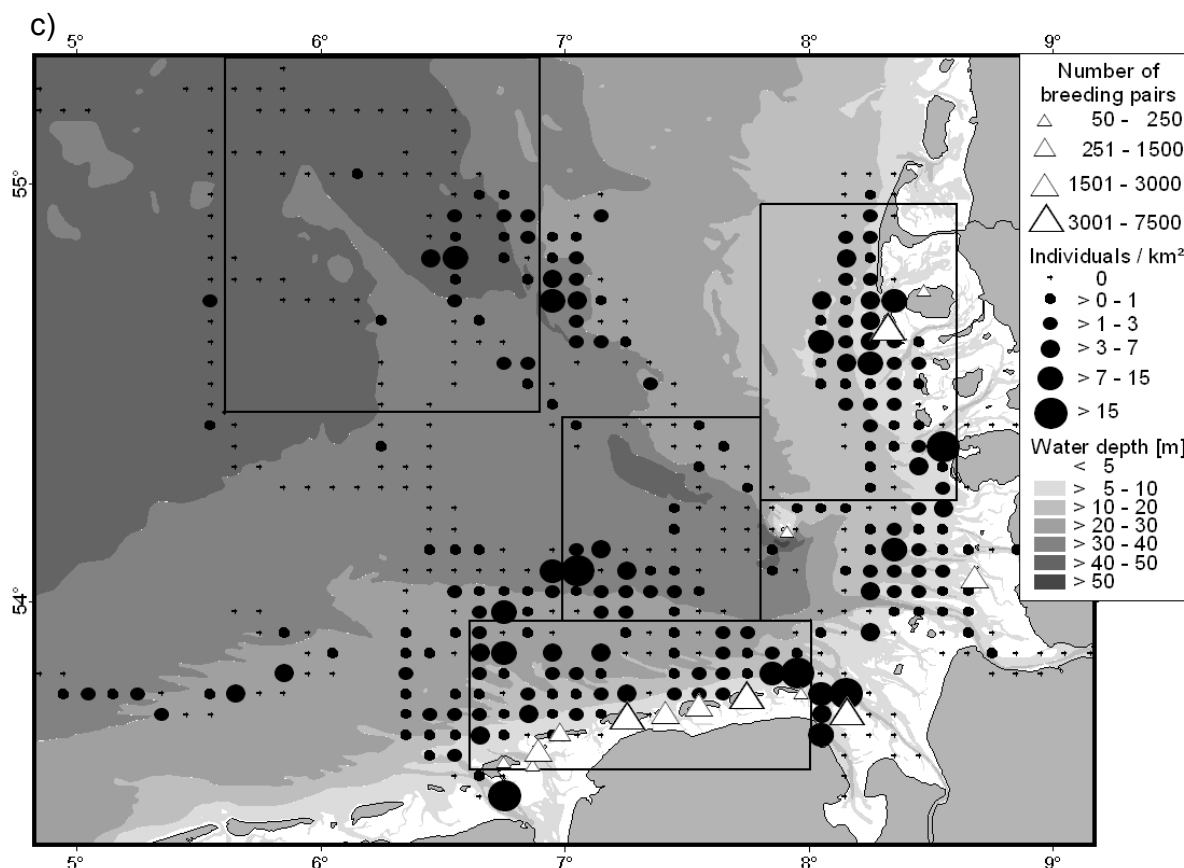
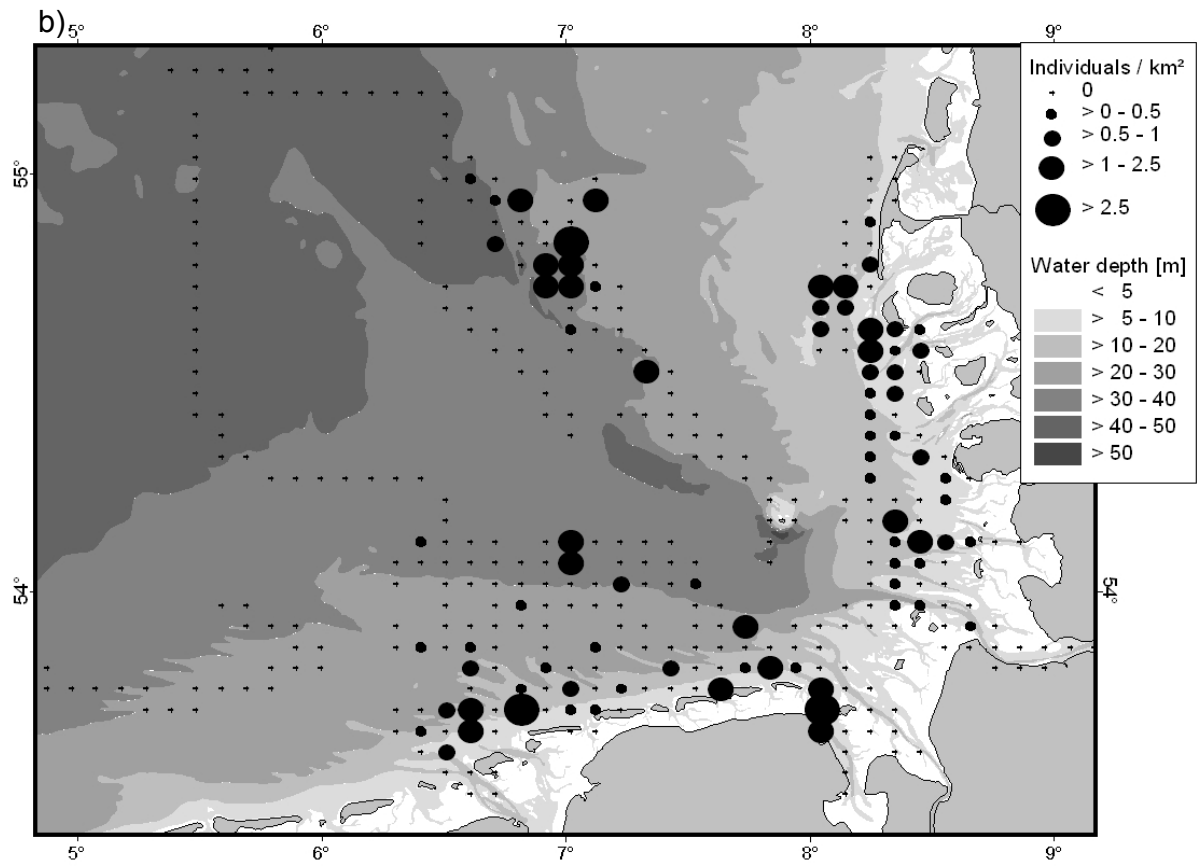
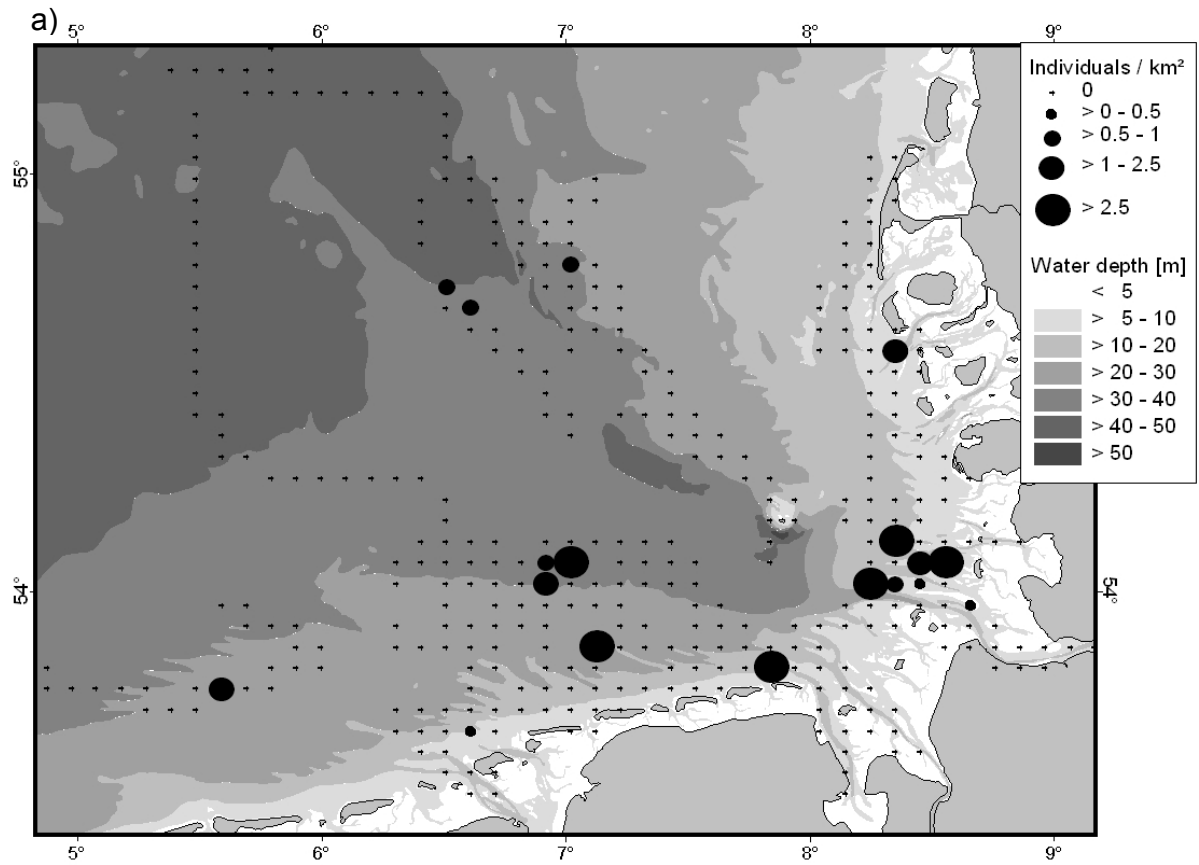


Fig. 11: Distribution of lesser black-backed gulls in May–August of the years a) 1992–1994, b) 1996–1998 and c) 2000–2002. Triangles represent breeding pair numbers (only colonies with > 50 pairs shown); data taken from Südbeck & Hälterlein (1994; 1995); Hälterlein & Südbeck (1996); Hälterlein & Südbeck (1998); Südbeck & Hälterlein (1999; 2001).

Behaviour at sea

Spatial distribution

During the research cruises in 2002, 55.3 % of all lesser black-backed gulls recorded were classified into the three behaviour categories. Most individuals were associated with fishing vessels (25.4 %) and therefore distribution of these gulls was strongly aggregated (Fig. 12a), with high numbers in coastal waters (mostly associated with shrimp trawlers) and highest numbers at 40 to 60 km distance from the shore (mostly associated with beam trawlers; see below) (Fig. 13). Birds actively searching for natural food (14 %) were much more evenly distributed and widespread over the whole study area (Fig. 12b), but appeared in highest numbers close to the shore as well as at 60 to 100 km distance from the coast (Fig. 13). Resting gulls (15.9 %) were only recorded within 60 km of the coast (Fig. 12c; Fig. 13). 44.7 % of the birds fell into no behaviour category. Densities within the six distance classes (Fig. 13) were significantly different among the four behavioural categories ($\chi^2 = 591.12$; $df = 15$; $p < 0.001$).



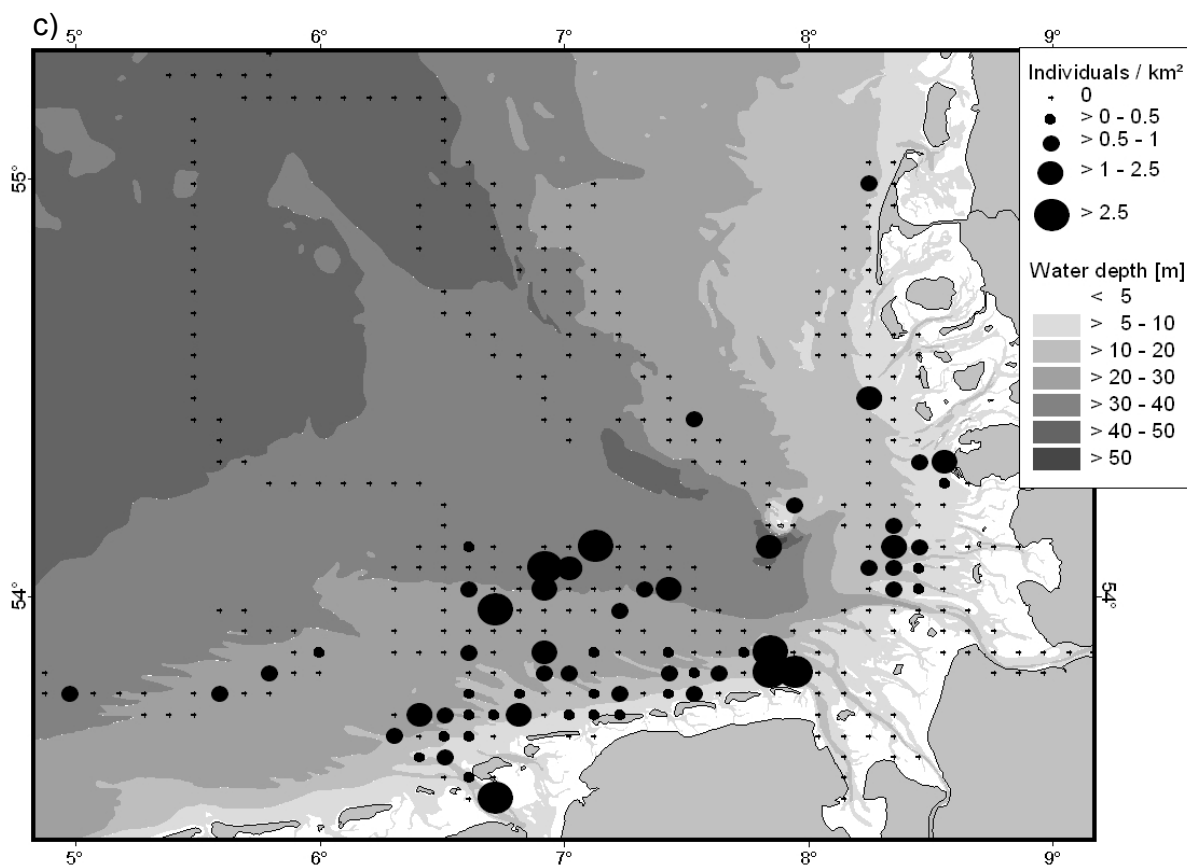


Fig. 12: Distribution of lesser black-backed gulls in May–August 2002 a) associated with fishing vessels, b) searching for or feeding on natural food and c) resting.

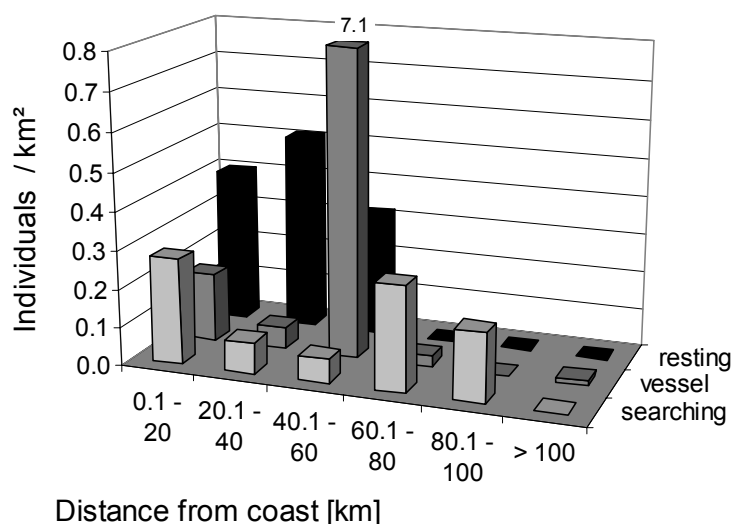


Fig. 13. Distance from coast (nearest point, including Wadden Sea islands, but excluding Helgoland) of lesser black-backed gulls resting, associated with fishing vessels (vessel) and searching for or feeding on natural food (searching).

Temporal variation in behaviour

The behaviour of lesser black-backed gulls at sea was partly influenced by time of day. The proportion of all individuals searching for natural food was highest during the morning and evening hours and decreased significantly during mid-day, whereas the proportion of gulls associated with fishing vessels showed the opposite pattern (Table 7). For resting gulls, no significant difference was recorded as a function of time of day.

Table 7: Temporal variation in behaviour and results of χ^2 -test examining behavioural differences between morning / evening and mid-day hours (n.s.: not significant).

Time of day [UTC]	No. of gulls		% displaying behaviour	χ^2 -test
	total number observed	displaying behaviour		
Searching for/feeding on natural prey				
3:00 - 8:59 and 15:00 - 19:59	551	95	17 %	$\chi^2 = 10.25$
9:00 - 14:59	1144	124	11 %	df = 1
3:00 - 19:59	1695	219	13 %	p < 0.001
Associated with fishing vessel				
3:00 - 8:59 and 15:00 - 19:59	551	19	3 %	$\chi^2 = 137.87$
9:00 - 14:59	1144	411	36 %	df = 1
3:00 - 19:59	1695	430	25 %	p < 0.001
Resting				
3:00 - 8:59 and 15:00 - 19:59	551	88	16 %	
9:00 - 14:59	1144	181	16 %	n.s.
3:00 - 19:59	1695	269	16 %	

Feeding behaviour

Items carried or hunted were recorded for lesser black-backed gulls searching for natural food. A total of 85 crustaceans (25 of these were *Liocarcinus spec.*), 39 fishes, 3 birds, 1 starfish and 1 bivalve were identified. As crustaceans seemed to be the most common food of naturally feeding individuals, this food item was studied in more detail.

First, there was a distinct spatial pattern in feeding on crustaceans in the study area. Most crustacean prey were recorded only at distances of up to 30 km from the coast (Fig. 14), and differences between the four boxes were significant ($\chi^2 = 54.39$; df = 3; p < 0.001). Second, there was a temporal variation in the feeding on crustaceans, both as a function of time of year and time of day. In regard to season, there was a significant increase in feeding events from May to August 2002 (May events 11; June events 21; July events 27; August events 41) ($\chi^2 = 19.28$; df = 3; p < 0.001) – observer effort was nearly constant during each month. In regard to time of day, 46 crustaceans were taken during the morning (0.12 crustacean consumed per gull present) and 25 during the evening (0.1 per gull) while during the mid-day hours only 14 crustaceans were taken (0.02 per gull) ($\chi^2 = 66.58$; df = 2; p < 0.001).

In addition to natural food, lesser black-backed gulls following fishing vessels were observed in high numbers (Fig. 12a; Fig. 13). However, during May and June, the months of main breeding activity, gull densities were not significantly associated with areas of highest fishing effort (data for 1990 to 1995, Spearman rank correlation; $r_s = 0.165$; not significant) as there were numerous gulls close to the shore (Fig. 15a). During July and August, the highest gull densities shifted to the areas of highest fishing effort ($r_s = 0.915$; p < 0.001, Fig. 15b).

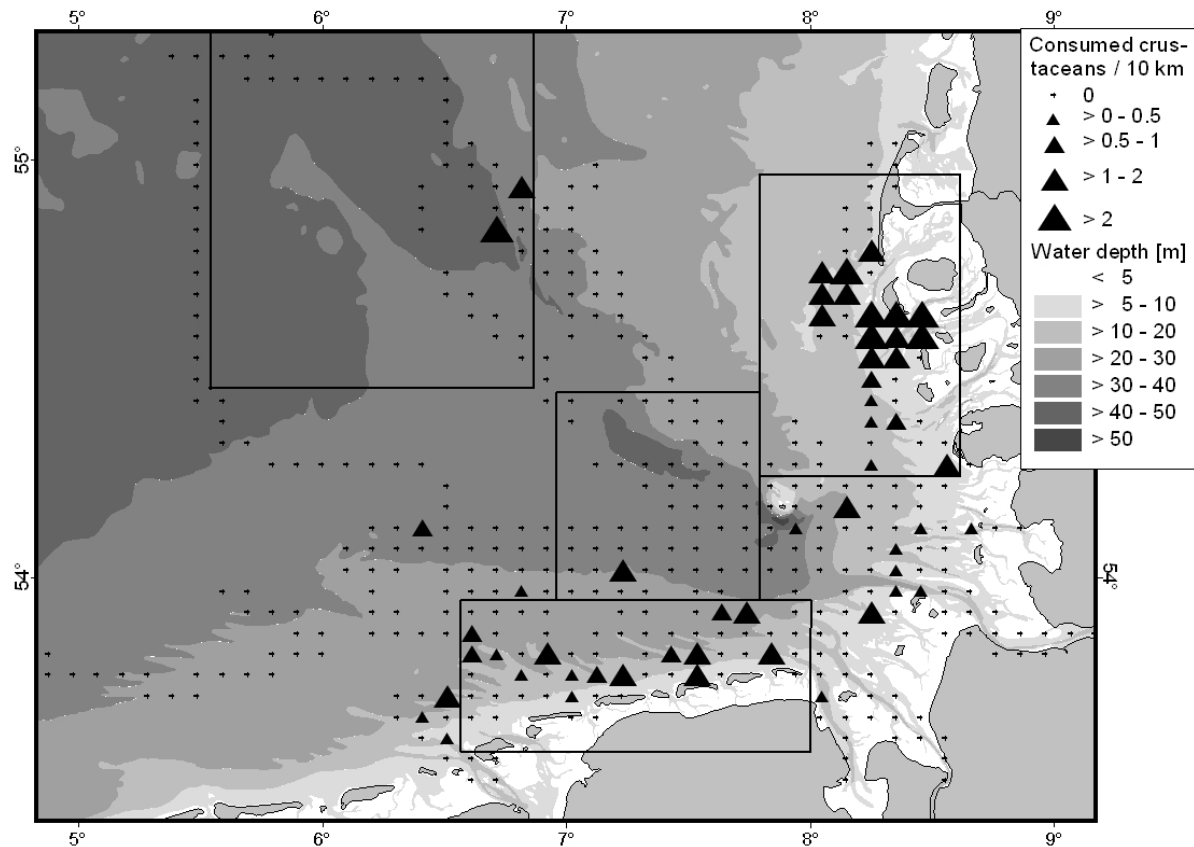


Fig. 14: Crustaceans consumed (per 10 km travelled) by lesser black-backed gulls in May–August 2002 and boxes used in statistical analyses.

Analysis of the main food items of lesser black-backed gulls from Norderney collected during the incubation period in 2002 revealed fishes and terrestrial invertebrates to be most frequent food items (both appearing in 45 % of the samples), followed by *Liocarcinus spec.* (23 %). During the chick-rearing period, *Liocarcinus spec.* was the most common prey type (44 %) with fishes ranking second (28 %) and terrestrial invertebrates less frequent (18 %). For the samples collected from Amrum in 2003 during the incubation period, *Liocarcinus spec.* was the most frequent dietary item (71 %), terrestrial invertebrates (28 %) and fishes (15 %) were less common. During the chick stage, the proportion of *Liocarcinus spec.* was slightly higher (78 %), while the proportions of terrestrial invertebrates (17 %) and fishes (7 %) were lower (see also Table 9).

Flight activity near the colony

Flight activity of lesser black-backed gulls near the colony of Norderney correlated with various factors (Table 8). The best ANOVA model was for birds leaving the colony ($R^2 = 0.51$), followed by that for birds returning to the colony ($R^2 = 0.39$). For both scenarios, time of day had a significant effect on flight activity, with a distinct pattern of strong morning and evening flight activity (means of 154.7 ± 37.5 and 195.2 ± 32.1 gulls crossed the counting line between 3:00 and 8:59 h and 15:00 and 19:59 h respectively).

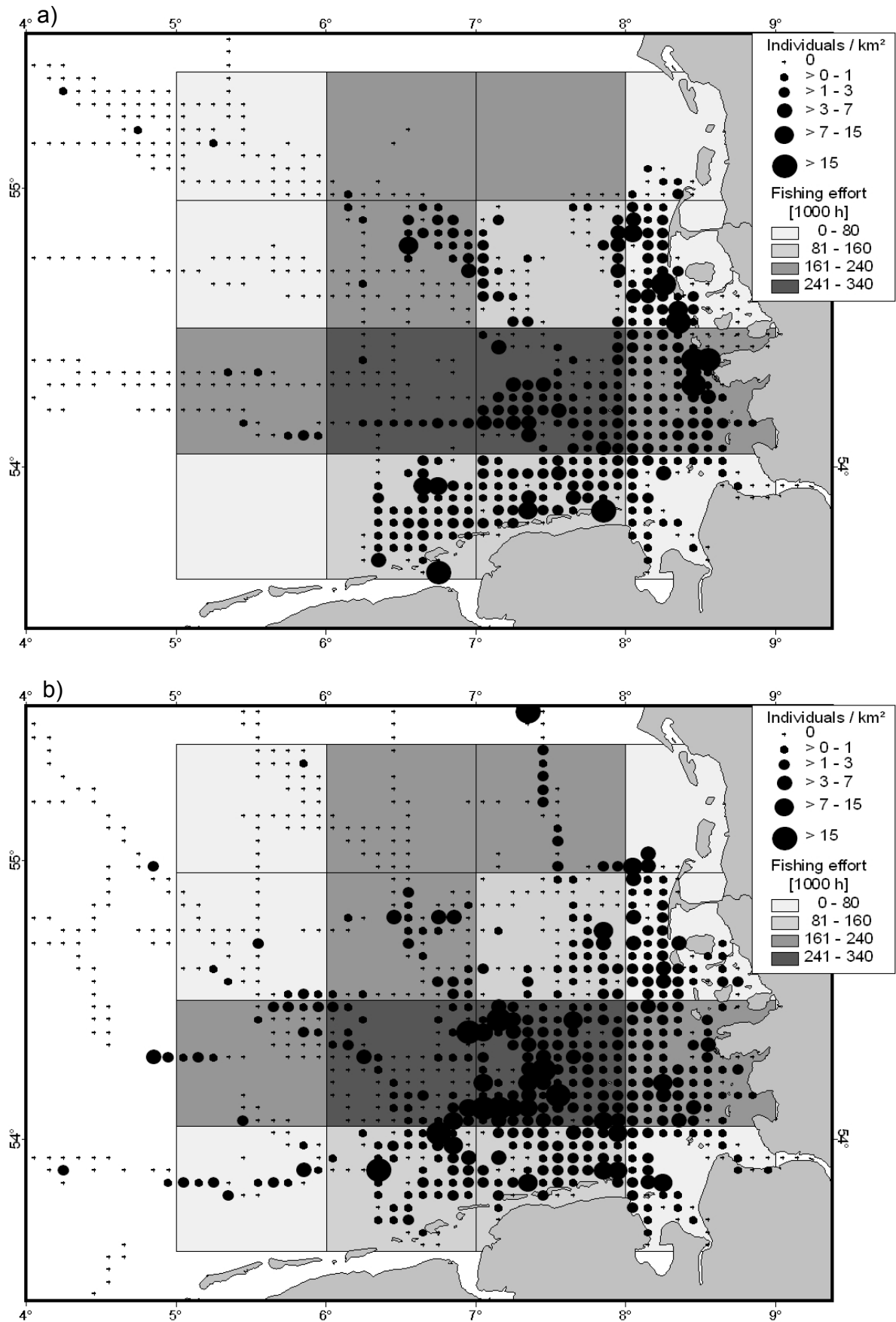


Fig. 15: Distribution of lesser black-backed gulls and fishing effort in a) May–June 1990–1995 and b) July–August 1990–1995. Grid represents statistical ICES rectangles. Data for fishing effort from Jennings et al. (1999).

In contrast, flight activity decreased substantially during mid-day (mean of 87.5 ± 18.1 gulls between 9:00 and 14:59 h). Wind force was the only variable which had no significant effect, while tide, wind direction, abundance of fishing vessels and the combined effects were significant only for gulls leaving the colony (Table 8).

Table 8: Results of 5-way ANOVA of two scenarios: Flight activity of gulls leaving colony (heading out to sea) and flight activity of gulls returning to colony (n.s.: not significant).

Parameter	df	F	p
Heading out to sea			
Main and combined effects	24	5.77	$p < 0.001$
Time of day	4	5.07	$p < 0.001$
Tide	3	4.61	$p < 0.01$
Wind force	2	1.13	n.s.
Wind direction	1	11.27	$p < 0.001$
Presence of fishing vessels (<10 km)	1	8.23	$p < 0.01$
Time of day x tide	12	2.29	$p < 0.05$
Wind direction x wind force	1	5.22	$p < 0.05$
Returning to colony			
Main and combined effects	24	3.50	$p < 0.001$
Time of day	4	7.93	$p < 0.001$
Tide	3	0.78	n.s.
Wind force	2	1.02	n.s.
Wind direction	1	0.78	n.s.
Presence of fishing vessels (<10 km)	1	0.5	n.s.
Time of day x tide	12	1.81	n.s.
Wind direction x wind force	1	3.67	n.s.

Discussion

Compared to other gull species, lesser black-backed gulls have a very extensive feeding range, resulting in a widespread distribution (see also Pearson 1968; Camphuysen 1995; Kubetzki & Garthe 2003). In the Wadden Sea area, the breeding population has increased almost exponentially during recent years (e.g. Spaans 1998; Garthe et al. 2000). The shift in areas of high abundance at sea during the three study periods are partly due to increases in the number of breeding pairs, resulting in an exponential population

growth off the German North Sea coast since the mid-1990s. The average numbers of breeding pairs for the three periods (1992-1996: 7,143 pairs; 1996-1997: 17,700 pairs; 2000-2002: 30,997 pairs) (Südbeck & Hälterlein 1994; 1995; 1999; 2001; Hälterlein & Südbeck 1996; 1998; Garthe et al. 2000) are reflected in the increasing densities at sea (see for instance densities in the offshore zone near the island of Amrum, where the increase of breeding pairs was particularly strong). However, it was yet still not clear what has caused particular hot-spots of lesser black-backed gull abundance and the reason for their shifts in the German Bight during the study period. To achieve insight into possible reasons, a combined investigation of the species' area utilisation at sea, behaviour patterns and main food types was made. This study is one of the first to undertake such an approach.

The results of dietary analyses may help to achieve a better understanding of the feeding ecology of this species and its relations to anthropogenic and natural food. With

Table 9: Comparison of results of different studies on diet of lesser black-backed gulls in the area of the German Bight. Values are given as frequency of occurrence [%] | = Incubation period; C = Chick-rearing period.

Location	Year	Chick status	Fish	<i>Liocarcinus</i> spec.	Molluscs	Other sub-littoral invertebrates	Terrestrial invertebrates	Plant material	Mammals and birds	Waste	Source
Terschelling	1985/1986	I/C	82/95	7/1	4/4	3/1	13/1	-/-	1/-	1/1	Noordhuis & Spaans (1992)
various ^a	1992	I + C	81	19	?	6	20	?	1	6	Spaans et al. (1994)
Amrum	1994	I/C	15/51	24/29	48/7	-/1	-/1	1/1	-/3	2/1	Garthe et al. (1999)
Juist	1997	I/C	65/40	29/52	20/16	-/-	16/18	8/9	7/3	2/-	Kubetzki & Garthe (2003)
Amrum	1997	C	13	79	6	2	10	6	6	3	Kubetzki & Garthe (2003)
Helgoland	2000-2002	I + C	69 ^(c) 48 ^(d)	4	-	-	4	6	-	2	Dierschke & Hüppop (2003) ^b
Norderney	2002	I/C	45/28	23/44	13/5	4/1	45/18	28/19	11/17	11/18	this study
Amrum	2003	I/C	15/7	71/78	14/4	4/3	28/17	31/33	7/9	4/14	this study

^a Average values from islands Terschelling, Vlieland, Texel, Schouwen and Maasvlakte; ^b Regurgitations; ^c Only discarded fishes, taken from fishing vessels
^d Only fishes taken as natural marine prey

an ability to dive only 0.5 m deep (Goethe 1975) or to take food items floating close to the surface, the lesser black-backed gull is only capable of hunting prey which occurs on or at least temporarily near the water surface. In both colonies studied, fishes and *Liocarcinus* spec. were the gull's most common food. Fishes can be captured naturally, but can also originate from discards or by-catch of fishing vessels. When identifying fishes from pellets of lesser black-backed gulls to species level, several authors found a high amount of fish species (such as gadids) that live close to the bottom, and thus can only become available to gulls by anthropogenic activities (e.g. Noordhuis & Spaans 1992; Spaans et al. 1994; Camphuysen 1995; Garthe et al. 1999; Dierschke & Hüppop 2003). Discard experiments have shown that lesser black-backed gulls following fishing vessels took up mainly fishes, and hardly fed on discarded crustaceans (e.g. Camphuysen et al. 1995; Walter & Becker 1997; my own

observations). Thus, it is very likely that the high proportion of *Liocarcinus* spec. found in the diet samples in both colonies were obtained by natural feeding. The frequent observations of lesser black-backed gulls feeding on crustaceans during the research cruises in 2002 (Fig. 14) strongly support this conclusion. Considering the high quantities of *Liocarcinus* spec. in the pellets, especially on Amrum in 2003, this type of prey obviously makes a very significant contribution to the diet of lesser black-backed gulls. This becomes even more obvious when considering the fishes / *Liocarcinus* spec. ratio for this particular colony (Table 9). The capture of free-living pelagic crustaceans has also been recorded in other gull species elsewhere (Stewart et al. 1984; Munilla 1997).

Comparison of the results of earlier studies on pellets with these of this study (Table 9) revealed the following: The abundance of *Liocarcinus* spec. in 1985 and 1986 (Noordhuis & Spaans 1992) as well as in 1992 (Spaans et al. 1994) was very low, but increased in subsequent years (except for Norderney in 2002 and Helgoland in 2003). This could be due to two factors: First, the study sites were different; thus, comparison is not possible without taking into account possible differences in the availability of the crustaceans in the different areas. Second, abundance of *Liocarcinus* spec. seems to have increased during the last 20 years. The following supports this: (1) An analysis of by-catches revealed an increase in the abundance of *Liocarcinus* spec. during the late 1980s, at least for the eastern German Bight (Tiews 1983; 1990); unfortunately no similar analysis has since been made. (2) Many studies have demonstrated that fishery activities support benthic scavengers such as *Liocarcinus* spec. that feed on dead or damaged fishes and other discarded species (e.g. Ramsay et al. 1997; Frid & Clark 2000; Demestre et al. 2000). (3) *Liocarcinus* spec. are present in significantly higher abundance in areas that have recently been trawled (Fonds & Groenewold 2000; Groenewold & Fonds 2000). Rumohr & Kujawski (2000) compared benthos data from 1902 to 1912 with data from 1986 and found five times higher numbers of that species in 1986. The authors named the possible effects of fisheries as responsible for that increase. (4) Besides direct effects of fishery, overfishing of large demersal fish species feeding on small crustaceans or its larvae could have led to an increase in crustacean abundance; e.g. the cod (*Gadus morhua*) is known to feed on benthic crustaceans to a large extent (e.g. Casas & Paz 1996; Gerasimova & Kiseleva 1998). However, considering the strong difference in the diet of the lesser black-backed gull between Juist and Amrum in 1997 and between Helgoland and Amrum in 2003 (Table 9) recorded in the present study, location would seem to play a decisive role in abundance of this species.

An obvious seasonal change in the diet of the lesser black-backed gull was indicated by dietary analysis and by the increasing number of gulls observed hunting crustaceans at sea. On Amrum as well as on Norderney, there was a consistent increase in the proportion of *Liocarcinus* spec. in the diet from the incubation to the chick-rearing period. These results agree with those of other studies that found a seasonal increase of crustaceans in the diet of gulls (Munilla 1997; Garthe et al. 1999; Kubetzki & Garthe

2003; see Table 9). Taking into account the fact that crustaceans have a much lower energy value than fishes (Cummins & Wuycheck 1971) and that fish diet can significantly enhance the survival rates of gull chicks (Pierotti & Annett 1990; Spaans et al. 1994), it is not clear why *Liocarcinus spec.* dominated the diet during the chick-rearing period. Again there may be more than one explanation for this: (1) There are several examples showing that the food choice of gulls can change during the season according to food availability (e.g. Burger 1976; Sjöberg 1989; Pierotti & Annett 1990; Chapter I). Analysing the by-catch of the German Brown Shrimp fisheries, Tiews (1983) found a strong increase in abundance of *Liocarcinus spec.* from spring to autumn. Aagaard et al. (1995) described increased activity of the shore crab *Carcinus maenas* in late summer and autumn, and this might also apply to *Liocarcinus spec.* Thus, increased feeding on crustaceans despite their lower energetic profitability may be the result of their superabundance at certain times of the year. (2) The pure energetic value of food is not always the main factor in food selection. Especially during the breeding season, birds require specific nutrients in their diet (Bezzel & Prinzing 1990). Calcium plays a major role in gull nutrition; it is an important component of eggshells and is necessary for bone development of chicks (e.g. Pierotti & Annett 1990; 1991). *Liocarcinus spec.* (and molluscs) may prove a valuable source of calcium, and capture of *Liocarcinus spec.* at sea would enable *Larus fuscus* to avoid the competition of other gull species on tidal flats. Thus, exploitation of crustaceans could potentially lead to niche partitioning with other gull species that do not use this source of food so intensively. Recent dietary analyses have revealed no major utilisation of *Liocarcinus spec.* by common, black-headed or herring gulls, which either forage in the sublittoral zone or at terrestrial sites (Dernedde 1993; Kubetzki & Garthe 2003; Chapter I and IV). In addition, competition for discards or by-catch of shrimp trawlers can be avoided by preying on crustaceans. Lesser black-backed gulls follow shrimp trawlers in coastal waters in high numbers at comparatively short distances from their colonies (Fig. 12a) and are in intense competition with other gull species (e.g. Camphuysen 1995; Walter & Becker 1997). In contrast, beam trawlers, which mainly fish far offshore, are followed almost exclusively by lesser black-backed gulls (often in high numbers) far away from their colonies, even during the breeding season (Camphuysen 1995; Garthe & Hüppop 1994; my own observations). After the breeding season, fishery activity determines the distribution of lesser black-backed gulls at sea even more strongly (Fig. 15).

Thus, by feeding mainly on pelagic crustaceans near the coast and following fishing vessels in offshore areas, the lesser black-backed gull tends to adopt two different feeding strategies resulting in different spatial and temporal distribution patterns. These findings are supported by observations of two different modes of departure on foraging trips in a lesser black-backed gull colony: During the breeding season, the gulls either leave the colony in direct flight or use a typical search flight, often diving for crustaceans in the early morning and evening hours (Schwemmer 2003). This indicates that the former were heading towards particular feeding sites such as beam trawlers

fishing far off the coast, whereas the latter were searching for natural food, hunting for *Liocarcinus spec.* as their main food item.

Besides *Liocarcinus spec.* and discards, pelagic fishes have to be taken into account as a further source of natural food. However, the importance of this food item for the lesser black-backed gull is not clear (Camphuysen 1995; Kubetzki & Garthe 2003). Spaans et al. (1994) found that pelagic shoaling fishes play a major role in the gulls' diet during chick-rearing. Dietary analysis and behavioural observations in the present study revealed utilisation of pelagic fishes by the lesser black-backed gull to be rare, indicating that this food may be taken as a supplementary rather than a major prey type (see also Table 9). However, pelagic fishes are probably underestimated in dietary analyses because of their high digestibility (see e.g. Duffy & Jackson 1986).

Robust relationships between avian feeding behaviour and daily activity patterns of their prey has been found in many studies (e.g. Bohl 1980; Piersma et al. 1988; Sjöberg 1989). For the lesser black-backed gull, this also appears to be the case. Increased availability of their main food item, *Liocarcinus spec.*, could have caused the strong peaks of flight activity in the morning and evening, although birds tend to show strong diurnal activity patterns with morning and evening peaks independent of external stimuli (Aschoff 1966). In terms of seasonal activity, the lesser black-backed gull tended to move into areas of higher fishing effort during July and August. Here, time of year did not seem to be the most important factor. Movements of the gull during this period could be due to the end of breeding activity, allowing foraging at longer distances from the shore, in the areas of higher food availability provided by fishing vessels.

In conclusion, the behaviour of lesser black-backed gulls in the south-eastern North Sea reflects anthropogenic and natural factors by distinct temporal patterns and changes in at-sea distribution, diet and prey-related foraging. This study has shown that – because of its high abundance and characteristic offshore distribution – this species is a suitable bioindicator species for evaluating changing conditions in both the natural marine environment and anthropogenic activities (see also Montevecchi 1993).

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Chapter III

Spatial patterns in at-sea behaviour during spring migration by little gulls (*Larus minutus*) in the south-eastern North Sea

Abstract

At-sea distribution and habitat use of seabirds has been studied on different scales and with different focus in many parts of the world. However, factors and / or processes causing certain patterns are often not easily explained. This holds also true for fast migrating species of international conservation concern such as the little gull (*Larus minutus*) in the German Bight (south-eastern North Sea). In this study, we used multi-year distributional data in combination with behavioural observations and food sampling to investigate spatial and temporal patterns of habitat use (and their possible causes) during the spring migration of this gull species. The results show a highly focused migration pattern during the last week of April and the first week of May. The river Eider seemed to play an important role as main migration route. Highest numbers of gulls were found either close to the mainland or close to the offshore islands. Different parts of the south-eastern German Bight revealed different ecological functions for this species: Little gulls used certain sub-areas for intense feeding (i.e. the region near Helgoland and the outlet of river Elbe) and others for migration. Hydrographic phenomena such as fronts and foam lines played an important role within the feeding sites and strongly influenced behaviour and distribution. Feeding behaviour as well as samples of probable prey revealed different quality of feeding sites according to the energy density of the most abundant probable food items (drowned insects vs. zooplankton and fish). In conclusion, the habitat use of *Larus minutus* during spring migration in the German Bight showed clear temporal and spatial patterns, and sites with main feeding action should be regarded as sensitive for little gulls at least during spring migration.

Introduction

At-sea distribution of seabirds has been studied intensively on a large scale in many regions of the world (e.g. Bailey 1968; Burger 1983; Abrams 1985). This also holds true for European waters where longer-term studies revealed spatial patterns of many seabird species and periods of time (e.g. Tasker et al. 1987; Camphuysen & Leopold 1994; Garthe et al. 2003). Current research temporarily focuses on which factors cause or influence distributions of different species in certain areas and several approaches have been undertaken to relate seabird distribution to various parameters (e.g. Garthe 1997; Camphuysen & Webb 1999; Markones 2003; Schwemmer & Garthe 2005).

Explaining the at-sea distribution and area utilisation of endangered, migrating seabirds is particularly relevant, as these species are even more sensitive to natural and / or anthropogenic changes of their marine environment during their passage when it is especially important to encounter reliable food sources and suitable abiotic conditions. The quality of staging sites can be relevant to provide good body condition and eventually ensure successful breeding (e.g. Evans et al. 1991; Ebbinge & Spaans 1995). The little gull (*Larus minutus*) is such a migrating seabird of high conservation concern, which uses the German Bight (south-eastern North Sea) intensively on its way to and from their Baltic breeding grounds, both in spring and autumn, while a small part of the Baltic breeding population winters in the North Sea (Glutz von Blotzheim & Bauer 1982; Cramp & Simmons 1983).

So far, the phenology of the spring migration has been described various times from regular counts over mainland (e.g. Looft 1971; Gloe 1973; 1987; Messenger 1993). Although some studies exist that focused at migration patterns along the coast or over water (e.g. Camphuysen & van Dijk 1983; White 1992; Dierschke et al. 2003), their results seem to be rather limited by their regional point of view and cannot provide information on offshore conditions. Due to the fact that the spring migration of this species can take place very rapidly (Woutersen 1980; Camphuysen & van Dijk 1983; Ouweneel 1989; Garthe 1993a), there is still a significant lack of knowledge about how this species distributes at sea during spring migration and it is unclear whether there are differences in the use of certain marine habitats (and their ecological function for this species) on the way to the breeding grounds. Thus, at-sea observations during ship-based counts can provide a more general overview on important relationships. The simultaneous analysis of a long-term set of at-sea distributional data, behavioural observations as well as analysis of the food supply can shed light on (1) the temporal and spatial patterns of *Larus minutus*, (2) the utilisation of different areas at sea, and (3) the location of sensitive offshore sites and their ecological function and quality.

It might be expected that the availability of food during migration acts as a decisive factor for distribution and area utilisation. At this stage, information on the diet of little gulls is only available for the breeding grounds or very few resting sites on land (Glutz von Blotzheim & Bauer 1982; Cramp & Simmons 1983; Zubakin 1990; Koop

1997), while there are hardly any indications on food types taken in the marine environment during migration.

In this study, we analysed multiple-year distributional and behavioural data of *L. minutus* as well as potential food availability. Furthermore, we assessed the different use of sub-areas by this seabird species in order to reveal the importance of the pelagic zone of the south-eastern North Sea coast during spring migration.

Material and Methods

At-sea distribution, behaviour and phenology during spring migration were analysed in the German Bight, south-eastern North Sea (for study period see below). The study area was defined as east of 6° 30' and south of 54° 30', including offshore areas and inner mouths of the rivers Eider, Elbe and Weser (Fig. 16). Little gulls were counted from the top deck of various research vessels in accordance with the method of Tasker et al. (1984) and Garthe et al. (2002). Although we applied the 'snapshot' method according to Tasker et al. (1984) to correct for densities of flying birds, we used every sighting as the present study emphasises the behaviour of each individual and is not aiming at estimating exact densities of birds. In order to correct each sighting for observer effort which was different over the years investigated, the sum of all individuals recorded per 3' latitude x 5' longitude grid (grid cell size equivalent to ca. 30 km²) was divided by the total km travelled within that grid (hexagons in Fig. 16). Data were taken from the German Seabirds at Sea database (Garthe & Hüppop 2000), version 4.03 (June 2004).

Because distance to coast can be one major factor affecting distributions of seabirds also during migration (Hutchinson & Neath 1978; Zubakin 1990; Garthe 1997) and may provide valuable information on possible mechanisms of interspecific competition and on utilisation of food resources (Kubetzki & Garthe 2003; Schwemmer & Garthe 2005), this factor was investigated for little gulls. Therefore the distance of each centre point of each of the 3' latitude x 5' longitude grid cells to the closest point on land (including the Wadden Sea islands but excluding the island of Helgoland) was calculated and related to the gull densities of the particular grid cell.

Behaviour at sea was analysed in accordance to the methods of Ashmole (1971) and Camphuysen & Garthe (2004). With an observer effort of 2,729 km travelled by boat, a total of 2,427 birds was observed, of which 1,697 could be classified according to one of the following four types of behaviour: (1) Heading towards certain direction; (2) searching for or feeding on natural prey; (3) heading towards certain direction while searching for or feeding on natural prey; (4) resting (gulls which were sitting on the surface with no activity, sleeping or preening). For birds of the second behaviour type, the feeding technique was recorded in all possible detail (see Camphuysen & Garthe 2004) using the categories (1) actively searching (flying with the head pointing towards the water surface); (2) dipping (taking small items from the sea surface during flight); (3) surface pecking (picking small items from the surface while sitting on the water); (4) surface

seizing (feeding on large prey while sitting on the water) and (5) kleptoparasitizing by aerial pursuit (hunting for prey carried by another bird). Additionally, birds associated with hydrographic fronts or with fishing vessels as well as little gulls which were involved in multi-species feeding flocks (Camphuysen & Webb 1999; Camphuysen & Garthe 2004) were recorded (574 birds in total).

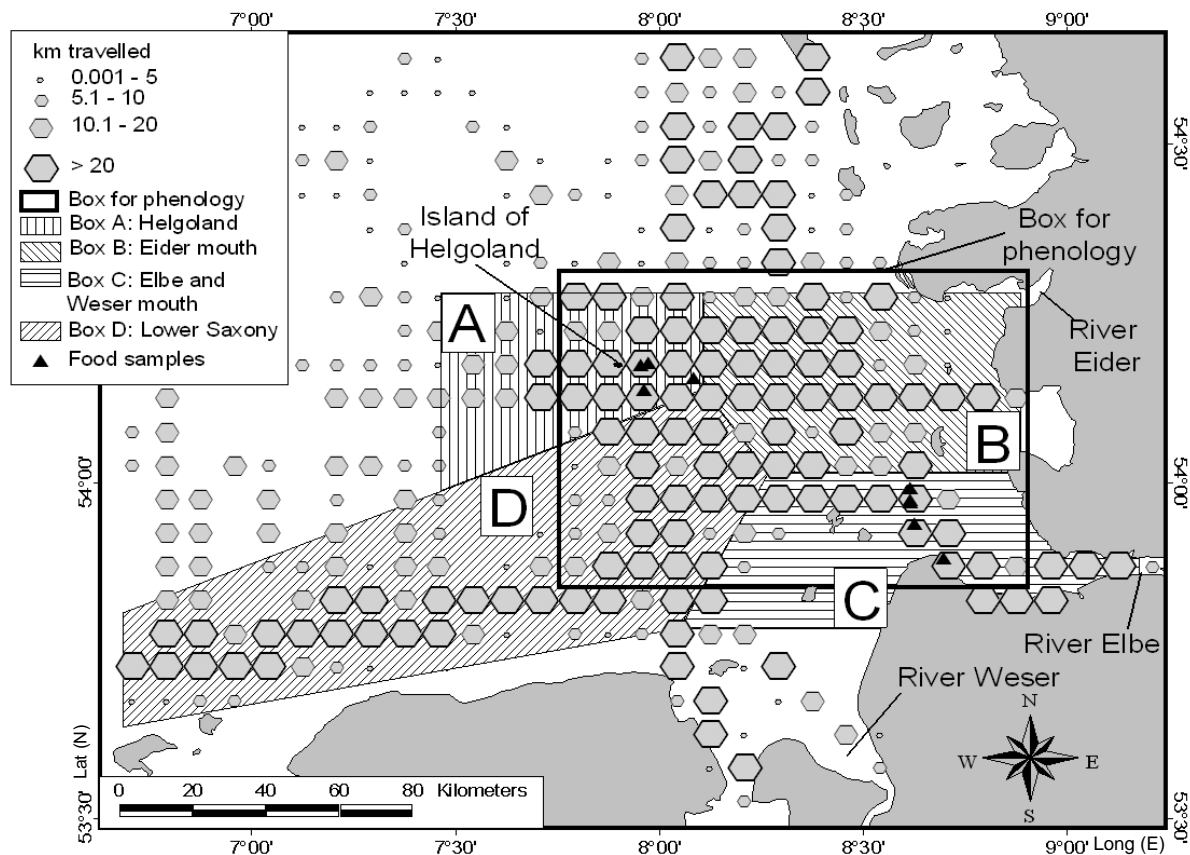


Fig. 16: Study area in the south-eastern North Sea. Hexagons indicate the observer effort during April and May over the years 1991-1993, 1997-1998 and 2000-2004. The boxes A-D served for detecting differences in habitat use by little gulls and were analysed on the basis of behaviour. Triangles represent locations of collection of food samples. The bold box was set for phenological analyses.

For information on habitat use by little gulls, behaviour patterns were compared between four different regions with distinct ecological functions for a migrating seabird in the southern German Bight (boxes A – D in Fig. 16): Box A is the 'Helgoland box', being the area with the highest distance to shore and including the offshore island of Helgoland. Box B is the 'Eider mouth box', located next to the river Eider. Box C is the 'Elbe mouth box', characterized by the influence of freshwater from the river Elbe and saline water during incoming tide. Box D is the 'Lower Saxony box', which covers the area along the coast of Lower Saxony and south of Helgoland, the expected main migration route of little gulls in the south-eastern North Sea. Each day of observation was taken into account for statistical considerations at which at least five little gulls with behaviour were detected. For each of these days, proportions of the four behaviour categories mentioned above were calculated and tested for differences between the four boxes applying

oneway-ANOVA and Student-Newman-Keuls post-hoc-test. The same was done for the proportion of little gulls associated or not-associated with hydrographic fronts.

For detailed phenological analyses of the migration, an area with high observer effort in all years of the study was selected (box for phenology in Fig. 16). Within that box, the totals of birds on each day observed (in total 102 days) were divided by the total distance travelled by boat on each day. In order to fit a normal distribution, the logarithm of that quotient was taken. For 2,381 out of 4,688 individuals recorded during March to May, age could be identified and the proportion of immatures and adults on the total was calculated within the same box. Little gulls in third year plumage were considered as adults. For the different analyses made, the study period was altered according to the available data: (1) Distribution was investigated from 15 April to 10 May (period of main migration intensity) during the years 1991-1993, 1997-1998 and 2001-2004. This time interval was also used for analysis of feeding associations (see below). (2) Behaviour was investigated from 15 April to 10 May during the years 2001-2004 as detailed observations of behaviour (Camphuysen & Garthe 2004) were not available from before. (3) Phenology was investigated from 1 March to 31 May during the years 1991-1993, 1997-1998 and 2001-2004 to gain detailed information on beginning and ending of the main migration period.

Many seabirds often feed in mixed or intraspecific feeding associations either to take advantage of prey becoming available due to hunting activities of other species (e.g. diving seabirds or marine mammals) or by being attracted by individuals of the same or closely related species, such as in gulls (e.g. Bayer 1983; Camphuysen & Webb 1999). Estimating the importance of interspecific groups for little gulls, 36 associations with other species were recorded and investigated on the basis of geographical variation and species composition.

Analyses of food remains in seabird colonies is a common and successful method to derive the foraging behaviour of seabirds during the breeding period (see overview in Duffy & Jackson 1986). Outside the breeding season and especially during migration, the collection of food samples is very difficult as most seabirds spend most of their time at sea. For information on potential food taken by little gulls during their migration, areas in which intense feeding behaviour occurred (e.g. hydrographic fronts / foam lines on the surface) were sampled six times in the area of the river Elbe outlet and five times in the area of the island of Helgoland (shown as triangles in Fig. 16). This was done with a net with a mesh size of 0.5 mm and 60 cm in diameter that was towed for 5 minutes close to the sea surface. Samples were analysed with a 8 x 23 binocular and species were determined to the lowest possible taxon. An ocular with a scale was used to measure approximate prey sizes.

In order to reveal detailed migration routes within different areas, little gulls with distinct flight directions observed during counts at sea were studied. For 440 individuals observed on 15 different days during the time mentioned under "behaviour" (see above), flight directions could be determined at various places within the study area. Directions

were classified in units of 30° and all sightings within the same area were plotted in eight different diagrams showing relative numbers of individuals.

Results

Phenology

Little gulls showed a distinct seasonal pattern during spring migration (Fig. 17). At the beginning of April, only few individuals were present, whereas highest numbers were found during the last ten days of April and the first ten days of May. Numbers decreased in the beginning of May and abruptly during the second half of May, indicating a short, highly focussed migration period.

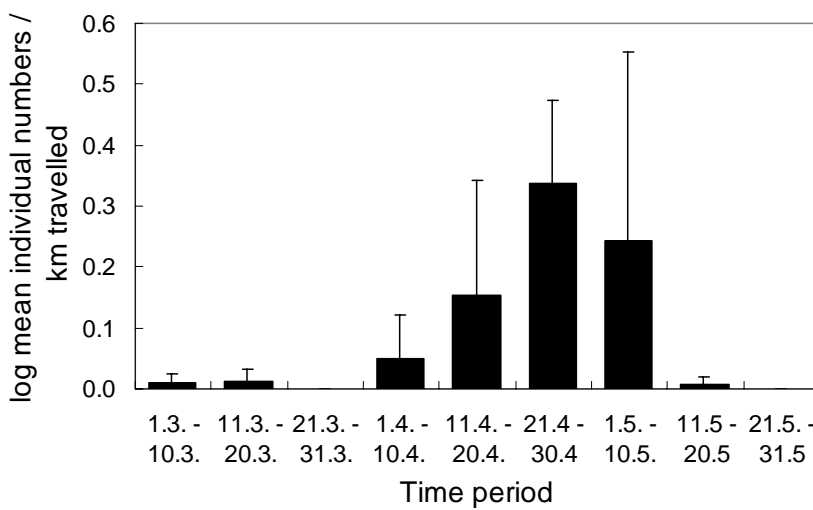


Fig. 17: Phenology of little gulls during March to May recorded within the bold box (Fig. 16), expressed as numbers of birds divided by observer effort (km travelled). Bars indicate standard deviation. The logarithm of the original numbers were taken to match a normal distribution.

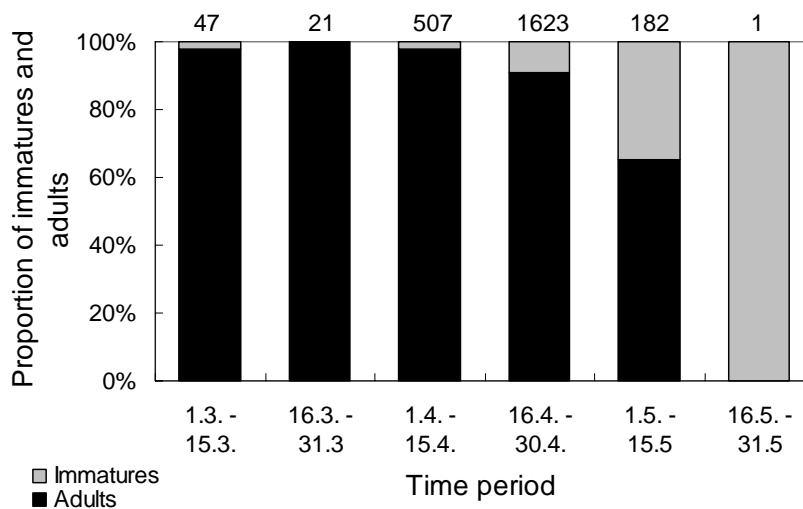


Fig. 18: Proportion of immatures and adults recorded within the bold box (Fig. 16). Number above the columns represent gull numbers.

Whereas almost solely adults were found until mid-April, the proportions of immatures increased above all in May (Fig. 18).

Distribution

Distribution patterns revealed highest numbers close to the offshore island of Helgoland up to 50 km from the shore (Fig. 19; Fig. 20). Most of the other individuals were found in the vicinity of the mainland (up to 20 km from shore) in a strip-shaped area from south-west to north-east between the eastern East Frisian islands and river Eider (Fig. 19). The offshore region, more than 50 km from shore, was hardly used by little gulls (Fig. 20).

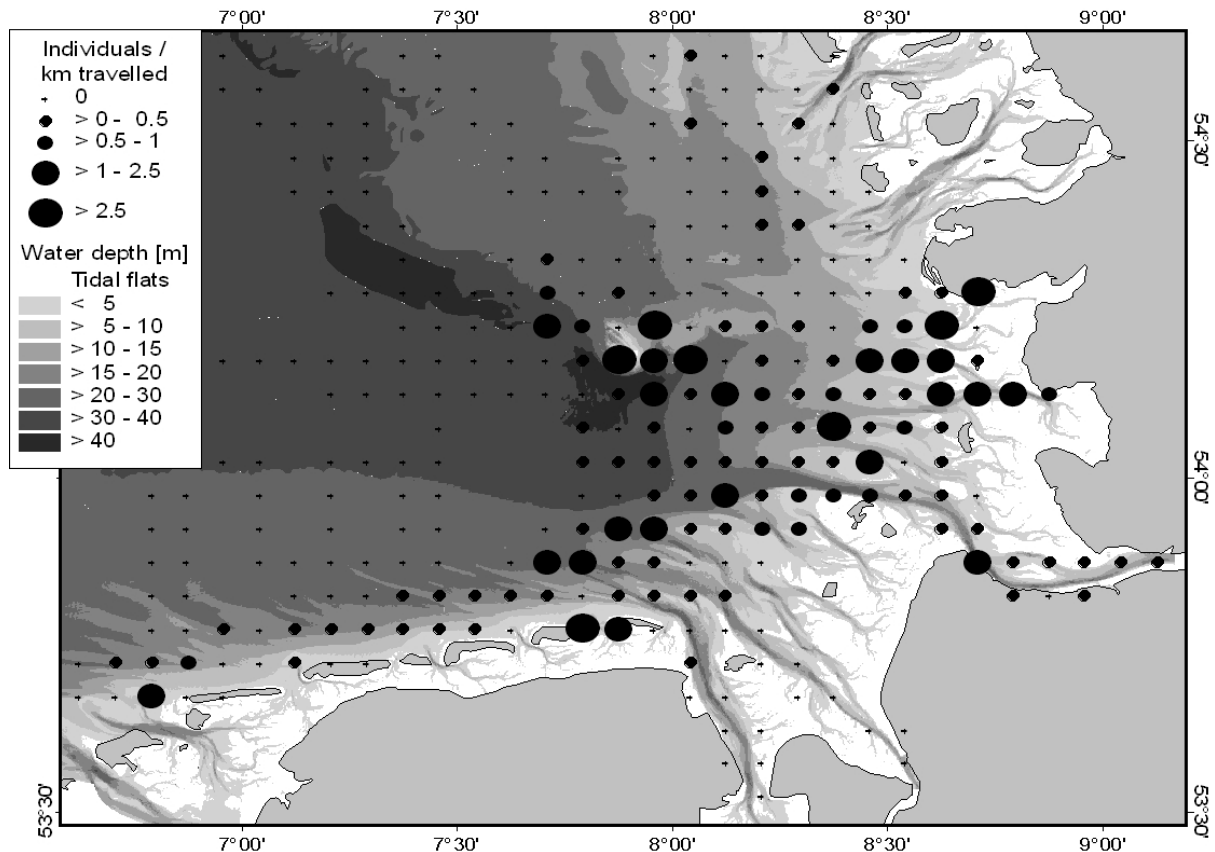


Fig. 19: Distribution of little gulls from 15 April to 10 May over the years 1991-1993, 1997-1998 and 2000-2004. Numbers of birds recorded were corrected for observer effort. The white triangle indicates the island of Helgoland.

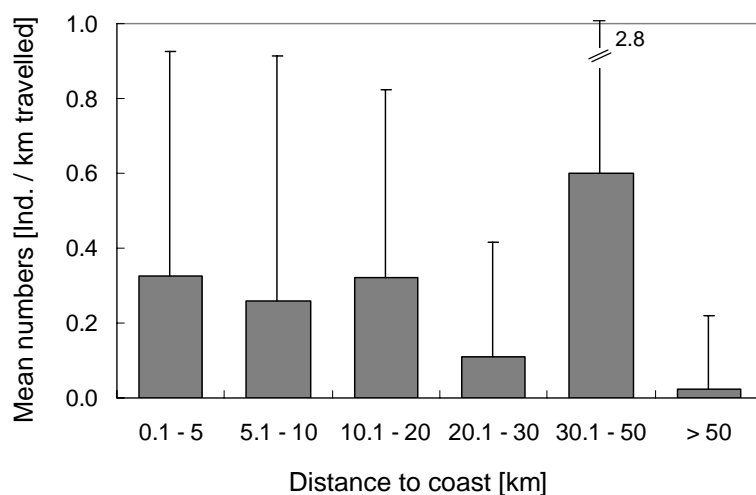


Fig. 20: Abundance of little gulls in relation to distance to the coast (including the Wadden Sea islands but excluding Helgoland).

Behaviour

Searching for or feeding on natural prey was the most common behaviour exhibited by little gulls over the whole study area (62.5 % of all birds with behaviour), followed by birds heading in a certain direction (23.8 %) and birds resting (13.7 %). A small number of individuals could be identified as searching for prey while heading in a certain direction

(7.4 %). Of all feeding gulls, dipping was the most common foraging technique (63.9 %), followed by actively searching for prey (28.3 %) and surface pecking (5.6 %). Only very few gulls were recorded surface seizing (1.8 %) and were involved in aerial pursuit with individuals of the same or different species (0.4 %). From the total of birds recorded, 19.1

% were associated with hydrographic fronts, 4.5 % were associated in multi-species feeding flocks and only 0.04 % joined fishing vessels (one single bird at one observation only).

Between the four spatial boxes (Fig. 16), significant differences could be detected in all but one behaviour type (resting) tested (Table 10). For individuals searching for or feeding on natural prey, highest proportions were found in Helgoland box and Elbe mouth box, those two areas being significantly different from the two others (Student-Newman-Keuls post-hoc-test). The proportions of gulls heading towards a certain direction were highest in the Lower Saxony box and the Eider mouth box (Table 10). Post-hoc-test revealed significant differences only between the Elbe mouth box and the Eider / Lower Saxony boxes while the Helgoland box differed only from the Lower Saxony box.

Highest proportion of birds associated with hydrographic fronts were found within the same boxes in which highest feeding activity occurred (Table 10). Significant differences were revealed only between the Helgoland and Lower Saxony boxes (Student Newman Keuls post-hoc-test).

Table 10: Proportions of the four categories of behaviour and of gulls associated with hydrographic fronts within the four boxes (for definition see Material and Methods section). Differences between the four boxes were tested by oneway ANOVA (see text for details; n.s.: not significant).

	Helgoland box	Eider mouth box	Elbe mouth box	Lower Saxony box	p
Searching for or feeding on natural prey	71.4%	29.0%	92.4%	29.9%	p < 0.001; df = 3
Heading towards certain direction	19.2%	38.0%	4.7%	55.9%	p < 0.01; df = 3
Resting	9.4%	33.1%	2.9%	14.2%	n.s.
Searching for prey with direction	10.8%	0.3%	0.1%	18.8%	not tested
Associated with hydrographic fronts	55.0%	19.4%	49.7%	11.6%	p < 0.05; df = 3
Not associated with hydrographic fronts	45.0%	80.6%	50.3%	88.4%	p < 0.05; df = 3

Food availability

In most cases, food taken by little gulls at sea was too small for identification by binoculars during the counts. Thus, the fishing samples collected at hydrographic fronts / foam lines in the vicinity of feeding little gulls may reflect potential diet (Table 11). In the area of the outlet of the river Elbe, drowned insects - floating on the surface - occurred most frequently in the six samples. Crustaceans (especially copepoda) were also found regularly and in high numbers. Other species occurred only rarely and infrequently. The five samples taken in the vicinity of the island of Helgoland revealed only few insects,

whereas fish larvae and fish eggs could be found in each of the five samples, mainly in high numbers. Planctonic crustaceans (mainly decapoda larvae and copepoda) occurred regularly (Table 11).

Table 11: Frequency and range of size of different species or groups found in fishing samples taken next to feeding little gulls at the mouth of river Elbe (n = 6) and the Helgoland region (n = 5); for location of sample sites see Fig. 16. x = 1 – 10 individuals in sample, xx = 11 – 25 individuals in sample, xxx > 25 individuals in sample.

Species / Group	Elbe sample no.						Helgoland sample no.					Range of size [mm]
	1	2	3	4	5	6	1	2	3	4	5	
Ctenophora:												
<i>Pleurobrachia pileus</i>	xxx	xx	-	-	-	xx	xxx	xx	x	-	-	1.9 - 11
Cnidaria:												
<i>Tima bairda</i>	x	-	-	-	-	x	-	-	-	-	-	4.8 - 6.2
Mollusca:												
Bivalvia	-	x	-	x	-	x	x	-	-	-	-	1.5 - 10.1
Crustacea:												
<i>Daphnia spec.</i>	-	-	-	xx	xxx	x	-	-	-	-	-	1 - 1.3
Copepoda	x	xx	x	xx	x	xxx	xxx	xxx	xxx	xxx	xxx	1.2 - 4
Cirripedia	-	-	xxx	xxx	xx	xxx	-	-	-	-	xxx	2.3 - 10.3
Decapoda (Larvae)	-	-	-	-	-	-	x	-	xx	xx	-	1 - 1.5
<i>Crangon spec.</i>	-	x	-	x	-	-	-	-	-	-	-	5.8 - 18
<i>Liocarcinus spec.</i>	-	-	x	x	-	-	-	-	-	-	-	1.1 - 22.2
<i>Carcinus maenas</i>	-	-	x	-	-	-	-	-	-	-	-	16 - 34.5
Amphipoda	-	-	-	-	-	-	-	-	-	-	xx	14.2
Insecta:												
Hymenoptera	-	xxx	xxx	xx	xxx	xxx	-	-	-	-	xx	1.3 - 8.2
Diptera	xxx	xx	xxx	xx	xxx	xxx	x	x	-	-	x	1 - 21.1
Coleoptera	x	xx	xxx	xx	-	x	x	-	-	-	-	1 - 10.2
Chaetognatha:												
Chaetognatha	-	-	-	-	-	-	-	-	x	-	x	14.2 - 17
Vertebrata:												
Teleostei (Eggs)	-	-	-	-	-	-	xxx	xxx	xxx	xxx	xxx	1.1 - 1.5
Teleostei (Larvae)	-	-	-	-	x	x	xxx	x	xx	xx	xxx	5.7 - 12
Others:												
Seeds	x	xxx	-	-	-	-	-	-	-	x	-	2.8 - 6.1

Interspecific aggregations

Most flocks consisting of little gulls and at least one other species could be classified as feeding associations. Each of it appeared rather close to shore (primarily in the catchments of river Elbe) or in the vicinity of the island of Helgoland (Fig. 21). Numbers of species associated with little gulls differed between flocks and ranged from 1 to 6. Many of the most diverse flocks occurred in the coastal area of river Elbe and south of the mouth of river Eider (Fig. 21).

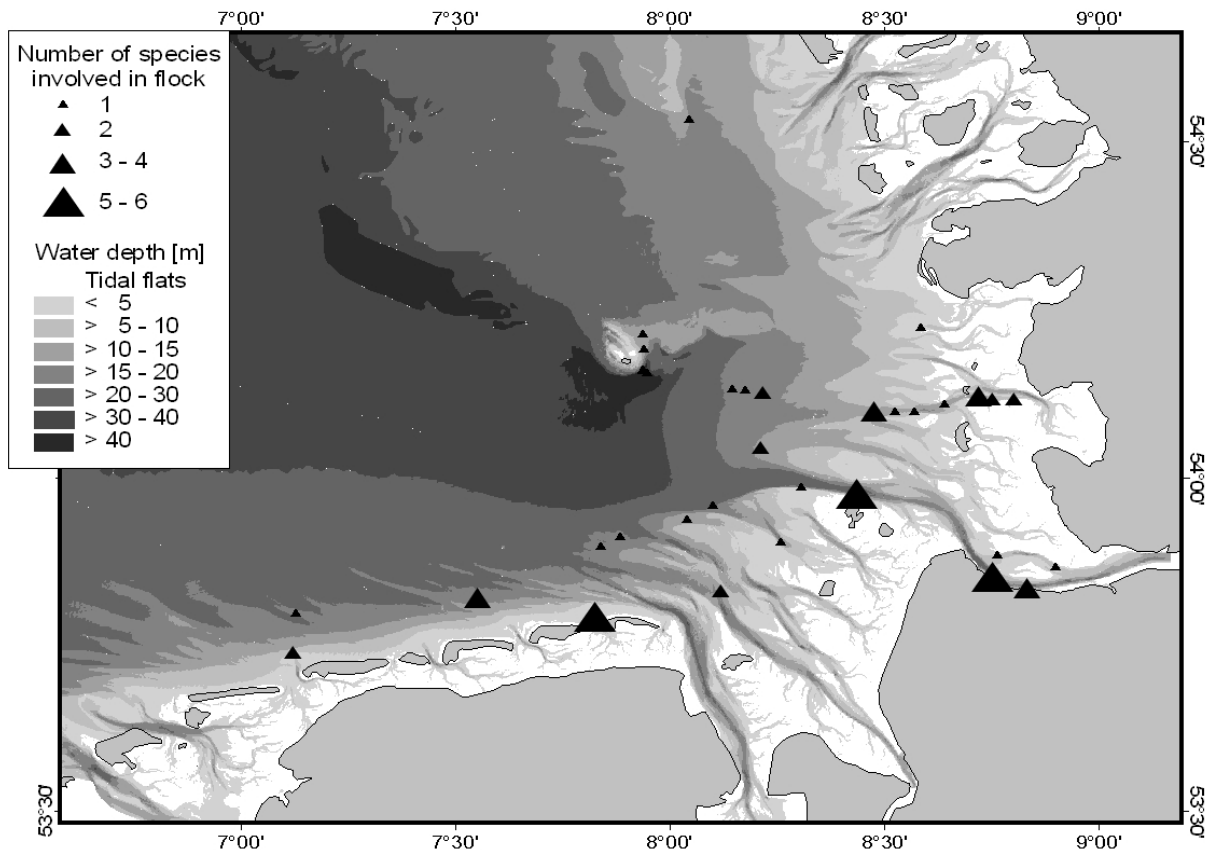


Fig. 21: Distribution of feeding flocks with little gulls involved. The size of the triangles indicate the number of other species participating in the flock.

In total, 14 species of birds and marine mammals were found in association with little gulls. *Larus minutus* did not seem to show a preference to associate with certain species, but common terns (*Sterna hirundo*) and Arctic terns (*Sterna paradisaea*) were recorded most frequently and appeared in half of the flocks noticed (Fig. 22). All species of gulls common in the North Sea were found participating in flocks rather often, while the non-surface-feeding seabirds and marine mammals appeared only very rarely. Species composition in the flocks showed regional differences on the basis of the four boxes. Common and Arctic terns as well as common gulls (*Larus canus*) were present in each of the boxes, whereas the highest regional variability was found in lesser black-backed gulls (*Larus fuscus*) which appeared in high numbers and at a high frequency in the Lower Saxony box but only very rarely elsewhere. The Helgoland box was the area with the highest diversity between flocks, every record showing different species in

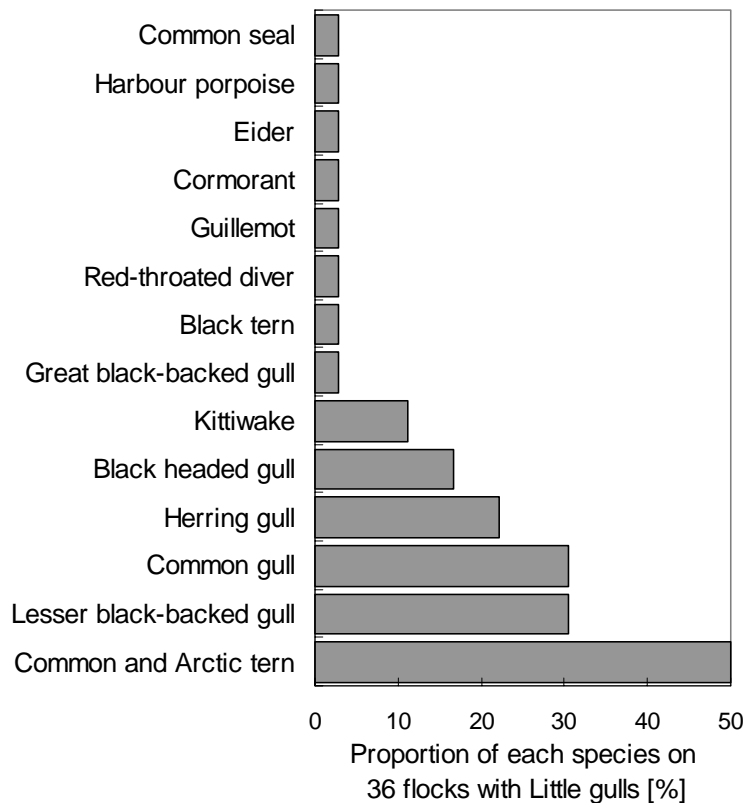


Fig. 22: Proportions of the 14 species found in 36 mixed flocks with little gulls.

association with little gulls, whereas the Elbe mouth box showed the lowest species diversity between flocks, consisting mainly of gulls and terns.

Flight directions

A clear preference for north-easterly directions towards the mouth of river Eider were found for almost any observation (Fig. 23). As only exceptions, the five individuals recorded in the Elbe mouth were heading north-west and most individuals recorded north of Helgoland were heading towards the island.

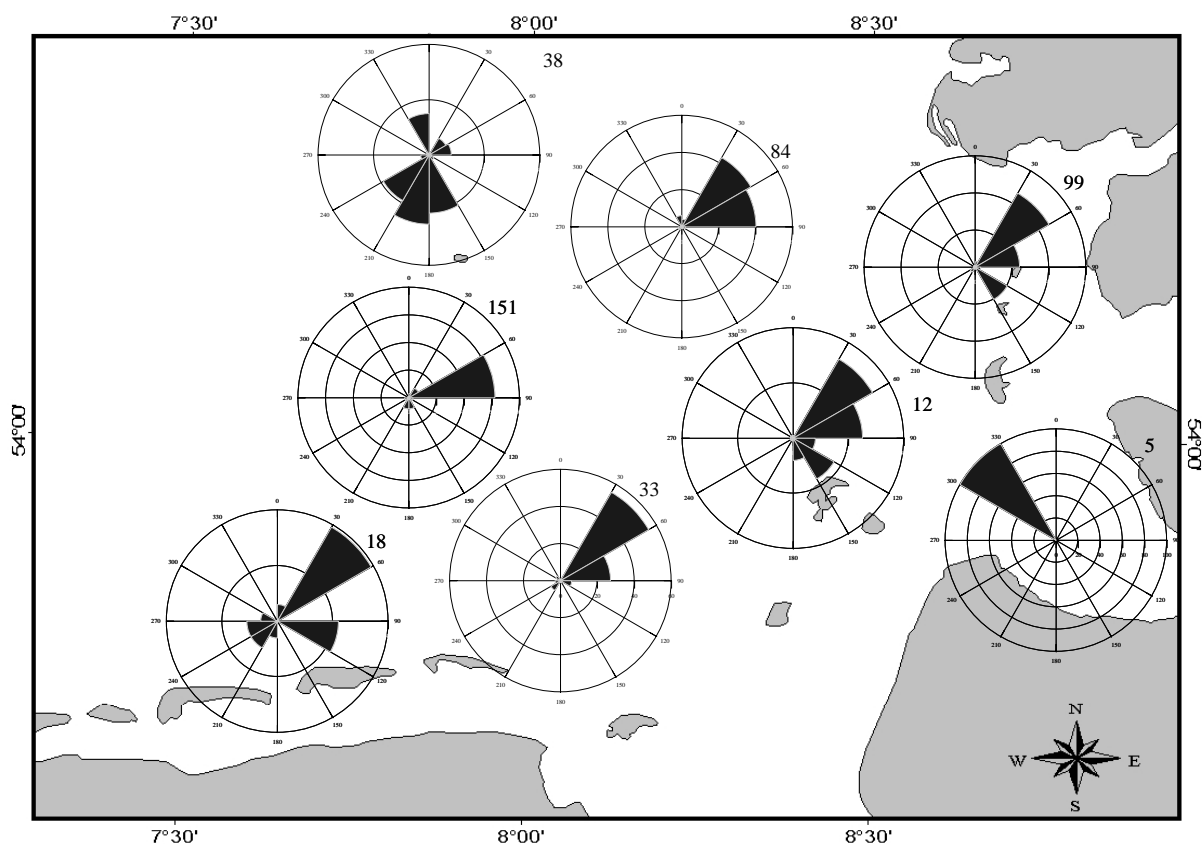


Fig. 23: Proportions of flight directions of little gulls in units of 30°. Every circle in flight diagram represents 20 % of all gulls recorded within the spot covered by each diagram. Numbers right to each diagram are absolute numbers of gulls. The study area was slightly reduced for a better overview.

Discussion

Different sub-areas of the German Bight seem to play an important role during spring migration of little gulls. In the following phenology, area utilisation and quality respectively ecological function of habitats for this species will be discussed.

Phenology of migration in the German Bight

Although spring migration takes place rather fast (Gloe 1987; Garthe 1993a; this study), little gulls seem to slow down their pace in the German Bight compared to other sites, before they head over the mainland towards the Baltic. In contrast, Woutersen (1980) found a highly focussed migration peak in the Netherlands which takes place within only 10 days (see also Camphuysen & van Dijk 1983; Platteeuw et al. 1994).

In this study, the peak of highest influx of individuals in the German Bight was recorded in late April and in the first 10 days of May. This temporal pattern matches very well findings of other studies: In many places in Britain and Ireland, highest numbers were recorded during the end of February and beginning of March (Lassey & Greenhaigh 1969; Hutchinson & Neath 1978; Madden & Rutledge 1993), while observations from the German mainland and the Baltic showed peak numbers for the last weeks of May (e.g. Koop 1985; 1997; Schirmeister 2002). Thus, timing of the migration leads to the assumption that the major part of gulls in the German Bight consists of individuals travelling along the Dutch and French coast as well as originating from the southern part of Britain and Ireland, whereas a northern influx can be negated due to very low numbers of little gulls in the northern part of Britain and Denmark during spring migration (Hutchinson & Neath 1978; Christensen et al. 1990). There are several authors that point out the relevance of trans-continental migration in little gulls, mainly along distinct river lines (e.g. Erard 1961; 1963; Albat 1993). These additional or alternative routes may become more important during unsuitable weather conditions, i.e. mainly strong winds (den Ouden & Stougie 1990; Temme 1991). However, high overall individual numbers recorded at sea in various meteorological conditions during different years of observation indicate the strong relevance of migration over the sea, particularly in the German Bight area.

The late arrival of immatures found in the study area agrees very well with many other studies (e.g. Lassey & Greenhaigh 1969; Garthe 1993a; 1993b). It can be assumed that some individuals do not migrate as far as to the breeding grounds, for some authors report long-term feeding actions and also summering at suitable sites (e.g. Hutchinson & Neath 1978; Madden & Rutledge 1993). In the German Bight, however, numbers during summer are very low (unpubl. data).

Spatial patterns and area utilisation

In general, the distribution of little gulls during spring migration is connected to the vicinity of the mainland and to the islands, e.g. Helgoland. This pattern might be explained either by the sheltering effect of the land or the higher food availability at these sites. The latter

seems to be the more decisive factor as the high proportion of individuals searching for or feeding on natural prey at coastal areas indicate. Suitable feeding sites are known to attract vast numbers of little gulls and may even lead to late migration peaks due to high numbers of non-breeders (Isenmann 1973; White 1992). Although feeding also takes place in other (even more offshore) regions and is also often combined with direct flight, indicating a certain prey availability at most parts of the study area, our results revealed that there are two different sites during spring migration in the German Bight which are intensely used for feeding, i.e. the area of Helgoland and the outlet of river Elbe (see below).

In contrast to these two sites, the more distant offshore areas and the most westerly part of the study area mainly serve as areas of more intense migration (although feeding action does occur, too). Analysing the flight directions in this areas, there is strong evidence that the river Eider was obviously used as main migration route. This finding is supported by Gloe (1987) who observed high numbers of little gulls on this river during spring. The general north-easterly direction which was visible remarkably far in the offshore area agrees very well with other land based studies (e.g. Eggers 1965; Garthe 1993a) and indicates the importance of the river Eider. It can be assumed that this route is particularly important during unsuitable weather conditions (compare den Ouden & Stougie 1990). Oppositely, the river Elbe does not seem to serve as an important migration route during spring migration as only few individuals were observed in direct flight ($n = 5$) and those were all heading down the river (Fig. 23). Although the sample size of migrating individuals in this region is too low to clearly indicate a general flight direction, regular coastal counts support that the majority of individuals head towards the river mouth (P Todt, pers. comm.). Taking into account the total numbers of individuals with flight direction towards the mainland, it can be assumed that a certain (although probably rather small) proportion of little gulls might not have spent a lot of time feeding in the German Bight.

Coming to an overall valuation of the southern German Bight in terms of area utilisation by little gulls, we can clearly define two important feeding sites: The outlet of river Elbe and the area near Helgoland, both characterized by frequent use of hydrographic fronts as main food sources (see below). These two sites are separated by a distinct migration corridor in which the gulls were heading towards the river Eider (Table 10; see also Fig. 24 for a simplified model).

Quality of sites in relation to food availability

Although the proportion of individuals searching for or taking up prey in the Helgoland region was slightly lower compared to the Elbe site (Table 10), there is some evidence that the former feeding site seems to be highly important with respect to prey availability: Of all individuals recorded within the Helgoland box which were classified as searching for or feeding on natural prey, only 13 % were searching for food without handling

captured prey items, whereas 77 % were actively taking up prey, most commonly by dipping at the sea surface, thus indicating favourable feeding conditions.

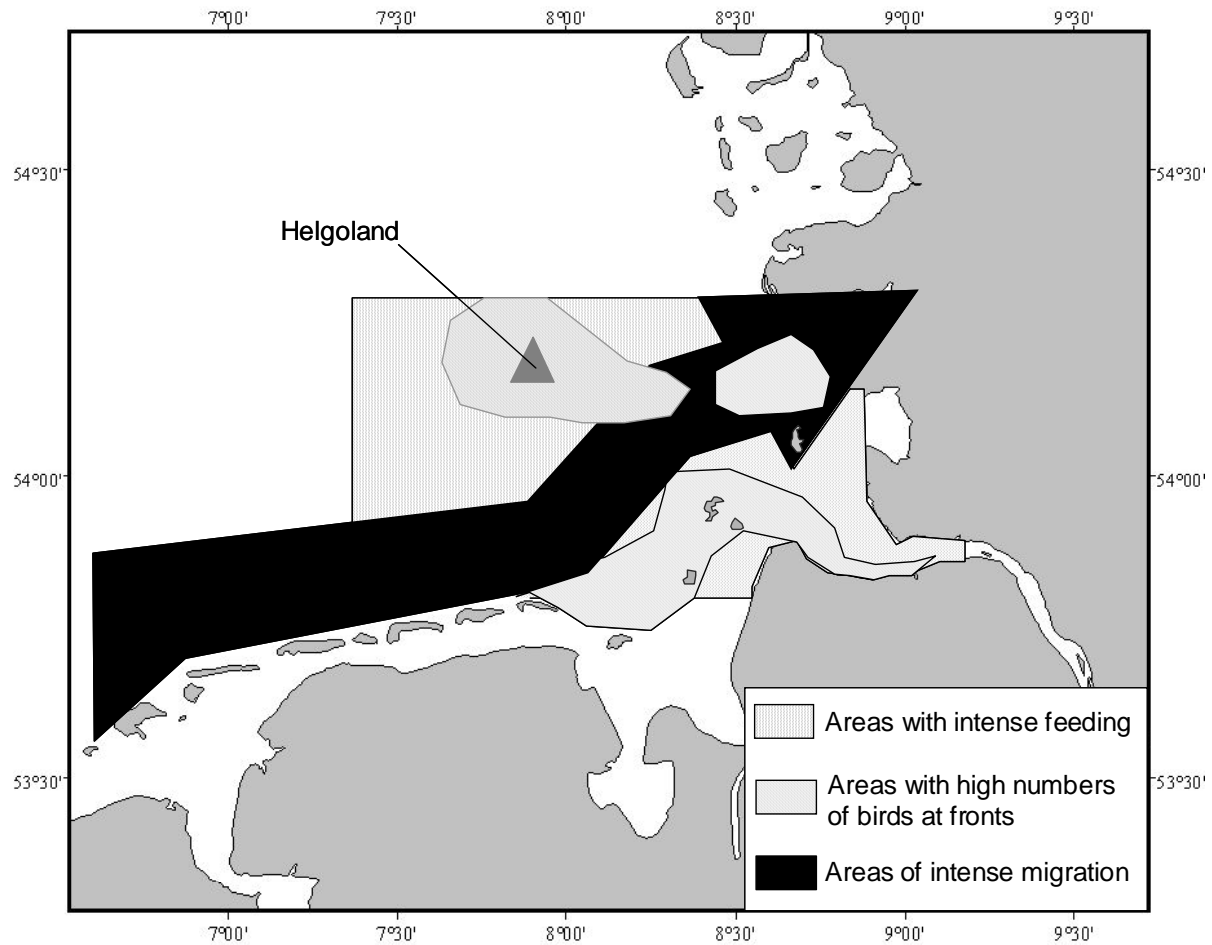


Fig. 24: Simplified scheme of area utilisation by little gulls in different regions of the southern German Bight.

Hydrographic phenomena might explain the good feeding conditions in this particular area: Becker et al. (1983) as well as Krause et al. (1986) found frequent upwellings in the post-glacial Elbe valley near Helgoland. This might have caused the obviously high prey availability. The large numbers of birds in association with clearly visible hydrographic fronts or foam lines support this conclusion (Table 10; Fig. 24). Krause et al. (1986) state that upwelling-fronts in that region are characterized by a significant high amount of zooplankton. The food samples from this area support these findings (Table 11). In contrast, nearly all individuals recorded in the outlet of river Elbe were found foraging (though the overall numbers and the proportion of gulls which were actually taking up prey were lower compared to the Helgoland region) and of these a high proportion took up prey at tidal fronts (Table 10). As fishing samples revealed, the most numerous potential prey category on which little gulls were likely feeding on were drowned insects (Table 11). Fronts in this region are characterized by the convergence of coastal freshwater from the rivers Elbe and Weser and saline water from the incoming tide, leading to a distinct area where floating material and potential prey aggregate (Becker & Prahm-Rodewald 1980; Krause & Reuter 1988). Additionally, strong tidal currents - found

commonly in this area - can cause high prey availability, too (Eades 1982; White 1992; Keijl & Leopold 1997; Zamon 2003).

However, there are indications that the outlet of the river Elbe is not of the same quality for little gulls than the Helgoland site at least during spring migration: (1) Overall individual numbers of gulls feeding are lower in the Elbe region, (2) the number of gulls handling prey is higher in the Helgoland region, (3) the use of the Elbe river as feeding and resting site seems to be much stronger during autumn migration (e.g. Albat 1993; Garthe 1993b; 1996). The different quality between the two sites might be determined primarily by different quality of food: The high amounts of zooplankton (i.e. primarily fish eggs and larvae as well as decapoda larvae and copepoda; Table 11) will provide a higher energy content compared to the mainly terrestrial food (i.e. insects) in the Elbe estuary. Additionally, drowned insects might also be a less predictable food source, because they could be available in considerable numbers only during certain wind conditions, that blow them out to the sea (Meyer et al. 1998). This can not be answered definitely by the relatively small number of food samples collected. Oppositely, MF Leopold (pers. comm.) reports of high amounts of fish larvae used by little gulls in the Dutch offshore area. Garthe (1993b, 1996) describes the intake of small pelagic fish, mainly smelt (*Osmerus eperlanus*), in the upper part of the river outlet of Elbe during autumn, which could not be observed during spring. Smelt is a very frequent pelagic fish of the Elbe river and is abundant throughout the year (Möller 1984; Thiel et al. 1995; Thiel & Potter 2001). The proportion of small 0-group smelt, that – according to its length – is suited best as prey for little gulls, is available from June onwards but seems to be super-abundant during August and September (Möller 1984). According to Garthe (1993b) this is the main autumn migration period of *Larus minutus* in the Elbe estuary. These findings may explain why the Elbe estuary might play a more important role during that migration period.

Although the content of fishing samples can only be regarded as potential prey items, there are various observations that proof that insects and zooplankton as well as small fish are the most likely food used during spring migration: (1) According to our behavioural observations, most feeding little gulls were recorded dipping or surface pecking. This is a typical behaviour for intake of small organisms which float close to the water surface. (2) Although investigations of stomach contents are very rare and only available from breeding grounds, insects and (to a smaller extent) fish larvae were found to be the most frequent food items as interpreted from the available literature (reviews in Cramp & Simmons 1983; Zubakin 1990). (3) Observations at resting sites during migration revealed frequent intake of insects either from the water surface or by aerial capture (e.g. Isenmann 1973; Morris 1992). The present study suggests that a diet consisting mainly of insects is not necessarily limited to freshwater lakes and breeding sites but may also occur in certain marine and coastal regions.

Prey capture technique and – perhaps even more important – food choice of little gulls seem to lead to an avoidance of competition with other gull species or terns: *Larus*

minutus can be classified as a typical social feeder and it can be assumed that this species benefits from foraging in interspecific groups, since terns and larger gull species that occur most frequently in such associations (Fig. 21) tend to feed on a different range of food (of larger size). Little gulls might take advantage of small prey or parts of prey which commonly become available during such feeding actions by other bird species. Evans (1989) reports that little gulls associated with hunting auks during winter, a phenomenon that we could observe frequently (unpubl. data). It is most likely that diving or plunging birds drive up suitable prey to the sea surface. However, during spring migration, little gulls were only rarely associated with diving birds and seem to benefit mostly from other surface-feeding species.

In conclusion, the present study revealed important patterns of habitat use by little gulls in the German Bight during spring migration. Although this species seems to be capable of using food in most areas of the German Bight while at the same time migrating very rapidly, there is strong evidence that different sites serve as major feeding grounds during spring migration and thus should be regarded as important and sensitive for little gulls at least during spring migration. Those staging sites can be of high importance for a far migrating seabird like the little gull, because they can provide significant carry-over effects between wintering / resting areas and the breeding grounds in order to provide good body condition and ensure high breeding success.

Acknowledgements

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Chapter IV

Area utilisation of gulls in a coastal farmland landscape: Habitat mosaic supports niche segregation of opportunistic species

Abstract

The intensively farmed coastal lowland landscape of Germany, adjacent to the North Sea, provides important foraging opportunities for black-headed, common, herring and lesser black-backed gull (*Larus ridibundus*, *L. canus*, *L. argentatus* and *L. fuscus*). We expected that spatial and temporal utilisation of the landscape mosaic as well as behavioural traits and utilisation of food resources would differ between these closely related species, facilitating niche segregation. We recorded the habitat types and their utilisation by the four species field by field over a whole year. In addition, we related species abundance to abiotic parameters. Black-headed and common gulls were the most numerous species in the study area throughout the year. In general, the former preferred habitat types with a higher level of farming activities and was often directly associated with farming tractors, whereas the latter was dominant on pastures. The black-headed gull seems to have a higher ability to exploit ephemeral, anthropogenic food sources and to exclude common gulls from such resources. Conversely, common gulls tend to prefer patches with naturally distributed prey. The most prominent abiotic parameter influencing gull abundance was farming tractors. Black-headed gulls are most likely to have benefited from recent changes in agricultural practice, while common gulls may have suffered from a decline in pastures. Our study indicates that, at present, interspecific competition is low, as two of the four gull species mainly forage in the marine environment, while there is significant habitat partitioning between the other two temporally, spatially and behaviourally.

Introduction

Gulls as opportunistic species can act as indicators for human induced changes in landscapes. Most species of (breeding) gulls at the German North Sea coast increased dramatically during the 20th century, which may to a large extent be explained by favourable food conditions due to anthropogenic activities (Garthe et al. 2000; Fig. 3). Higher numbers of gulls on terrestrial sites seem to be strongly positively correlated with the increase of industrial farming as well as with utilisation of anthropogenic waste (e.g. Mudge & Ferns 1982; Horton et al. 1983; Flore 2006; Gloe 2006). Anthropogenic activities in general can be highly relevant for different species of gulls to carry breeding populations, provide food resources but also even to facilitate coexistence (Hunt & Hunt 1973).

The coastal lowland landscape of Germany, adjacent to the North Sea coast, holds such intense anthropogenic (agricultural) activities. Its importance for gulls has perhaps been underestimated for a long period of time due to its vicinity to the Wadden Sea which carries huge quantities of seabirds and shorebirds (Blew et al. 2005b). Recent investigations deal with area utilisation and niche segregation of gulls at sea (e.g. Kubetzki & Garthe 2003; Schwemmer & Garthe 2005; 2006), but most interestingly there are only few studies that focus at these topics in terrestrial landscapes: Vernon (1970a; 1972) points out the importance of different mainland habitat types for two gull species in the mainland of the UK during winter. However, a longer period of observation and a fine-scale resolution of different habitat types will be necessary to reveal the function of the landscape mosaic for gulls. Such fine-scale patterns might play a subtle but important role in terms of niche segregation. Furthermore, abiotic parameters may indirectly influence the spatio-temporal dynamics of different species in a different way by steering prey availability (e.g. Steele 1989; Honza 1993).

Closely related species within the same geographical area are expected to exhibit niche segregation by (1) spatial habitat partitioning, (2) temporal differences, (3) utilisation of different resources as well as (4) differences in behaviour (Begon et al. 2006). The aim of this study is to shed light on the utilisation of the landscape mosaic by the four closely related gull species of the North Sea coast, black-headed, common, herring and lesser black-backed gull (*Larus ridibundus*, *L. canus*, *L. argentatus* and *L. fuscus*) and to elucidate niche segregation patterns with regard to these ecological principles. We compared observed and expected gull numbers on various farmland habitat types (with different anthropogenic influence) and in relation to abiotic parameters and additionally conducted detailed recordings of behaviour. The design of this study is based at a regional scale and high temporal resolution and thus should allow to derive the principles of coexistence of closely related species in a highly dynamic agricultural landscape. Finally, it should enable to draw general conclusions of the relationship between niche segregation and the (future) development of industrial farming.

Methods

Study area

The study area is located on a peninsula close to the North Sea coast in the northernmost German Federal State, Schleswig-Holstein, (central coordinates: $8^{\circ} 53' 24$ E and $54^{\circ} 09' 36$ N; Fig. 25). We conducted a total of 115 counts of all four gull species using fields along a 16.8 km long transect route. The study area is a typical German coastal mainland area mainly consisting of fields with intensive tillage and a smaller number of pastures. The transect covered a total area of 7.8 km² and encompassed all fields that the route went through ($n = 208$). It was set nearly perpendicular to the coast from a point close to the shore line near the city of Büsum to another point in the mainland (linear distance 11.2 km; Fig. 25).

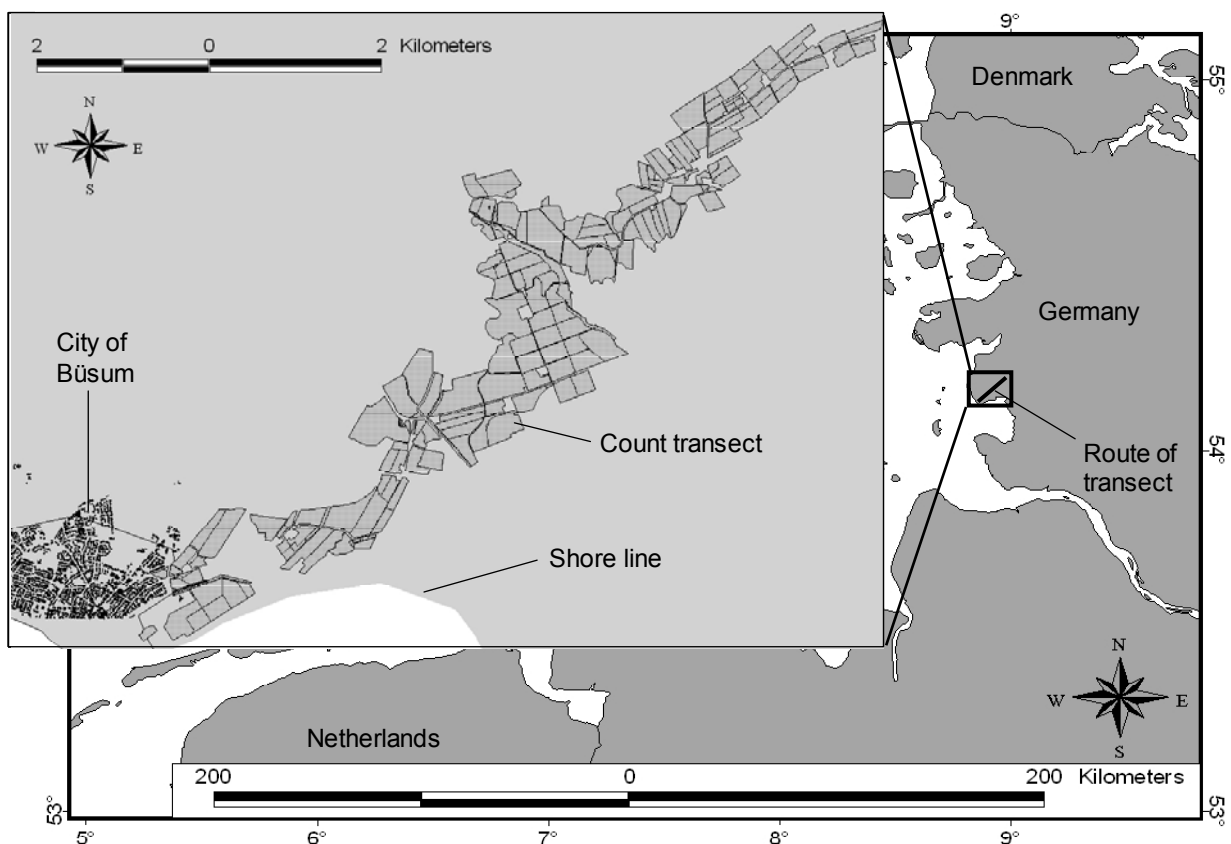


Fig. 25: Study area near the German North Sea coast. Rectangle indicates the location of the count transect from the city of Büsum to another point away from the shore line. Polygons in the detailed map represent single fields along the count transect. Additionally, the whole section of the detailed map was recorded once per month to calculate abundance values of gulls on different habitat types within a larger study area. Data source: Digital ALK data provided by Vermessungs- und Katasterverwaltung Schleswig-Holstein.

Observations took place from October 2004 to September 2005. Between 8 to 15 counts were carried out in each month (except only 4 counts in February due to heavy snow). During each count, gull numbers and associated habitat type (for habitat availability see Table 12) as well as behaviour of gulls were recorded. Taking into account that gull abundance as well as habitat preference would depend on season (see Atkinson et al.

2002), we split the data set into four periods: (1) Winter (November to February), (2) spring migration (March to April), (3) breeding time (May to July) and (4) autumn migration (August to October).

Table 12: Mean habitat availability [km²], proportion on the total and n number of fields with the respective habitat in the transect area during the four seasons. Habitat types were classified into three classes (level of farming) according to the degree of agricultural activity.

Habitat type	Level of farming	Winter		Spring migration		Breeding		Autumn migration	
		Availability [km ²] and proportion	n	Availability [km ²] and proportion	n	Availability [km ²] and proportion	n	Availability [km ²] and proportion	n
Fallow	1	0.15 (1.9%)	5	0.16 (2.1%)	6	0.27 (3.4%)	9	0.27 (3.4%)	9
Pasture	1	2.03 (25.9%)	91	1.62 (20.7%)	82	1.62 (20.7%)	82	1.62 (20.7%)	82
Potatoes	2	0	0	0.04 (0.6%)	1	0.54 (6.9%)	12	0.47 (6.0%)	9
Cabbage	2	0.07 (0.8%)	5	0	0	0.29 (3.6%)	7	0.21 (2.7%)	7
Carrots	2	0.24 (3.1%)	4	0	0	0.26 (3.3%)	5	0.18 (2.3%)	4
Colza	2	0.87 (11.1%)	15	0.96 (12.2%)	16	0.96 (12.2%)	16	0.35 (4.5%)	8
Stubble	2	0.26 (3.3%)	7	0.07 (0.9%)	2	0	0	1.03 (13.2%)	19
Winter Wheat	2	2.19 (28.0%)	45	3.16 (40.2%)	63	3.56 (45.4%)	69	1.45 (18.5%)	29
harvested crops	3	0.22 (2.9%)	4	0	0	0	0	0.10 (1.3%)	2
drilled	3	1.74 (22.2%)	31	1.78 (22.7%)	36	0.35 (4.5%)	9	1.78 (22.7%)	35
ploughed	3	0.07 (0.8%)	1	0.05 (0.6%)	2	0	0	0.36 (4.6%)	5

Recording of behaviour

We classified behaviour into three categories: (1) Foraging behind tractor, (2) resting or sleeping, (3) searching for prey naturally. Individuals belonging to the third category could be subdivided into (1) walking over the ground, (2) flying while dipping to the ground, (3) aerial pursuit for insects. Additionally, we recorded species composition behind 124 farming tractors within the larger study area (total section of the detailed map in Fig. 25) throughout the year. Behaviour of these gulls associated with farming tractors was classified as (1) foraging within flock, (2) foraging outside of the flock, (3) resting. We computed the proportions of gulls that were associated with tractors on the total number of gulls recorded during the 115 transect counts.

Habitat preference

Total habitat availability [km²] of each agricultural habitat type was recorded field by field. According to farming activity the total area of each habitat type varied over the course of the year, thus habitat availability was recorded whenever changes took place (Table 12).

We calculated total area of each habitat type using a detailed digital map containing information on the area of each land parcel (software: Arc View 3.2). We analysed the preference for habitat types with different levels of farming for each species. Habitats were classified as: (1) Recently farmed fields with open soil = high level of farming, (2) fields under farming with crops = medium level of farming, (3) pastures and fallow = low level of farming (see Table 12 for detailed habitat classification).

In order to analyse habitat preference and to avoid statistical bias due to differences in gull numbers between the four species and habitat availability we computed a habitat preference score (HP), separately for each day of observation, each level of farming and each species: First, expected values (EXP) of gull numbers of each species (s) within each level of farming (l) and day (d) were calculated by multiplying the available area of habitats of each level of farming (A_l) by the total number of each species of gulls (n_s) observed during that day and subsequently dividing by the total area (A) available:

$$EXP_{dls} = \frac{(A_l * n_s)}{A}$$

Subsequently, we derived the habitat preference score for every day, level of farming and species (HP_{dls}) by subtracting the observed gull numbers of each species and day within each level of farming (OBS_{dls}) from corresponding expected values and dividing this difference by the expected values:

$$HP_{dls} = \frac{(OBS_{dls} - EXP_{dls})}{EXP_{dls}}$$

This would lead to a preference score of -1 if no gulls of the species (s) had been observed on the respective observation day (d) and within the respective level of farming (l), to a score of 0 if the observed gull numbers exactly matched the expected values, while a positive score would indicate a preference for the respective level of farming. We added all preference scores 2 to allow for logarithmic scaling. We computed medians as well as the 5% and 95% percentiles of the habitat preference score. The score served to detect differences of preferences of levels of farming within and between species: (1) We tested separately for each species and season whether certain levels of farming were used more than others. (2) To compare the four gull species we conducted tests separately for each combination of level of farming and season. We used Friedman tests to detect general significant differences between preferences of farming levels within species and seasons as well as species differences within levels of farming and seasons. In case of a significant result of a Friedman test, Wilcoxon tests were applied as post-hoc tests. For these analyses observation days served as sampling units. If a species was not observed at a particular day or never observed within a certain level of

farming, corresponding data were excluded from the data set. Tests were only conducted if after exclusion at least six observation days remained. Wilcoxon rather than Friedman tests were applied when only two species or farming levels remained in the data set after exclusion. Since the same two null-hypotheses (no preferences of certain levels of farming within species and seasons as well as no species differences within levels of farming and seasons, respectively) were both tested several times (i.e. for different seasons, species and levels of farming), an α -level adjustment was necessary in order to avoid reporting spurious significances. This was achieved using Fisher's Omnibus test. This procedure 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 & Meelis 1994).

Densities on different habitat types

In order to gain information on abundance values of the four gull species on each agricultural habitat type we recorded gull numbers within a larger study area (28.3 km²; total section of the detailed map in Fig. 25) once per month. Densities were computed by dividing individual numbers of each species associated with each habitat type by the total area available of each habitat type. Finally, we calculated mean densities for each season.

Abiotic factors

We related total gull abundance to the following abiotic parameters: (1) Wetness of the soil (as wet or dry), (2) presence / absence of farming tractors (as present or absent), (3) wind force [Beaufort], (4) time of day (as minutes before or after noon [UTC]) and (5) stage of the tide (as minutes after high tide). Time of day and stage of tide were initially assumed to influence gull numbers also with their square values, but since a visual inspection of the data did not yield any hints for such a relation, linear relations were considered appropriate. For statistical analyses the first two parameters were considered as factors while the other three were treated as covariates.

We analysed the data in two different ways: (1) Using a multi-factorial approach a general linear model (ANCOVA) was applied. Here, we tested the influence of the two factors (presence of farming tractors and wetness of the soil) in combination with one covariate on the total gull numbers, separately for each combination of species and season. This analysis was conducted separately for each covariate because otherwise error degrees of freedom were too small. Initially, also the interactions between the two factors and the covariate were included into the model. In case interactions between the factors and the covariate did not reveal significance, they were removed from the model and testing was repeated. If such an interaction revealed significance we refrained from applying the ANCOVA for that analysis (Engqvist 2005). Both factors were treated as fixed-effects factors and Type III sum-of-squares were applied. (2) In a non-parametric and uni-factorial approach we tested the influence of each factor separately for both levels of the other factor using Mann-Whitney U-tests. The relation between total gull

numbers and each of the covariates was tested using Spearman rank correlation applied separately to each combination of the two factors. Again, we used Fisher's Omnibus test to account for multiple testing. In addition, to investigate whether correlation coefficients revealed a consistent effect across different seasons, levels of factors (e.g. tractor presence) etc., we used a one-sample t-test of the correlation coefficients (expected value: 0). Non-parametric tests were only carried out if the sample size was sufficiently large to principally enable a significant result (Spearman's rank-correlation: $n \geq 5$; Mann-Whitney U-test: $N_1 = N_2 \geq 4$ or $N_1 \geq 5, N_2 \geq 3$). As a consequence, some combinations of species, season and abiotic parameter were not tested.

For the ANCOVA data were partly log- or rank-transformed in order to achieve normally distributed and homogeneous error variances. For combinations of species and seasons for which none of the transformations did yield a normal distribution we carried out no ANCOVA but permutation tests. These two-factor permutation tests were based on a restricted permutation keeping the structure of the data, i.e. in tests of differences between species days were permuted within seasons, whereas in tests of differences between seasons, days were permuted within species. The test of the interaction between the two factors can be done using both permutation procedures. As test statistics we used the sum of the squared differences between means per level of a factor and the overall mean or, in case of the interaction, the sum of the squared differences between means per combination of levels of the two factors and the overall mean. For winter the factor abundance of farming tractors was not tested as hardly any tractor was present during that time of the year.

We present results of both, the parametric multi- and the non-parametric uni-factorial approach, as the assumptions of the ANCOVA were hardly fulfilled in several cases, mainly because response variables were severely skewed particularly if they comprised larger proportions of tied observations. Nevertheless we consider the multi-factorial approach as useful, as it is able to reveal interactions between different abiotic parameters. In addition, its power could be superior compared to the non-parametric approach since it does not require splitting the data in order to control for the effects of potentially confounding additional factors (which cannot be included into a non-parametric analysis) and hence is based on larger samples. The presentation of both methods also allows to cross-validate the results.

We carried out most statistical standard procedures using SPSS, whereas Spearman's rank correlation was applied using self written software (R Mundry). For non-parametric tests of small samples we used exact tests (Siegel & Castellan 1988; Mundry & Fischer 1998). Non-parametric tests of larger samples with larger proportions of tied observations were not tested using the standard approximation with correction for ties but using a permutation procedure (e.g. Manly 1997; Monte-Carlo significance, SPSS). Where not stated otherwise, 10,000 permutations were conducted. All indicated p-values are two-tailed.

Results

Abundance and phenology

Overall numbers of gulls in the coastal mainland differed between the four species: The black-headed gull was most frequent, followed by the common gull, while herring and lesser-black-backed gull did not play a quantitatively important role during most of the year (Fig. 26; Table 13). Phenology of black-headed and common gull were rather

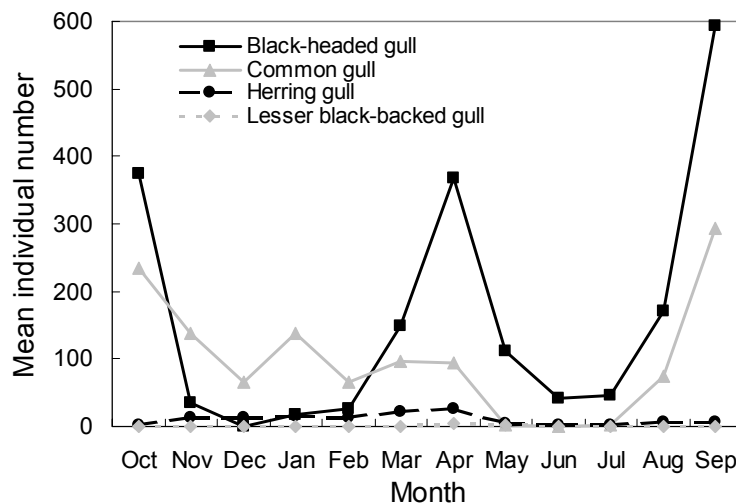


Fig. 26: Phenology of black-headed, common, herring and lesser black-backed gull in the transect area in the German coastal mainland during October 2004 to September 2005.

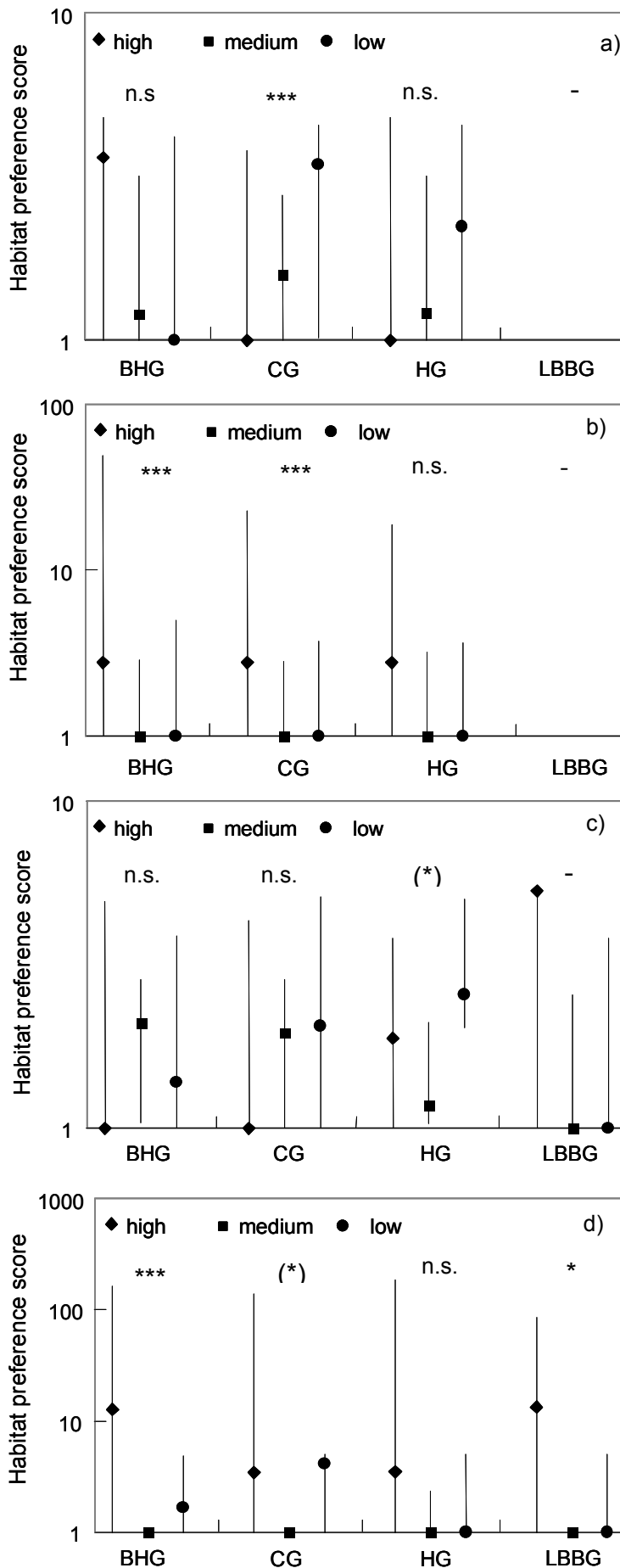
similar, both showing a clear peak with maximum numbers during autumn migration, while during spring migration at least black-headed gull revealed a second peak (Fig. 26; Table 13). The common gull was the most frequent species during winter, and all species showed lowest numbers during the breeding period. Black-headed gull was present in more than 90 % of all counts during breeding, but mainly in small numbers (Table 13).

Table 13: Proportion of transect counts with sightings of at least one individual per corresponding species and maximum number (in brackets) for each season. BHG = black-headed gull, CG = common gull, HG = herring gull, LBBG = lesser black-backed gull.

	BHG	CG	HG	LBBG	n counts
Winter	44% (180)	84% (527)	81% (53)	0% (0)	32
Spring migration	78% (798)	78% (481)	56% (105)	28% (16)	18
Breeding time	92% (433)	26% (12)	36% (23)	21% (9)	39
Autumn migration	96% (1311)	89% (1180)	50% (28)	12% (1)	26

Preference of levels of farming

There were general significant differences in the preference for habitats of the three levels of farming, both between and within species (Fisher's Omnibus tests: $\chi^2 = 46$; $df = 22$; $p < 0.005$; $\chi^2 = 144.1$; $df = 26$; $p < 0.001$, respectively; Fig. 27a-d). Throughout the year black-headed and lesser black-backed gulls revealed the strongest preference for habitats with the highest level of farming, whereas common (despite of autumn



migration) and herring gulls (despite of autumn migration and breeding) showed strongest preferences for habitats with low and medium levels of farming (see asterisks in Fig. 27a-d for significant differences between levels of farming within each species). Winter was the only season that revealed significant differences between the species, i.e. in the levels of high and low farming (Friedman tests, high: $\chi^2 = 6.57$; $df = 2$; $p < 0.05$; low: $\chi^2 = 13.17$; $df = 2$; $p < 0.005$, respectively; Fig. 27a): Black-headed gulls revealed a significantly higher preference for habitats with the highest level of farming compared to common gulls (Wilcoxon test: $T^+ = 75$; $N = 10$; $p < 0.005$), while the latter showed a significantly higher preference for habitats with lowest levels of farming compared to black-headed gulls (Wilcoxon test: $T^+ = 87$; $N = 12$; $p < 0.005$).

Fig. 27: Preference of habitat types with different levels of farming (low, medium and high) during a) winter, b) autumn migration, c) spring migration, d) breeding. No or not sufficient lesser black-backed gulls were encountered during winter and autumn migration. Asterisks refer to tests of differences between the three levels of farming within each gull species ((*): $p \leq 0.1$, (*): $p \leq 0.05$, **: $p \leq 0.005$, ***: $p \leq 0.001$, n.s.: not significant, -: not tested due to small sample sizes; see Table 13 for species abbreviations).

Table 14: Mean densities (individuals / km²) of black-headed (BHG), common (CG), herring (HG) and lesser black-backed gulls (LBBG) on different habitat types during the four seasons recorded during 12 counts within the larger study area (total area: 28.3 km²; see Material & Methods section for details; - = habitat type not available).

	Winter				Spring migration				Breeding				Autumn migration			
	BHG	CG	HG	LBBG	BHG	CG	HG	LBBG	BHG	CG	HG	LBBG	BHG	CG	HG	LBBG
Harvested	1.7	3.3	0.2	0	-	-	-	-	305.8	0	0	0	684.4	3.9	0	0
Fallow	0	0	0	0	23.3	0	0	0	0	0	0	0	4.4	1.5	0	0
Drilled	0	0.2	0	0	29.7	1.3	0	0	393.5	15.1	17.4	2.4	175.7	74.0	4.0	0.3
Ploughed	10.3	31.3	0.3	0	255.1	21.7	95.7	1.3	61.5	6.4	28.9	0	474.2	200.6	7.0	0
Pasture	8.9	44.9	7.9	0	36.9	8.1	3.5	0	15.3	15.1	15.5	1.9	32.2	44.3	7.7	0.7
Vegetables	0	0	0	0	0	0	0	0	50.0	9.9	20.5	4.0	13.7	2.9	0	0
Colza	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0
Stubble	1.1	2.5	0.5	0	0	0	0	0	2.1	0	3.2	4.2	31.4	12.2	6.3	0.3
Winter wheat	0.2	3.8	2.6	0	30.0	4.7	0.4	0	0.7	0	0	0	6.0	16.7	0.1	0
total density in study area	3.1	14.3	2.8	0	33.4	4.7	3.6	0.0	15.4	3.7	4.7	0.6	54.9	32.5	2.7	0.2

During breeding a trend (though not significant) was found for more black-headed gulls on habitats with high level of farming compared to common and herring gulls (Fig. 27d), while during both migration periods no significant differences were detected between the species (Fig. 27b-c).

Mean gull densities on different habitat types

Black-headed gulls showed the highest total densities in the study area except in winter, when common gulls dominated (Table 14). Herring and lesser black-backed gulls revealed total densities of < 5 individuals km⁻² during each season. Black-headed gulls reached highest densities on ploughed, drilled and harvested fields, while common gulls were mainly found on pasture except during both periods of migration. Values of herring gulls were highest either on pasture or ploughed fields. Generally, vegetables (except during breeding) and colza as well as fallow did not show high densities of any species (Table 14).

Gull abundance in relation to abiotic factors

Uni-factorial approach

Each of the abiotic parameters influenced gull abundance significantly, except wetness (Table 15). Presence of active tractors as well as time of day had a consistent effect on gull numbers (see arrows in Table 15): Presence of active tractors lead to an increase in total numbers in all cases (no test for consistence necessary). In all but one case (black-headed gull during breeding) numbers decreased during the course of the day (consistence tested by t-test of Spearman's rank correlation coefficients: mean $r_s = -0.29$; $t = -3.42$; $df = 6$; $p < 0.05$). Wind force and tide did not show consistence effects (mean $r_s = -0.004$; $t = 0.02$; $df = 6$; $p = 0.99$ and mean $r_s = -0.18$; $t = -1.05$; $df = 6$; $p = 0.33$, respectively). Although wetness itself had no significant effect, numbers increased most drastically during wet conditions when tractors were present (Table 15), indicating a combined effect of both parameters (see below).

Multi-factorial approach

The combined results of the ANCOVA and the permutation tests revealed an overall significant influence of the abiotic factors on total gull numbers (Fisher's Omnibus test: $\chi^2 = 268.9$; $df = 178$; $p < 0.001$). In detail, presence of active tractors as well as wind force had significant effects on gull abundance (Table 16). The multi-factorial design revealed a trend of an interaction between the two factors presence of tractors and wetness of the soil (Table 16), that was most prominent for black headed gulls during breeding and autumn migration: Numbers of black-headed gulls reached highest values when tractors where present during wet conditions (Fig. 28). Unlike the uni-factorial approach, the multi-factorial design did not detect general significant effects of time of day and tide on gull abundance.

Behaviour of gulls

Behaviour of the four gull species differed significantly according to the three behaviour classes ($\chi^2 = 2851.3$; $df = 6$; $p < 0.001$; Fig. 29a). All species but common gulls spent more than 40 % of their time resting, while the latter was found foraging naturally during most of the time. Of all species black-headed gulls foraged most intensively behind farming tractors (23 %). Naturally foraging individuals most commonly walked over the ground while searching, but a small proportion of common and black-headed gulls (< 5 %) foraged flying while continuously dipping to the ground. A small number of naturally foraging black-headed gulls was recorded in aerial pursuit for insects (4 %), whereas no other species foraged that way.

Table 15: Influence of abiotic parameters on individual numbers, tested separately for each species and season (indicated by left two columns). In order to exclude potentially confounding effects, Mann-Whitney U-tests of each of the two factors (tractor presence and wetness) were conducted separately for both levels of the respective other factor. Correspondingly, correlations between the covariates (wind force, time of day or tide, respectively) were calculated separately for all four combinations of levels of the two factors. The first row indicates the factor or covariate tested, the second row indicates the respective level(s) of the factor(s) controlled for. (*): $p \leq 0.1$, *: $p \leq 0.05$, **: $p \leq 0.005$, ***: $p \leq 0.001$, n.s.: not significant, -: not tested. + tractor: with tractor present, - tractor: without tractor present. Arrows indicate decreasing (↓) or increasing (↑) gull numbers with increasing value of a covariate or smaller (↓) or larger (↑) gull numbers on wet days or days with tractors present. General significance was tested using Fisher's Omnibus test. See Table 2 for species abbreviations.

	tractor		wetness		wind force		time of day		time of day		tide		tide	
	wet	dry	+ tractor	- tractor	+ tractor, wet	+ tractor, dry	+ tractor, wet	+ tractor, dry	+ tractor, wet	+ tractor, dry	+ tractor, wet	+ tractor, dry	+ tractor, wet	+ tractor, dry
BHG	Winter	* ↑	-	n.s.	n.s.	-	n.s.	*** ↓	n.s.	n.s.	-	*** ↓	n.s.	n.s.
	Spring	-	-	n.s.	n.s.	-	n.s.	n.s.	n.s.	n.s.	-	n.s.	n.s.	n.s.
	Breeding	* ↑	n.s.	(*) ↑	n.s.	* ↓	n.s.	n.s.	*** ↑	n.s.	n.s.	n.s.	*** ↑	n.s.
	Autumn	** ↑	n.s.	(*) ↑	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*** ↑	* ↓	n.s.	n.s.
CG	Winter	n.s.	-	n.s.	n.s.	-	n.s.	n.s.	*** ↓	n.s.	-	*** ↓	n.s.	n.s.
	Spring	-	-	n.s.	n.s.	-	n.s.	n.s.	n.s.	n.s.	-	n.s.	n.s.	n.s.
	Breeding	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*** ↑	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Autumn	* ↑	n.s.	n.s.	n.s.	*** ↓	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
HG	Winter	n.s.	-	-	(*) ↑	n.s.	-	n.s.	n.s.	n.s.	-	n.s.	n.s.	n.s.
	Spring	-	-	-	n.s.	n.s.	-	n.s.	n.s.	n.s.	-	n.s.	n.s.	n.s.
	Breeding	n.s.	n.s.	n.s.	n.s.	n.s.	(*) ↑	*** ↑	n.s.	n.s.	n.s.	n.s.	n.s.	*** ↑
	Autumn	* ↑	n.s.	n.s.	(*) ↓	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
LBBG	Winter	-	-	-	-	-	-	-	-	-	-	-	-	-
	Spring	-	-	-	n.s.	n.s.	-	n.s.	n.s.	n.s.	-	n.s.	n.s.	n.s.
	Breeding	n.s.	n.s.	n.s.	* ↑	n.s.	n.s.	*** ↑	n.s.	n.s.	n.s.	n.s.	n.s.	*** ↓
	Autumn	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*** ↓	n.s.	n.s.	n.s.
General signi- cance	$\chi^2 = 59.3$ df = 38 p < 0.05		$\chi^2 = 51.9$ df = 46 n.s.		$\chi^2 = 129.2$ df = 58 p < 0.001		$\chi^2 = 157.5$ df = 58 p < 0.001		$\chi^2 = 155.4$ df = 58 p < 0.001					

Table 16: Results of multi-factorial tests (ANCOVA / permutation tests) of the influence of abiotic parameters on numbers of individuals, conducted separately for each species and season. The two factors tractor presence and wetness were tested simultaneously and in combination with one covariate at a time. (*): $p \leq 0.1$, *: $p \leq 0.05$, **: $p \leq 0.005$, ***: $p \leq 0.001$, n.s.: not significant, -: not tested. Only those combinations of species and seasons were tested that comprised at least five values (days) per each combination of the levels of the two factors. Lesser black-backed gulls were not tested due to too low sample size. General significance was tested using Fisher's Omnibus test. See Table 13 for species abbreviations. PERM = permutation test.

		active tractor	wetness	wind force	time of day	tide	active tractor x wetness	method
BHG	Spring	n.s.	n.s.		n.s.		n.s.	ANCOVA
	Spring	n.s.	n.s.			n.s.	n.s.	ANCOVA
	Breeding	**	n.s.	n.s.			(*)	ANCOVA
	Breeding	**	n.s.		n.s.		(*)	ANCOVA
	Breeding	**	n.s.			(*)	*	ANCOVA
	Autumn	*	n.s.	*			n.s.	ANCOVA
	Autumn	*	n.s.		n.s.		n.s.	ANCOVA
	Autumn	*	n.s.			n.s.	(*)	ANCOVA
CG	Winter	-	n.s.	n.s.			-	ANCOVA
	Winter	-	n.s.		*		-	ANCOVA
	Winter	-	(*)			n.s.	-	ANCOVA
	Spring	n.s.	n.s.	n.s.			n.s.	ANCOVA
	Spring	n.s.	n.s.		n.s.		n.s.	ANCOVA
	Spring	n.s.	n.s.			n.s.	n.s.	ANCOVA
	Breeding	n.s.	*				n.s.	PERM
	Autumn	*	n.s.	***			n.s.	ANCOVA
	Autumn	(*)	n.s.		n.s.		n.s.	ANCOVA
	Autumn	(*)	n.s.			n.s.	n.s.	ANCOVA
HG	Winter	-	(*)	n.s.			-	ANCOVA
	Winter	-	(*)		n.s.		-	ANCOVA
	Winter	-	(*)			n.s.	-	ANCOVA
	Spring	n.s.	n.s.	n.s.			n.s.	ANCOVA
	Spring	n.s.	n.s.		n.s.		n.s.	ANCOVA
	Spring	n.s.	n.s.			n.s.	n.s.	ANCOVA
	Breeding	n.s.	n.s.				n.s.	PERM
	Autumn	n.s.	n.s.				*	PERM
General significance	$\chi^2 = 91.9$ df = 40 p < 0.001	$\chi^2 = 57.8$ df = 52 n.s.	$\chi^2 = 25.9$ df = 14 p < 0.05	$\chi^2 = 19.5$ df = 16 n.s.	$\chi^2 = 20.1$ df = 16 n.s.	$\chi^2 = 53.6$ df = 40 p = 0.073		

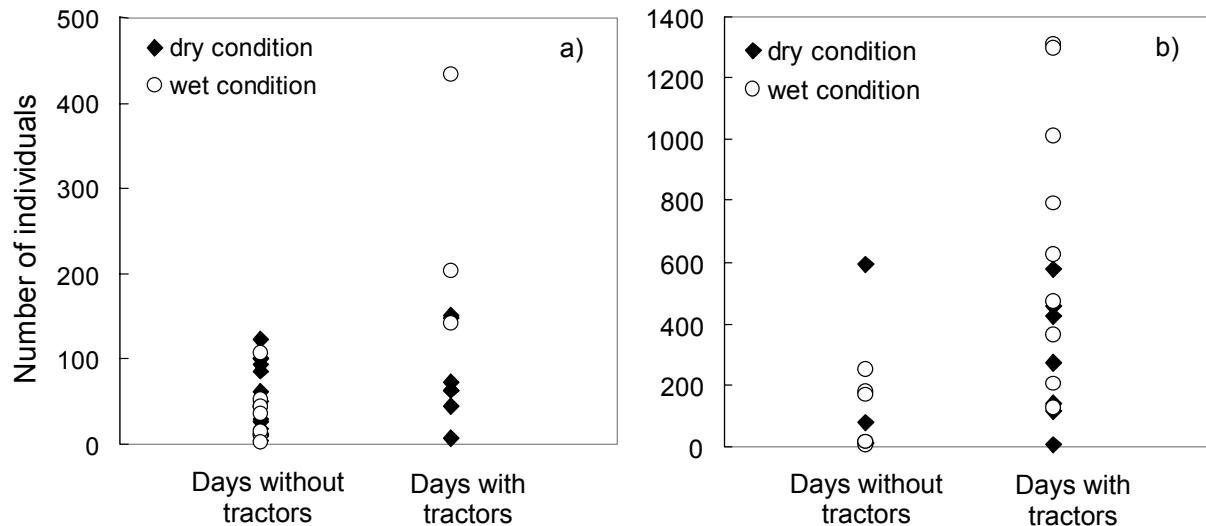


Fig. 28: Influence of the interaction between presence / absence of tractors and wetness on total numbers of black-headed gulls within the counting transect during a) breeding ($n = 39$ observation days) and b) autumn migration ($n = 26$ observation days).

26 of the total of 124 farming tractors recorded were not attended by gulls (21 %). Most tractors encountered were cultivating the soil by ploughing or drilling (85 %). These generally attracted the largest flocks of gulls (mean number of all individuals: 182). A smaller number of tractors (15 %) that usually did not attract as many birds as the former (mean number of all individuals: 63) were harvesting, mowing, or deploying dung. Species composition behind farming tractors was clearly predominated by black-headed gulls (78.7 % of all gulls associated with tractors), followed by common gulls (20.6 %) while herring (0.6 %) and lesser black-backed gulls (0.1 %) were not frequently found behind tractors.

Proportions of gull associated with tractors on the total during each season differed significantly between the four species ($\chi^2 = 826.4$; $df = 9$; $p < 0.001$; Table 17). Black-headed and common gulls reached highest values during autumn migration. Throughout the year black-headed gulls revealed the highest proportions, followed by common gulls, while herring gulls revealed the lowest values (Table 17). Lesser black-backed gulls were only encountered during breeding and spring migration and showed medium numbers. The behaviour of gulls behind farming tractors differed significantly between species according to the three behaviour classes ($\chi^2 = 6323.8$; $df = 6$; $p < 0.001$): Most black-headed gulls foraged within the dense flock in the vicinity of the tractor, while common gulls showed a higher proportion of individuals foraging aside of the dense flock and most herring gulls were found resting (Fig. 29b).

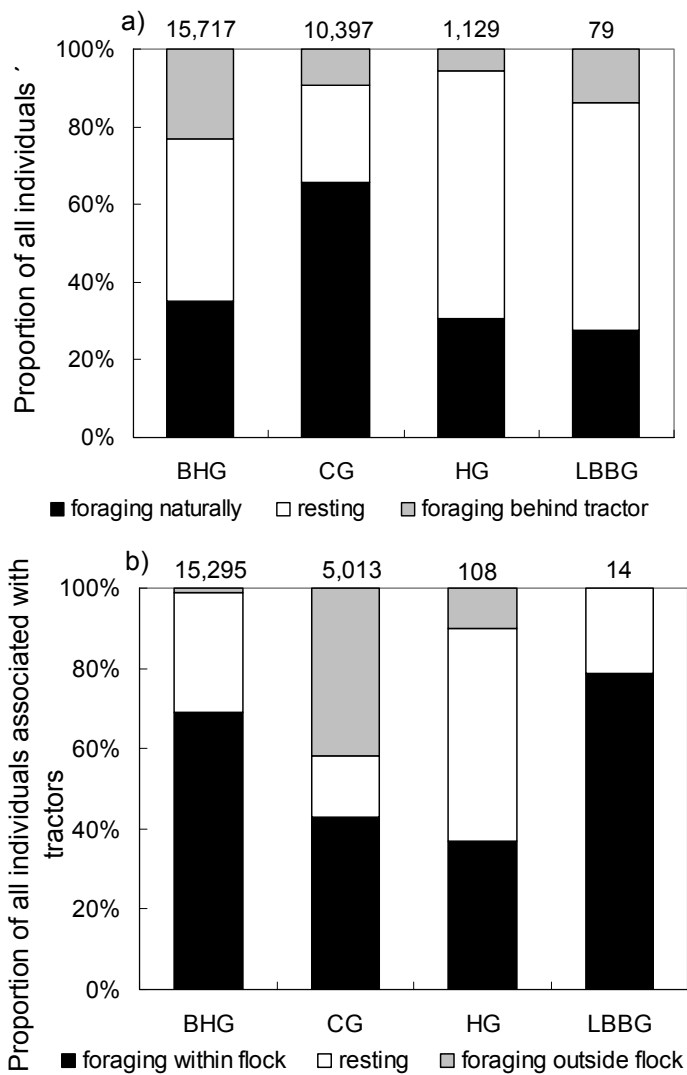


Fig. 29: a) Behaviour of all gulls within the transect area during all counts expressed as proportions on three behaviour categories. b) Behaviour of gulls associated with 124 farming tractors within the transect and larger study area expressed as proportion on three behaviour categories. Numbers above the columns depict the numbers of gulls included.

Discussion

Our findings suggest an important role of terrestrial (near shore) habitats at least for the two small gull species. This fits well studies from the UK where larger gull species mainly foraged on tidal flats or – when feeding inland – used refuse tips, while the small species were frequently observed on fields (e.g. Vernon 1970a; 1972; Mudge & Ferns 1982; but see Sibly & McCleery 1983). Low numbers in our study area throughout the year highlight the importance of adjacent marine feeding sites for herring and lesser black-backed gull at the German North Sea coast, which is also confirmed by dietary analyses (e.g. Verbeek 1977; Kubetzki & Garthe 2003; Chapter II). As black-headed and common gulls must be regarded as the most important species in terrestrial habitats, they will be emphasised in the subsequent discussion.

Table 17: Proportion of gulls associated with farming tractors on the total of all gulls recorded during each season.

	BHG	CG	HG	LBBG
Winter	25.9 %	5.9 %	5.6 %	0 %
Spring migration	33.2 %	11.2 %	8.2 %	24.4 %
Breeding	31.2 %	18.5 %	11.4 %	12.9 %
Autumn migration	39.4 %	28.5 %	1.8 %	0 %
Overall average	32.4 %	16 %	6.8 %	9.3 %

Temporal and spatial habitat use

Although none of the species investigated showed a distinct preference for a single habitat type or level of farming, the most obvious and basic difference existed between common and black-headed gulls: The former species preferred low levels of farming and particularly pastures more than the latter, which was frequently associated with high levels of farming and recently cultivated fields. But our findings also show that this general pattern was not consistent throughout the year. We found significantly higher preference values for high levels of farming in black-headed gulls compared to common gulls during winter and a trend for the same relationship during breeding, whereas no such significant difference was found during both times of migration. Reasons for this patterns can be explained by taking into account the influence of agricultural practices which cause seasonal variation in habitat availability: Whereas the availability of the ploughed, harvested and drilled habitats changed dramatically, the availability of fallow and pasture stayed more or less constant during the year (Table 12). It is important to investigate the seasonal differences in habitat use in more detail:

Migration: During both times of migration (but particularly during autumn), farming activity is most intense causing a superabundance of food as a consequence of highly available drilled, ploughed and harvested fields. This generates a weak preference for habitats with low levels of farming in all species, including common gulls. Food availability in the whole area should be sufficient for all species, even for those being less successful in foraging directly behind farming tractors (see below). Peak numbers of gulls in the mainland during both periods of migration (Fig. 26) are confirmed by other studies (Platteeuw 1987; Pedersen et al. 2000; see also Chapter I). However, because of the superabundant food, interspecific competition might be considered moderate despite high total individual numbers.

Breeding: In contrast to migration, the total area of suitable foraging habitats can be considered as particularly low, because (1) vegetation on most fields is high and thus not suitable for foraging (Morris 2000; Butler & Gillings 2004; Devereux et al. 2006), (2) intensity of soil cultivation providing artificial food sources is low shortly before harvesting. This might lead to constant numbers of all species but particularly black-headed gulls on the few available fields with open soils and grazed or mowed pastures (Table 14; Fig. 27d). The main reason for the low numbers of common gulls in the mainland may be seen in their low breeding pair numbers at the German North Sea coast (Garthe et al. 2000; Kubetzki 2001).

Winter: Although during winter there is still a moderately high availability of fields with open soils (Table 12), this is the time with the lowest farming activities during the whole year. Gulls are forced to gain their food by natural foraging. Black-headed gulls seem to be most dependent on anthropogenic food resources as indicated by habitat preference and significant correlations to farming tractors. Thus, it can be assumed that common gulls might be able to outcompete the latter during times of low anthropogenic

activities by mainly foraging on pastures, which requires a different feeding strategy (see below).

Generally, it should be considered that the patterns of temporal and spatial habitat use by the four gull species are highly variable. This is certainly caused by the rapidly changing food availability related to anthropogenic activities as well as by the general flocking behaviour of gulls (see below). However, despite of this variability, the general different preferences for certain habitats and levels of farming among the species are obvious.

Dietary and behavioural habitat partitioning

As revealed by dietary analyses of common gulls, earthworms (Lumbricidae) can make up to 90 % of the gull's food (Vernon 1970b; 1972; Kubetzki 2001). Earthworms show much higher biomass values under pastures compared to any type of arable land, as a result of a higher content of organic matter (Cuendet 1983; Edwards 1983). Furthermore, the age of the pasture is positively correlated with earthworm densities (Eijsackers 1983). Also, abundance of arthropods in grazed pastures (e.g. dung-dwelling specialists) was found to be higher compared to mowed sites (Vickery et al. 2001; Barnett et al. 2004). As most of the pastures in the study area are rather old and grazed by animals instead of being cut for hay production or silage, organic matter content and thus earthworm and arthropod abundance can be expected to be high. Biomass of earthworms under pasture reaches highest values during late autumn and early winter (Watkin & Wheeler 1966). This should offer good feeding opportunities for common gulls and is presumably a crucial factor for their high numbers on pastures during (early) winter. As black-headed gulls are more dependent on food related to farming, they might suffer stronger disadvantages when this ephemeral food resource vanishes.

Despite temporal and spatial habitat partitioning apparently existing between common and black-headed gulls, we found a high variance in habitat preference and frequent feeding in mixed flocks. A suitable explanation for this is the effect of local enhancement: According to this theory, the exploitation of food resources can be increased by high numbers of individuals (also of different species) joining in foraging actions (e.g. Waite 1981). Individual food intake rate can be increased by foraging within larger flocks, as high individual numbers indicate high food availability. Competition should be low as far as natural food resources are rich enough. This would contradict our findings of niche segregation between black-headed and common gulls to some degree. However, one essential difference between the use of pastures and of recently cultivated fields / farming tractors is the prey distribution: Although earthworms are known to aggregate in patches close to the surface according to microclimatic conditions, their distribution under pasture can be characterized as more or less even (Kruuk 1978; Waite 1981). Thus, earthworms present a type of food that is not defendable unlike anthropogenic waste, discards behind fishing vessels or the high quantities of soil invertebrates that become accessible during soil cultivation. Whereas we could observe

aggressive interactions and kleptoparasitism behind farming tractors mainly between black-headed gulls, this behaviour never occurred in naturally foraging individuals. Brockmann & Barnard (1977) state that the rate of kleptoparasitism should increase if the prey is superabundant (which is not necessarily the case in naturally foraging individuals). Furthermore, the even distribution of earthworms under pasture causes large distances between foraging individuals which would reduce the success of kleptoparasitism and aggressive interactions (Thompson 1986). Consequently, black-headed gulls are not capable of preventing common gulls to feed on pastures in mixed flocks. Furthermore, the scattered food under pastures requires a more intense searching time (Fig. 29a) that black-headed gulls might not be able to spend and are therefore possibly outcompeted by common gulls particularly during winter, when anthropogenic food availability is low. Thompson (1986) found that black-headed gulls using agricultural pasture in England completely relied on kleptoparasitising plovers (that fed on earthworms) instead of foraging on their own, which is supporting this assumption.

The utilisation of farming actions can be considered as the most important feature in niche segregation between the two small gull species. Hunt & Hunt (1973) revealed that small gull species tend to utilise habitats which provide small food items that can be handled more easily. As tractors stir up insects and other comparatively small prey, this might explain why the large gulls were hardly foraging behind farming tractors and their abundance was not significantly correlated with the presence of tractors, but it does not account for comparably low numbers of common gulls. Since this species also reveals low foraging success in the utilisation of fishery waste behind fishing vessels (e.g. Garthe & Hüppop 1994; Camphuysen et al. 1995), it can be assumed that common gulls generally seem to be less competitive in dense feeding flocks related to defendable, anthropogenic food sources. The exploitation of anthropogenic activities will lead to energetic advantages for the black-headed gull, as indicated by its frequent resting behaviour (Fig. 28a). The high proportion of resting herring gulls does not seem to be a result of frequent utilisation of anthropogenic food, but can be explained by taking into account that this species mainly exploits tidal flats (e.g. Verbeek 1977; Kubetzki & Garthe 2003) and thus might use the coastal mainland primarily for resting purposes.

Gull abundance in relation to abiotic parameters

The availability of natural food resources and thus gull abundance is supposed to correlate with meteorological parameters (e.g. Steele 1989; Honza 1993). Earthworms are most available during wet conditions as well as in the early morning hours (Kruuk 1978; Sibly & McCleery 1983). This suits to the findings of our study, as at least the uni-factorial approach detected significantly higher numbers of all gulls in the morning hours compared to the rest of the day. Wetness, however, did not significantly influence gull abundance in general (although we found indications for higher gull numbers during wet conditions). Presumably, wet soil alone did not suffice to increase the availability of soil invertebrates, but in connection with soil cultivation it seems to lead to higher prey

availability. As earthworms migrate towards the upper soil layers during wet conditions (e.g. Satchell 1967), the proportion of the total earthworm population that becomes available during soil cultivation can be considered much higher compared to dry conditions, when many individuals are located below the depth of the ploughshare.

Wind force is able to influence prey availability (especially earthworms) only indirectly via air humidity (Kruuk 1978). Nevertheless, we found that wind force strongly affected gull abundance (though very inconsistently; Tables 15 and 16). Reasons for that are probably not connected to foraging but result from the flocking behaviour of gulls during severe weather (Vernon & Walsh 1966; my own observations): A high proportion of individuals is forced to abandon the submerged high tide roost sites near the shore and shelter in flocks inland. This aggregated dispersal would lead to low individual numbers, in case the flocks built up outside our study area or it would lead to high values if flocks were located within the study area. Thus, it is most likely that high wind forces generally have an increasing effect on numbers, but our methodological design (too small study area) was not able to detect this. As high tide roosts (also during calm conditions) can be located in the mainland, too, stage of the tide might show similar inconsistent results. These effects additionally enhance the variability of the data.

The presence of farming tractors influenced gull numbers most explicitly and possibly superimposed effects of other parameters. We tried to account for that by splitting the data set into observation days with and without tractors. However, the analysis of the other abiotic parameters may still be biased if farming tractors were present outside but in the vicinity of the study area. We believe that the rather high numbers of observation days might account for such a bias. An increase in observation days as a possible solution was rejected as it would have led to dependent data due to temporal autocorrelation.

Uni- and multi-factorial analyses of the abiotic parameters revealed similar results apart from influence of the tide and time of day. As the demands for the multi-factorial approach were only reached by transformation of the data, the uni-factorial analysis should be considered as more reliable. But, since the results of both methods agree in the most important parameters, we believe that the multi-factorial approach is basically correct and reasonable, as indicated also by the interaction between wetness and presence of tractors, which led to higher gull numbers.

In general, our analyses of abiotic parameters does not suggest any substantial differences between the species that would indicate niche segregation patterns, except presence of tractors that clearly seemed to be most favourable for black-headed gulls.

Conclusions

It has been shown that differences in area utilisation in the coastal mainland between black-headed and common gulls and partly also the two larger species were explicitly connected to anthropogenic activities which black-headed gulls were able to exploit most. Common gulls were found to depend on sites with the lowest level of farming at

least during certain seasons. The availability of a mosaic of different habitat types seems to support coexistence. However, during the last 30 years profound changes in agricultural practices throughout northern Europe have taken place (Chamberlain et al. 2000; Buckwell & Armstrong-Brown 2004). Such long-term habitat modifications can significantly influence habitat use, species diversity and population sizes as already shown for various bird species (Duncan et al. 1999; Chamberlain et al. 2000; Atkinson et al. 2002). The most crucial changes must be seen in the overall and continuous decline of the total area of pastures for the benefit of tillage as well as intensification of grasslands (Chamberlain et al. 2000; Kubetzki 2001; Vickery et al. 2001; Barnett et al. 2004). This development is certainly most favourable for black-headed gulls (see Barnett et al. 2004), while it might cause long-term severe effects for common gulls which are much more dependent on carefully managed pastures at least during winter. Thus, in case the population of black-headed gulls at the German North Sea coast will continue to increase (Garthe et al. 2000), common gulls might suffer from competition. At present, also the latter species is still able to take advantage of the high prey availability provided by farming activities at least during the most intense farming period in autumn. However, with increasing numbers of black-headed gulls that are more competitive behind farming tractors, it can be assumed that common gulls will be excluded from that food source. At present, competition between different gull species within the German coastal mainland seems to be low, as the two large species show low numbers in coastal mainland, while the two smaller ones reveal temporal and spatial habitat partitioning patterns as well as important differences in behaviour.

Acknowledgements

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Chapter V

Influence of water flow velocity and water depth on distribution and foraging patterns of a surface-feeding seabird in the German Wadden Sea

Abstract

In contrast to diving species, surface-feeding seabirds are far more dependent on biological or physical processes that cause enhanced prey availability close to the water surface. The highly structured Wadden Sea of the German North Sea coast is primarily dominated by the influence of strong tidal currents as one major physical factor. We investigated the influence of water flow velocity and water depth on the foraging behaviour of the surface-feeding Arctic tern (*Sterna paradisaea*) to test the following hypotheses: (1) We expected relationships between times and areas of highest water flow velocity and foraging activity of Arctic terns as a consequence of turbulences that might enhance prey availability. (2) We predicted that areas of highest foraging success should be located within areas of highest water currents and low water depth (as a result of enhanced biological productivity). (3) As Arctic terns are known to exhibit comparatively small foraging radii, we expected that the location of breeding grounds should be predictable as well using these environmental data. We carried out direct observations on prey brought into Arctic tern colonies as well as on foraging success in relation to different tidal stages. Furthermore, we analysed a long-term data set on at-sea distribution and behaviour of Arctic terns and modelled probabilities to encounter foraging individuals in relation to water currents and depth using a Generalised Additive Model (GAM). Prey choice of Arctic terns differed significantly between different tidal stages. Foraging success was highest during flood and ebb tides (i.e. during highest water flow velocities). Areas of major foraging activities were located primarily within the mouths of large tidal streams of the Wadden Sea and within areas of shallow water and high water currents. The breeding colonies of Arctic terns were located within a mean distance of 4.9 ± 4.7 km to areas where the probability to encounter a foraging individual was > 50 %. In conclusion, our findings clearly show the overall importance of physical processes to directly influence prey availability for surface-feeding seabirds. Moreover, we are for the first time able to reveal distinct foraging areas of Arctic terns in the Wadden Sea. In contrast to situations elsewhere, the Wadden Sea can be regarded as a very good foraging habitat for Arctic terns due to its high biological productivity and the physical processes that enhance prey availability.

Introduction

In contrast to diving seabirds, purely pelagic, surface-feeding species such as terns respond most sensitively to changes in food availability as they are only able to exploit a small part of the upper water column (e.g. Ashmole 1963; Monaghan 1996). Unlike gulls that may switch to terrestrial foraging habitats during times of low prey availability, terns may only feed on pelagic food either in marine or freshwater sites. Thus, they depend on prey made available at the water surface either by biological or physical processes. The former can be caused, for instance, by interactions with other marine predators that drive suitable prey close to the water surface (Safina & Burger 1985) or it may be related to diurnal vertical migration patterns of suitable prey (e.g. Sjöberg 1989; Stienen et al. 2000; Schwemmer & Garthe 2005). The latter can be a result of hydrographic phenomena such as upwelling or eddies caused by strong tidal currents in mutable coastal systems (Irons 1998; Holm & Burger 2002; Zamon 2003).

The Wadden Sea in the south-eastern part of the North Sea is such a highly dynamic ecosystem. Its morphology is shaped primarily by tidal currents that are particularly strong within deep and greatly structured tidal channels (Stanev et al. 2003). There are three main reasons to expect increasing prey availability during times (and within areas) of strong water currents: (1) A higher water mass with a higher number of suitable prey items per unit time will pass a certain area. (2) Due to upwelling, turbulences and eddies, prey will be driven closer to the water surface. (3) Feeding conditions might improve as a consequence of schools of planktivorous fish occurring near the surface which feed on plankton brought to the water surface by tidal rips and jets (Zamon 2003). Thus, tidal currents might significantly influence prey availability and provide spatially and temporally predictable food sources.

For Arctic terns (*Sterna paradisaea*) breeding at the German North Sea coast the tidal cycle has already been described to affect diet choice and foraging behaviour (Boecker 1967; Frick & Becker 1995). The same holds true for the closely related common tern (*Sterna hirundo*) (Boecker 1967; Becker & Specht 1991; Frank 1992; Frank & Becker 1992; Frick & Becker 1995). Furthermore, Becker et al. (1993) stated tide-related use of distinct foraging areas by common terns in the south-eastern German Wadden Sea. Yet, for Arctic terns such areas have not been revealed so far, and the link between tide-induced temporal foraging patterns and their spatial distribution is still missing.

The aim of this study is to elucidate the influence of the tidal cycle on diet, foraging activity and at-sea distribution of Arctic terns in the Wadden Sea. Moreover, we tried to reveal distinct foraging sites of this species at sea. In detail, we derived the following three hypothesis:

(1) We expected the highest foraging activity of Arctic terns during times of highest water flow velocity (i.e. during ebb and flood tide). As biological production is highest within shallow water which is attracting small fishes (Vorberg & Breckling 1999), we expected a negative relationship between foraging activity and water depth. As water

flow velocity is positively related to water depth (Stanev et al. 2003) we expected that also the interaction of both parameters would significantly influence foraging behaviour. Furthermore, we assumed tide-induced differences in prey choice. (2) If Arctic terns would show a strong association with high tidal currents and shallow water areas, then location of foraging sites should be predictable using environmental data on water flow velocity and depth. (3) Arctic terns at the German North Sea coast showed a comparatively high frequency of feeding intervals of chicks (Frick & Becker 1995; Niedernostheide 1996) and exhibited a short foraging radius (Boecker 1967; Hartwig et al. 1990). Consequently, Arctic tern colonies should be established in the vicinity of foraging areas and thus, location of these colonies should be predictable as well, using the same environmental data.

To test these hypotheses, we conducted colony-based observations on Arctic tern diet and foraging behaviour in relation to tidal stage. Additionally, we recorded distribution patterns and foraging actions of terns during various seabirds-at-sea counts. Eventually, we modelled the probable locations of foraging sites. Finally, the quality of the Wadden Sea and adjacent areas as foraging habitats for Arctic terns is discussed with respect to the present status of this species at the German North Sea coast and compared with situations elsewhere.

Material and Methods

Study area

The offshore study site is located in the south-eastern German Bight and covers the whole coastal zone off the northernmost German federal state, Schleswig-Holstein, east of 7° E; west of 9° 20' E and south of 55° N (Fig. 30). Detailed at-sea observations were conducted in a nearshore area east of 8° 06' E; west of 9° 20' E and south of 54° 20' N (rectangle in Fig. 30). Colony observations were carried out in an Arctic tern colony with approximately 140 breeding pairs at the mouth of the river Eider (8° 51' E; 54° 16' N; triangle in Fig. 30). Terns breed at the base of an artificial ear dike which is a part of the river barrier. Public access is possible to the breeding colony (the closest nests being located approximately 3-4 m away from a foot path bordered by a balustrade), providing excellent observation opportunities. Due to intense public traffic, the birds are habituated to humans and were thus not disturbed by our observations.

Prey brought into the colony

In total, we recorded $n = 1,124$ prey items brought into the breeding colony by Arctic terns. Observations were conducted on five days during the late chick-rearing period between 15 and 22 July 2006. We used binoculars to identify food items which adults carried in their bill when returning to the colony to feed their chicks (see Duffy & Jackson 1986 as well as Cezilly & Wallace 1988 for a critical review of this method). Size of prey

was estimated by comparison with mandible length. We used the length of the whole bill, from the tip to the most proximal point. Length of prey items were estimated as a multiple of the bill length (from 0.8 times to 2.5 times). To convert these estimates to numeric length units, we measured the bill length of six museum specimens of Arctic terns and received a mean value of 4.7 cm.

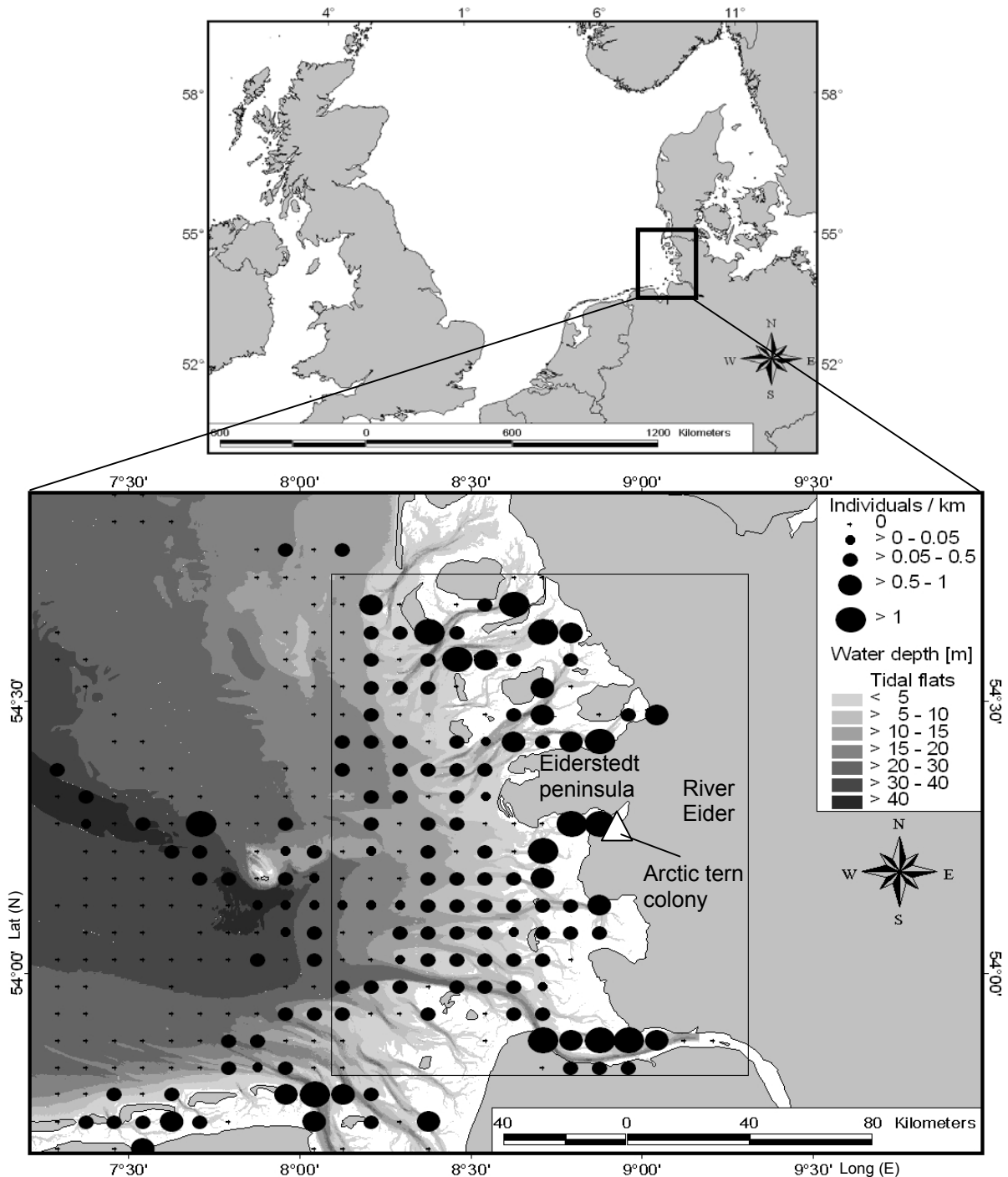


Fig. 30: Location and details of the study area at the eastern German North Sea coast. Black dots and small crosses indicate the distribution of Arctic terns at sea as derived from seabirds-at-sea counts (see Material and Methods for details). Rectangle in the lower image: Area chosen for detailed at-sea observations. Triangle: Location of the Arctic tern colony (ca. 140 breeding pairs) at the mouth of the river Eider.

The lengths of the prey species were used to calculate species-specific biomass values [g]. For fish species, length-mass ratios after Leopold et al. (2001) were applied. For unidentified clupeids we calculated a mean of the ratio of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). Twait shad (*Alosa alosa*) was not found in the diet. For North Sea shrimp we used an approximation of a mean of 2 g (own measurements), as estimates of length of this prey type in the field were too inaccurate due to its small size. For Brachyuran crustaceans we conducted our own series of (n = 1,191) measurements of biomass (y) in relation to length (x) that yielded a ratio of $y = 0.271 x^{2.81}$ (H Dries unpubl. data). 25 prey items could only be determined as fish without further details. For these we calculated a mean biomass value on the basis of the frequency of occurrence of all other fish in the diet. In seven cases we were only able to identify a small object, in two cases we identified polychaete worms and in 19 cases we were not able to estimate lengths. These cases were excluded for calculations of biomass values (n for calculations of biomass values = 1,096; flood tide n = 267; high tide n = 260; ebb tide n = 289; low tide n = 280).

Over the five days we conducted a total of 8 h of constant observations of prey brought into the colony. To relate prey type and biomass to different stages of the tide, we distributed the observation effort equally over the whole tidal cycle. Four tidal stages were distinguished: (1) Flood tide (one hour after low tide to one hour before high tide, i.e. 4 h); (2) high tide (one hour before high tide to one hour after high tide, i.e. 2 h); (3) ebb tide (one hour after high tide to one hour before low tide, i.e. 4 h); (4) low tide (one hour before low tide to one hour after low tide, i.e. 2 h). We covered each of the four tidal stages by 2 h of observation. The Friedman test was applied to test for significant differences of prey between the four tide classes.

To relate biomass brought into the colony to stage of the tide, total biomass and median biomass per prey item and tidal stage class were calculated. Overall differences were tested applying Kruskal-Wallis tests. Mann-Whitney U-tests were applied as post-hoc procedure (with α -level correction after Bonferroni). In contrast to foraging behaviour observed at the colony (see below) we were not able to test for significant differences between observation days as the number of days was too low.

Foraging behaviour at the colony

To relate foraging behaviour to the stage of the tidal cycle, we followed single individuals that were starting to a foraging trip from the colony towards the Wadden Sea / offshore area with a telescope. The time span from departure (defined as crossing a line of buoys in the Eider mouth adjacent to the colony) from the colony to the first feeding attempt (either by dipping or shallow plunging into the water surface; Camphuysen & Garthe 2004) was recorded and related to the stage of the tidal cycle as defined above. We did not note whether the hunting event was successful or not, as we only aimed to obtain an indication of prey availability during different stages of the tide. As foraging behaviour within same stages of the tidal cycle were recorded repeatedly on different days of

observation, we tested for differences between days within each of the four tidal stage classes. Kruskal-Wallis tests revealed no significant differences of either tidal stage between different observation days (flood tide: $\chi^2 = 7.2$; $df = 3$; high tide: $\chi^2 = 3.6$; $df = 2$; ebb tide: $\chi^2 = 3.6$; $df = 3$; low tide: $\chi^2 = 0.9$; $df = 2$; $p > 0.05$, respectively). Subsequently, data of the same tidal stages were pooled. Again, we tested for overall differences in foraging behaviour between the four tidal stages using Kruskal-Wallis test and applied Mann-Whitney U-tests (with α -level correction after Bonferroni) as post-hoc procedure.

Distribution at sea

Distribution of Arctic terns at sea was recorded during the whole breeding period (i.e. May to July) of the years 2002–2006 following the standardized method described by Tasker et al. (1984) and Garthe et al. (2002); (German Seabirds at Sea database, version 5.07; as of October 2006). Total observer effort covered 8,473 km. Following this method, we carried out counts in an area of a 90° scan on one side of the steaming observation vessel. Both, birds sitting on the water surface and flying across the respective area were recorded. The position of the observation platform and thus the distance travelled was automatically noted by GPS within intervals of 1 min. Mean individual numbers were computed for (1) the whole study area applying a grid of 3' latitude x 5' longitude and (2) for the nearshore area (rectangle in Fig. 30) applying a grid of 2' latitude x 3' longitude. This was achieved by dividing the total tern numbers within each grid cell by the total distance travelled within each grid cell. To reveal areas that were used for foraging, we divided all bird records into individuals that were feeding or attempted feeding (i.e. shallow or deep plunging, dipping or surface pecking; see Camphuysen & Garthe 2004 for details) and those without feeding behaviour.

As the correct identification of Arctic terns at sea is problematic due to confusion with the closely related and very similar common tern, a certain proportion of terns recorded at sea could not be identified to species level. In order to consider this proportion of birds, we calculated the number of identified Arctic (total $n = 782$) and common terns (total $n = 3,007$) per grid cell and calculated the respective proportionate number of undetermined individuals (total $n = 4,814$). Finally we added this number to the number of identified Arctic terns. This procedure was considered appropriate, as Arctic and common terns show no distinct differences in their at-sea distribution (unpubl. data). We are aware of the fact that a certain bias might occur due to differences in ecological aspects (others than visible by distribution patterns) of these two species. However, we believe that for the questions raised within the scope of this study such a potential bias would not cause any confounding effects.

Foraging behaviour at sea

We expected foraging activity to increase in areas with high water currents, as a consequence of better prey availability. Furthermore, we assumed that water depth might influence foraging behaviour. We used data on water flow velocity [m / s] on an hourly

basis for a whole tidal cycle of the south-eastern German Bight (resolution: Grid of 1 x 1 nautical mile) to calculate the mean water flow velocity for each grid cell (source: "Bundesamt für Seeschifffahrt und Hydrographie"). 11 classes of water flow velocity were defined (from 0.1 to > 1 m / sec). Furthermore, water depth was divided into six classes in steps of 5 m (from 0 to 25 m). Numbers of feeding (total n = 2,258) and non-feeding individuals (total n = 2,719) were related to water flow velocity and depth. We modelled the probability to encounter foraging seabirds within a given water depth and water flow velocity applying a Generalised Additive Model (GAM) (Hastie & Tibshirani 1990; Wood 2006). Therefore, the type of feeding behaviour (as feeding or non-feeding) was correlated with water flow velocity and depth, separately, as well as with the interaction of both. The model selection was achieved by performing a ten-fold cross-validation procedure, and the best model was selected according to the resulting cross-validation error statistics (Hastie et al. 2003). To fit the model, a quasibinomial distribution was selected (since the maximum probability to encounter a feeding bird was 1). Finally, we plotted the resulting model estimation (probability of feeding) against latitude and longitude and conducted a spatial interpolation (too.far = 0.05) of the probability values (Wood 2006).

GAM as well as interpolation procedures were performed with the open source software package of R 2.4.1 (www.r-project.org) using the MGCV library (Wood 2000), while Kruskal-Wallis, Mann-Whitney U, Friedman and t-tests were conducted using SPSS. All indicated p-values are two-tailed.

Results

Diet

In general, fish dominated the diet brought into the colony by Arctic terns, while crustaceans contributed a much lower proportion (Table 18). Smelt (for scientific names see Table 18) was the main prey species showing the highest individual and overall biomass values, followed by unidentified clupeids (Tables 18 and 19). Most of the latter were probably herrings. Other fish taxa, including pipefish species, flat fish species, gobies and ruffe were only recorded occasionally. Among the crustaceans, North Sea shrimps were the most important prey (Table 18).

Influence of tide on diet and foraging behaviour at the colony

Prey composition among the four tidal stage classes differed significantly (Friedman test: $\chi^2 = 7.8$; $df = 3$; $p = 0.05$; Fig. 31). The proportion of smelt was highest throughout all tidal stages and reached a maximum (> 90 %) during low tide. Clupeids were caught mainly during high tide. Other prey components reached their highest values particularly during ebb tide, when many North Sea shrimps, flat fish and other crustaceans were

found. Pipefish reached highest numbers (ca. 5 % of all prey types) during high tide (Fig. 31).

Table 18: Number, proportions, total and mean biomass of prey types brought into the breeding colony by Arctic terns.

Prey type	Number	Proportion	Total biomass [g]	Mean biomass [g]
Smelt (<i>Osmerus eperlanus</i>)	700	62.3%	2285	3.3
Clupeidae unident.	266	23.7%	231	0.9
Smelt or clupeidae unident.	32	2.8%	21	0.6
Herring (<i>Clupea harengus</i>)	3	0.3%	5	1.5
Gobiidae unident.	2	0.2%	0	0.2
Ruffe (<i>Gymnocephalus cernuus</i>)	2	0.2%	5	2.4
Pleuronectiformes unident.	17	1.5%	17	1.0
"Round fish" unident.	25	2.2%	18	0.7
Syngnathidae unident.	16	1.4%	3	0.2
North Sea shrimp (<i>Crangon crangon</i>)	33	2.9%	83	2.0
Shore crab (<i>Carcinus maenas</i>)	5	0.4%	13	2.7
Brachyura unident.	13	1.2%	31	2.4
Nereidae unident.	1	0.1%	?	?
Unident. small prey	9	0.8%	?	?
Total	1124		2713	

Table 19: Frequency of occurrence [%] and number (in brackets) of biomass classes of clupeids and smelt brought into the colony by Arctic terns.

	Biomass [g]					total n
	> 0 - 0.5	> 0.5 - 1.5	> 1.5 - 3	> 3 - 6	> 6	
Clupeidae	23% (63)	56% (150)	18% (49)	3% (7)	0%	269
Smelt (<i>Osmerus eperlanus</i>)	1% (7)	6% (44)	49% (340)	37% (268)	7% (48)	700

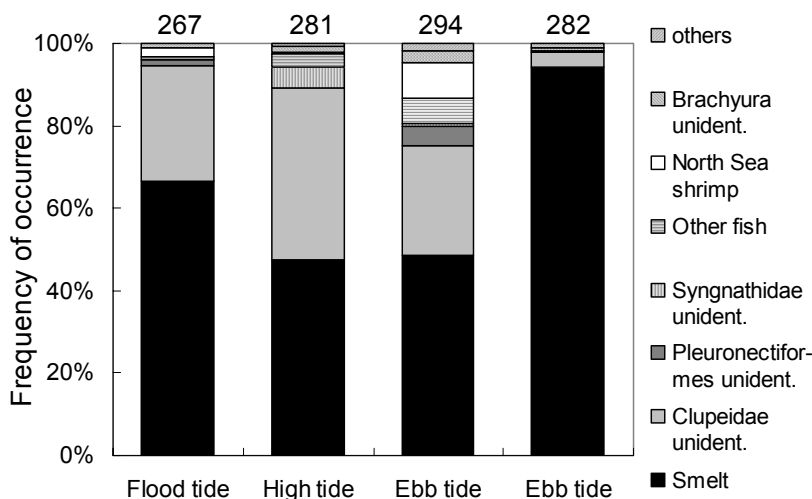


Fig. 31: Proportions of different prey types brought into the colony in relation to tide (several prey types with low frequency of occurrence were pooled; see Table 18 for all prey types; numbers above the columns indicate the number of prey items per tide class).

Biomass per prey item differed significantly among the four tidal stage classes (Kruskal-Wallis test: $\chi^2 = 209.4$; $df = 3$; $p < 0.001$; 5 out of 6 post-hoc tests being significant; Fig. 32; Table 20). Highest median biomass values were reached during low tide, while lowest values occurred during high tide (Fig. 32). Consequently, total biomass brought into the colony within one tidal stage class reached 1.139 kg during low tide, followed by flood tide (0.678 kg) and ebb tide (0.508 kg), while it was lowest for high tide (0.388 kg). Biomass values were mainly influenced by the proportions of smelt in the diet, which had the highest mean biomass (3.3 g) of all prey species (clupeids: 0.9 g; Tables 18 and 19). Biomass values between smelt and clupeids differed significantly (t-test: $t = -27.2$; $df = 505.1$; $p < 0.001$; Table 19).

Foraging behaviour based on feeding attempts of individuals leaving the colony differed significantly among the four tidal stage classes (Kruskal-Wallis test: $\chi^2 = 19.86$; $df = 3$; $p < 0.001$; 3 out of 6 post-hoc tests being significant; Fig. 33; Table 20). Time until first dive or dip was shortest during ebb tide, while it was highest during high tide. Differences between high tide and the other three tide classes were most obvious and significant in two out of three cases (Fig. 33; Table 20). In general, tidal stages with higher water flow velocity (i.e. flood and ebb tide) obviously revealed shorter foraging times of Arctic terns.

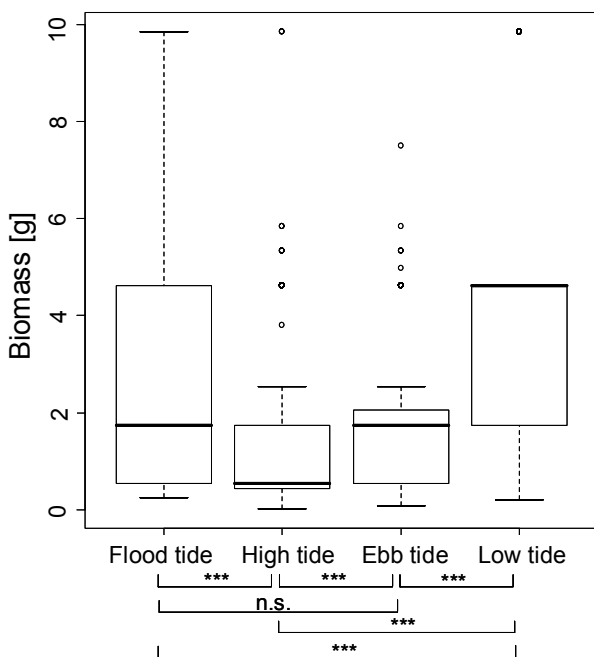


Fig. 32: Boxplot (bold line = median; rectangle = quartile; dashed line = 95 % percentile; dots = outliers) of biomass [g] of prey items brought into the colony by Arctic terns in relation to tide. Significance levels have been adjusted according to Bonferroni correction (*: $p \leq 0.0125$, **: $p \leq 0.0025$, ***: $p \leq 0.00025$, n.s.: not significant).

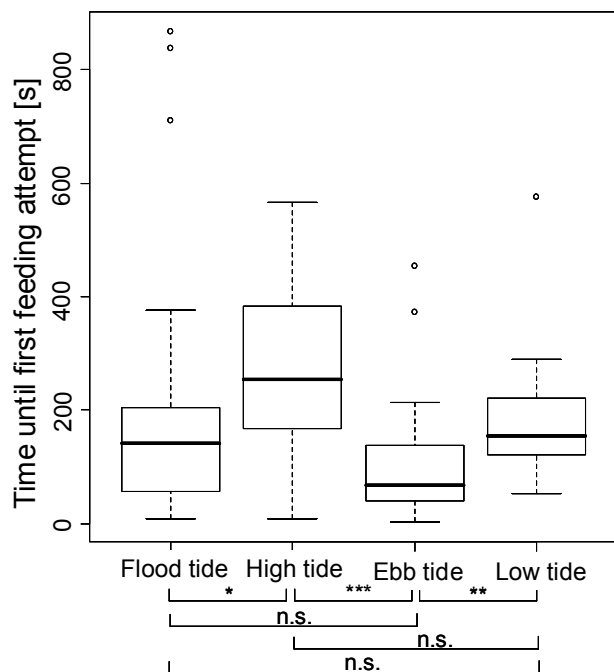


Fig. 33: Boxplot (for further description see Fig. 32) of searching time [s] of foraging Arctic terns until their first feeding attempt in relation to tide.

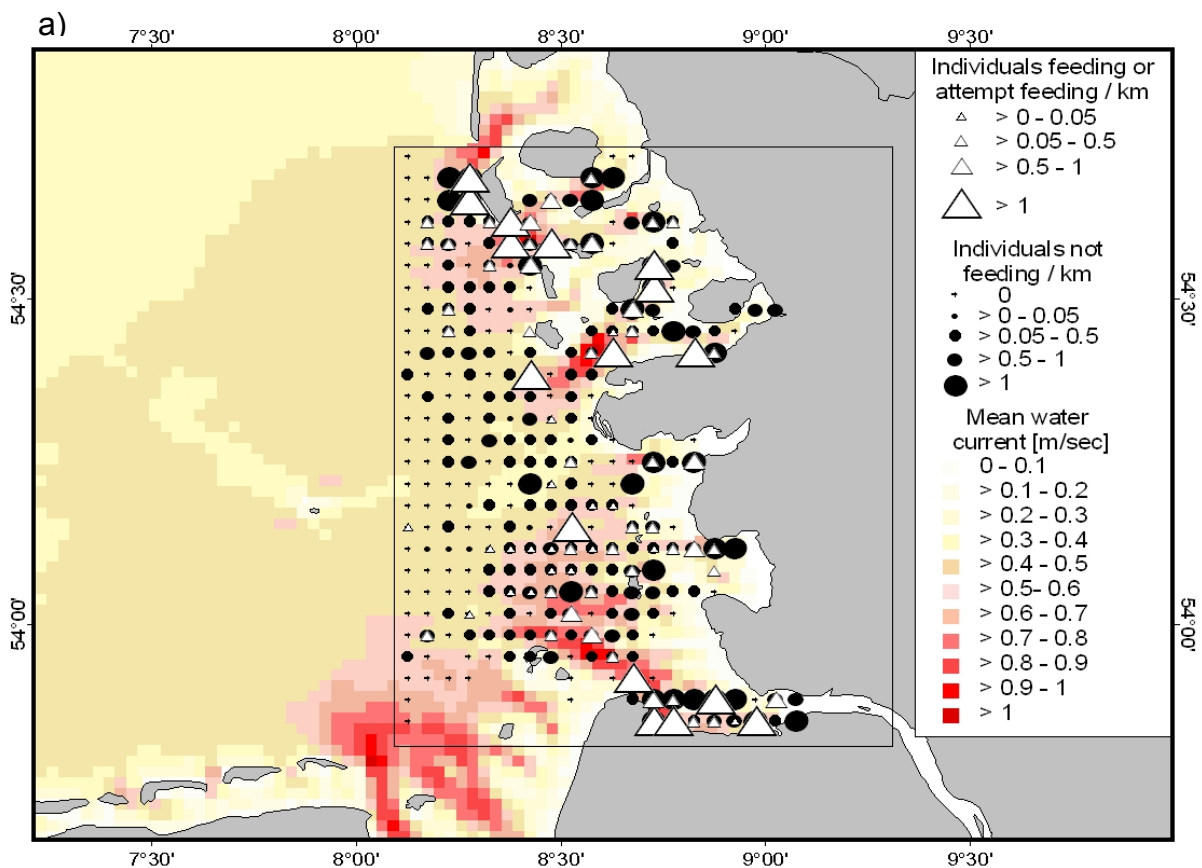
Table 20: Results of Mann-Whitney U-tests referring to differences in biomass per prey item and to time to first feeding attempt in relation to stage of the tide, respectively. Significance levels have been adjusted according to Bonferroni correction (n.s.: not significant).

	Biomass				Time to first feeding attempt			
	N ₍₁₎	N ₍₂₎	U	p	N ₍₁₎	N ₍₂₎	U	p
Flood tide ₍₁₎ - High tide ₍₂₎	267	260	23699	< 0.00025	37	20	221	< 0.0125
Flood tide ₍₁₎ - Ebb tide ₍₂₎	267	289	18420	n.s.	37	22	431	n.s.
Flood tide ₍₁₎ - Low tide ₍₂₎	267	280	24028	< 0.00025	37	32	342	n.s.
High tide ₍₁₎ - Ebb tide ₍₂₎	260	289	28810	< 0.00025	20	22	140	< 0.00025
High tide ₍₁₎ - Low tide ₍₂₎	260	280	13069	< 0.00025	20	32	119	n.s.
Ebb tide ₍₁₎ - Low tide ₍₂₎	289	280	19640	< 0.00025	22	32	156	< 0.0025

Distribution at sea in relation to water flow velocity and water depth

The general at-sea distribution of Arctic terns during the breeding period was rather limited to the nearshore area (Fig. 30). Highest densities were reached in the Wadden Sea and in the mouths of the tidal streams adjacent to the pelagic offshore zone (Fig. 30).

The mouths of the large tidal streams as well as the mouth of the river Elbe revealed the highest water flow velocities. High numbers of feeding birds occurred within these areas (Fig. 34a), while in the most western zone of the study area as well as in an eastern strip close to the shore mainly non-feeding individuals were found.



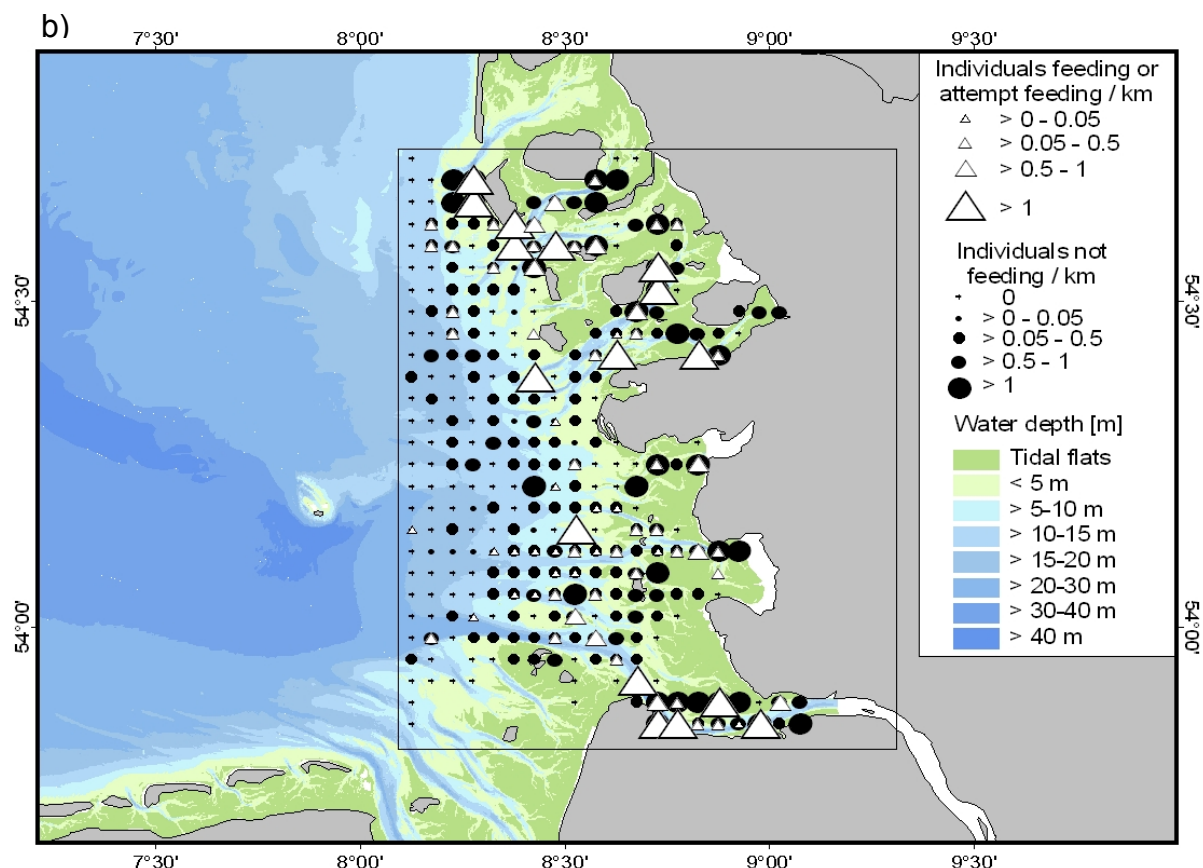


Fig. 34: Distribution of Arctic terns feeding or attempted feeding and those not feeding (a in relation to mean water flow velocity [m / s]; (b in relation to water depth [m]).

Additionally, no feeding events occurred west of the peninsula of Eiderstedt (for location see Fig. 30), an area with particularly low water flow velocity. Feeding events mainly occurred within areas of rather shallow water, despite some feeding events within some deeper tidal streams (Fig. 34b). There was an almost linear positive relationship between proportion of feeding individuals and water flow velocity (Fig. 35a), while increasing water depth had a general negative effect on feeding activity (Fig. 35b). For a GAM keeping all three parameters (i.e. water flow velocity, water depth and their interaction) the cross-validation procedure revealed the best model fit using 5 knots for the parameter water depth and the interaction. The model detected a significant influence of all three parameters (variance of the intercept: 2.13; $p < 0.001$; water flow velocity: $F = 55.5$; $p < 0.001$; water depth: $F = 67.65$; $p < 0.001$; water flow velocity x water depth: $F = 111.7$; $p < 0.001$). The model explained 26 % of the total deviance of the data and revealed a prediction error of 24 %. According to the cross-validation procedure, the model with the highest deviance explained (29 %) and with the lowest prediction error (21 %) was based on water depth and the interaction only (i.e. water flow velocity should be removed). However, we have chosen to present the model with the best fit in which all three parameters were kept (in accordance with our hypothesis). Since an ANOVA of both model outputs revealed no significant difference between the two, we selected this approach. In general, the probability to encounter feeding behaviour was highest within

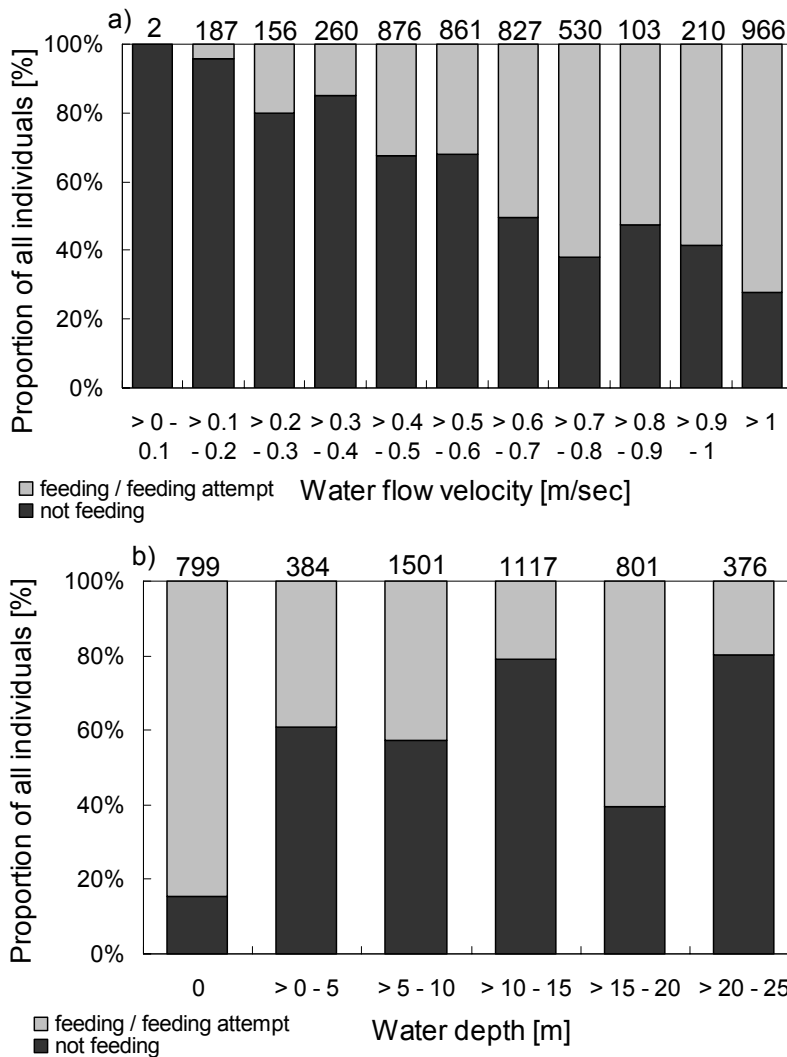


Fig. 35: Proportion of Arctic terns feeding or attempted feeding and those not feeding a) in relation to mean water flow velocity [m / s], b) in relation to water depth [m]. Numbers above the columns depict numbers of observed individuals.

areas of high water flow and low water depth (in areas < 5 m water depth and water flow velocity > 0.9 the probability to encounter feeding activities reached 0.9; Fig. 36). Within deeper water the probability of feeding is predicted to be only high when the water flow velocity is also high (Fig. 36). The model detected a lower probability of feeding within medium water depth, which seemed to be more or less independent of water flow velocity (Fig. 36).

The spatially interpolated model revealed highest probabilities of feeding mainly in areas with high water flow velocity (Fig. 37; compare Fig. 34a for distribution of water flow velocities). Particularly the tidal stream system of the

“Hever”, which is located north of the peninsula of Eiderstedt showed high probability values. Furthermore, another hot spot is located south-east of the island of Amrum in the north-west corner of the study area. The mouth of the river Elbe showed moderate probability values, whereas the mouth of the river Eider, where the study colony is located, revealed low values.

A high proportion of Arctic tern colonies are located in the vicinity of areas that showed a high probability of feeding behaviour (Fig. 37). These colonies are mainly located in the northern part of the study area. However, there is a number of larger colonies at the mainland and also in the southern part of the study area (including the study colony of the river Eider), which are not located close to proposed feeding sites. Overall, the 20 breeding colonies shown in Figure 37 are located at a mean linear distance of 4.9 ± 4.7 km from areas, where feeding probability reached a value of 0.5.

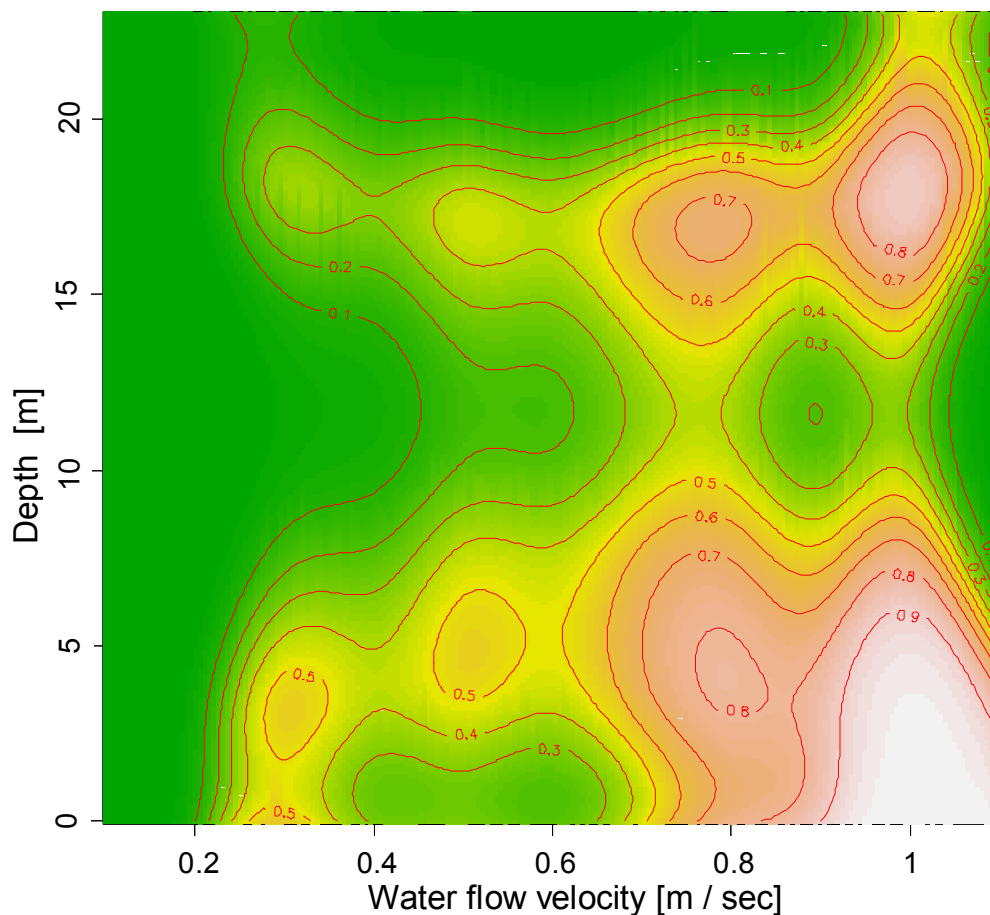


Fig. 36: Model of probability (range 0-1) to encounter feeding behaviour of Arctic terns in relation to water flow velocity, depth and its interaction. The model was performed with a Generalised Additive Model (see text for details).

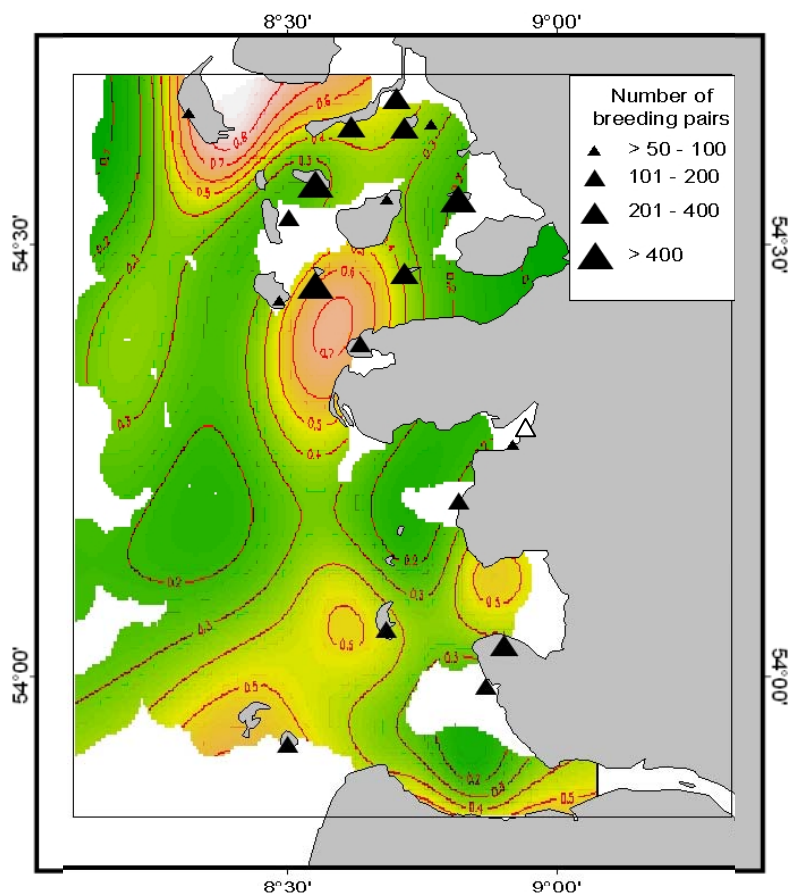


Fig. 37: Spatial interpolation of the estimation of the GAM (probability to encounter feeding terns in relation to water flow velocity, depth and its interaction; see text for details). Black triangles indicate breeding pair numbers of Arctic terns (source: Hälterlein unpubl. data), white triangle indicates the study colony at the river Eider.

Discussion

Diet

The Arctic tern colony at the Eider mouth is highly suitable for direct observations of prey brought into the colony due to the short distance from the observer to the nests. Thus, only 7 out of 1024 observed prey items (< 1 %) remained unidentified. Due to these excellent conditions we believe that the observational bias that is subject to this method (see Cezilly & Wallace 1988) was very small and that we were able to identify most prey items appropriately. Duffy & Jackson (1986) state that prey brought into colonies by terns reflect the overall diet properly. Still, it might be important to state that particularly observations of smaller prey items might be biased as they are more difficult to identify (Duffy & Jackson 1986). Moreover, diet of terns can vary during the breeding period (Boecker 1967; Pearson 1968; Safina & Burger 1985; Lyons et al. 2005; but see Lemmetyinen 1973). Thus, it can not be excluded that the diet recorded in the present study differed from the prey fed to the chicks during the early chick-rearing period. Since this was not the main focus of our study, we believe that such a potential bias can be neglected.

The prey species found in the diet of Arctic terns reflect a typical profile of prey of an intertidal river mouth in German North Sea waters: Particularly smelt is a characteristic species of such habitats. This fish species might originate both from the Wadden Sea area and from the lower mainland river section (Thiel et al. 1995; Vorberg & Breckling 1999; Thiel & Potter 2001). As revealed by biomass values, smelt must be considered a very suitable prey which additionally seems to be highly abundant in the vicinity of the colony. Moreover, the energy content of smelt is similarly high as that of herring (Massias & Becker 1990). In contrast to other studies on diet of Arctic terns in the Wadden Sea (Boecker 1967; Frick & Becker 1995; Niedernostheide 1996), our findings show a rather low proportion of crustaceans (both in terms of number and biomass). Furthermore, stickleback (*Gasterosteus aculeatus*) was not found in the diet of Arctic terns, although it would belong to a typical river mouth fauna (Thiel et al. 1995; Vorberg & Breckling 1999; Thiel & Potter 2001) and it has been described as important prey for Arctic terns elsewhere (Lemmetyinen 1973; Dierschke & Klümman 1988). The absence of this species might have had mainly three reasons: (1) Other more suitable prey in terms of energy density (see Massias & Becker 1990) and availability might have been preferred; (2) sticklebacks were indeed absent; (3) due to its spines it might be considered as poor food particularly for chicks.

It is generally important to consider that diet of terns might differ considerably among different sites (e.g. Becker et al. 1987; Frank 1992; Lyons et al. 2005). Frank (1992) found that the diet of terns mirrors the prey availability in the vicinity of the breeding colony. Our findings support this conclusion. Moreover, our colony-based observations on foraging activity (in which terns leaving the colony were followed using telescope) revealed that most feeding actions occurred only a few km or even several

100 m away from the colony (also see discussion about foraging radii below). Also, the time span between leaving the colony and performing the first feeding attempt (although significantly different between tidal stages) was generally short, with a median not exceeding 300 s. It is however important to note that in most cases the first diving attempt was not successful and birds went on foraging. Various feeding attempts until the first foraging success are a common phenomenon in terns (Safina & Burger 1985).

Effects of tide on diet and foraging behaviour

Our colony-based observations on foraging behaviour revealed shortest searching time during high water currents (i.e. during ebb and flood tides). In contrast, high tide seemed to be the worst time for foraging as searching time of Arctic terns was longest (Fig. 33) and biomass intake was lowest (Fig. 32). Moreover, (although not recorded systematically) a high number of birds could be observed to head towards the mainland during high tide. Frank & Becker (1992) reported the same phenomenon for common terns. This indicates that prey availability and quality might be poorest during low water currents. The comparatively high proportion of pipefish taken during high tide, which is the prey type with the lowest biomass values and an adverse length-biomass ratio (Leopold et al. 2001; Harris et al. 2007), indicates that the availability of other, more suitable prey might be slightly reduced. These findings match well other studies that found that the chick provisioning rate in Arctic terns decreases during high tide (Boecker 1967; Frick & Becker 1995).

In contrast, the searching time of Arctic terns was significantly lower during stages of high water currents (Fig. 33). It can be expected that prey within reach of Arctic terns can not escape these foraging predators as easy as during low water flow velocity, as escape reactions might be restricted by the power of the water and its direction. The influence of water currents on locomotion has already been stated for different marine species (Levington et al. 1995; Ghalambor et al. 2003). Particularly during ebb tide the proportions of prey species from the intertidal area (such as North Sea shrimps, Brachyuran crustaceans and flat fish species) increased markedly. As all of these species are benthic, it can be assumed that water turbulences might have driven them closer to the surface. Zamon (2003) found higher numbers of seabird flocks during strong flood currents and assumed that schools of planktivorous fishes would become more available for predators as a consequence of a higher amounts of plankton driven to the surface.

During low tide the proportion of smelt in the diet reached a maximum, while clupeids were only taken in very small numbers. This effect might be consistent with a higher rate of freshwater intrusion into the river mouth and fits the complementary higher proportion of pipefish and clupeids during highest saltwater intrusion at high tide (Fig. 31; compare with Lyons et al. 2005). A strong increase of benthic organisms during low tide as revealed by Frick & Becker (1995) was not found for our study and might again emphasize the high availability of smelt during this tidal stage.

Location of foraging sites

The general at-sea distribution of Arctic terns exposed highest concentrations close to the coast (Fig. 30; compare with Mitschke et al 2001), which matches well with the comparably low foraging radius of this species (e.g. Boecker 1967; Hartwig et al. 1990; see below). However, the fine-scale distribution of feeding and non-feeding individuals differed (Fig. 34), indicating the use of distinct foraging sites. For radio-tagged common terns, Becker et al. (1993) already proofed the existence of such foraging areas as well as of transit areas where feeding was less intense. We were able to reveal similar patterns of foraging and non-foraging zones for Arctic terns: Our results clearly show that zones of intense foraging actions were mainly located in rather shallow areas of high water flow velocity in or at the outer border of the Wadden Sea. Transit areas of low feeding activities did mainly exist close to the mainland as well as in the offshore regions of the study area. In both of these areas, water flow velocity is comparatively low. The (rather small) proportion of non-feeding individuals in the westernmost part of the study area might result either from late or early migrating individuals or from a number of non- or failed breeders, a phenomenon that has already been described before in Arctic terns (Camphuysen & Winter 1996).

For surface-feeding seabirds it is essential that prey is available close to the water surface. In other marine ecosystems predatory fish species have been found to drive smaller fish to the surface and that the distribution of surface-feeding seabirds was significantly correlated with those feeding actions (e.g. Safina & Burger 1985; Zamon 2003). It can be assumed that, in the Wadden Sea, the physical effect of tidal currents might have a similar effect to cause patches of enhanced and predictable prey availability. The spatial probability values of feeding actions as revealed by the GAM (Figs. 7 and 8) support such a conclusion. The combination of shallow water and strong tidal currents seem to be most beneficial for Arctic terns. Boecker (1967) observed similar effects. In shallow areas strong currents produce a strong friction with the ground (Stanev et al. 2003), which might lead to turbulences causing higher prey availability. Furthermore, in shallow waters (particularly of the Wadden Sea) biological production is highest and may attract various prey species (Vorberg & Breckling 1999). This positive interaction between physical and biological processes might be extremely beneficial for Arctic terns. The slight increase of foraging activity in deep water (Fig. 35b and 36) might again be mainly an effect of physical processes related to highest water flow velocities. In general, tidal current speeds seemed to play a superior role compared to water depth.

For the interpretation of our model it is important to bare in mind that it is only based on classified values of water depth and mean water flow velocity. Moreover, values of water flow velocity were only available at a rather rough spatial grid. Since feeding actions of Arctic terns might be steered also by fine-scale processes, such as regional patches of food becoming available or strong turbulences causing local prey availability in a small section of a tidal stream, our model would not be able to detect such patterns (compare with Hunt & Schneider 1987). However, as the explained

deviance of 26 % of the model output indicates, correlations between feeding activity and water currents / depth could be identified very well at a broader spatial scale. For more detailed results on foraging behaviour and distribution it might be useful to equip birds with radio tags or data loggers.

If ephemeral patches of prey close to the water surface last long enough, it can be assumed that the information about this food source will be passed on from foraging to non-foraging individuals. This is a common phenomenon of flock-feeding seabird species (e.g. Götmark et al 1986; Camphuysen & Webb 1999) and would amplify aggregations of terns within areas of high prey availability caused by tidal currents. Furthermore, it can be assumed that areas of high water flow velocity are spatially and temporally predictable food sources for surface-feeding seabirds. Individuals might thus exhibit foraging-site fidelity (Irons 1998), which could have supported the clear separation between feeding and non-feeding sites (Fig. 34).

Location of Arctic tern colonies in relation to feeding sites

The foraging radius of Arctic terns breeding along the north-western North Sea and those breeding along the German Bight seems to be different: Pearson (1968) estimated a foraging radius of approximately 20 km for Arctic terns breeding on Farne Island, whereas Hartwig et al. (1990) estimated a radius of 4 km and Boecker (1967) calculated a radius of 3-6 km for Arctic terns from the Wadden Sea. These comparatively small foraging radii fit well our findings: For all Arctic tern colonies we found a mean linear distance of 4.9 km to the closest area where the probability value of feeding events reached 50 % (Fig. 37). However, some colonies (including the Eider colony) are located more distant to optimal feeding sites. This seems to contradict our findings to some degree. However, there are a number of possible reasons for the establishment of the colony at this site: (1) Distance to feeding spots is not the only factor which accounts for location of colonies. Of course, also breeding habitats and nest site quality are important issues. Arctic terns are known to prefer open breeding sites in an early stage of natural succession (e.g. Südbeck et al. 1998). Such breeding sites are rare, as a consequence of management measures for coastal protection and lower intensity of grazing of salt marshes. The study colony at the mouth of the river Eider is an example for the preference of such open breeding habitats by Arctic terns. (2) It is important to bare in mind that we were only able to sample foraging actions at sea within larger tidal streams which were accessible by vessels, though we were able to use boats that could enter very shallow water. Smaller tidal streams, however, might also play an important role for Arctic terns (Boecker 1967), and there is a high number of those available in the vicinity of the Eider mouth. Moreover, local currents within the main flow of the Eider mouth must be considered as comparably high, but might have not been reflected by the rough resolution of our model data (see above). Additionally, our ship-based observation effort within the Eider mouth unfortunately was comparably poor. (3) Arctic terns at the Eider (as well as in some other mainland sites) may forage at different inland freshwater sites

(compare with Frank & Becker 1992 for common terns). The Eider itself seems to hold an ample food supply of estuarine fish species such as smelt. (4) During certain environmental conditions, the river barrier itself can cause turbulences, which may enhance food availability. (5) Terns are able to continue foraging at night in a restricted area around the river barrier due to its extensive artificial lighting (own observations) and thus can increase their foraging effort and number of feeding bouts.

Most Arctic tern colonies (also those with the highest breeding pair numbers) are located on islands in the northern part of the study area (Fig. 37; Südbeck et al. 1998). Hence, they are located very close to areas with the highest mean water flow velocity in the whole study area.

Conclusions

Our findings clearly show the important role of strong tidal currents to provide patches of (high) prey availability for surface-feeding seabirds in the Wadden Sea. Furthermore, our data state the existence of distinct foraging sites of Arctic terns that were mainly determined by water flow velocity and water depth. In general, it seems that in a highly dynamic coastal zone physical processes are of major importance to influence food availability even at a relatively small spatial scale (see Hunt & Schneider 1987). The location of feeding sites compared with the location of breeding colonies as well as the distinct temporal pattern of foraging behaviour and diet choice demonstrate the high affinity of Arctic terns to tide-induced processes in the Wadden Sea. Since the temporal and spatial occurrence of prey supplied by tidal currents will be highly predictable for predators, the foraging conditions for Arctic terns in the Wadden Sea seem to be very favourable. The establishment of breeding colonies in the vicinity to optimal foraging sites might be considered as a consequence of the reliable food supply.

Since the tidal cycle will provide a variety of food on a regular daily basis, it is unlikely that Arctic terns in the Wadden Sea will suffer from shortages in food supply in the near future, as reported for instance from breeding colonies along the north-western North Sea coast (e.g. Bailey 1991; Monaghan et al. 1992; Furness & Tasker 2000). Many studies in this region have shown that Arctic terns may highly depend on single marine prey species, such as the lesser sandeel (*Ammodytes marinus*), and that the lack of such species can severely affect breeding success (Bailey 1991; Monaghan et al. 1992; Furness & Tasker 2000). Our dietary data does not state the dependence on single prey species in the Wadden Sea (compare also with Boecker 1967; Hartwig et al. 1990; Frick & Becker 1995; Niedernostheide 1996). Furthermore, the breeding population of Arctic terns at the German Wadden Sea is rather stable and in some areas even showed a slight increase during the last 20 years (Südbeck et al. 1998; Koffijberg et al. 2006).

A bottleneck in terms of food supply in the Wadden Sea might only occur (despite of the predictable effect of tidal currents), in case that the food web of the Wadden Sea might change fundamentally (compare Harris et al. 2007 for a case study in the northern

North Sea). Small fish which is still highly abundant in the Wadden Sea and particularly within tidal estuaries (Thiel et al. 1995; Thiel & Potter 2001) might play the most crucial role for Arctic terns. Presently, there is no indication that these excellent foraging conditions for Arctic terns in the Wadden Sea might be threatened.

Acknowledgements

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General Discussion

Each of the previous five chapters provided an example of unravelling patterns of habitat use by different seabird species and underlying habitat quality of different systems of the coastal zone of the south-eastern North Sea coast. Each chapter contains a detailed discussion of the specific results. To evaluate the overall applicability, universal validity and conclusions of the integrative approach used throughout this study, this general discussion will respond to most of the general points addressed (see Introduction), as far as not already discussed within the dedicated chapters. The questions discussed within this general scope are:

- (1) What are the overall patterns of habitat use by the investigated species within the coastal zone of the German North Sea coast?
- (2) How powerful is the bioindicator approach, i.e. investigating distribution and behaviour of seabirds as well as prey availability and prey used by birds to judge habitat quality and ecological functions of sites?
- (3) What are the consequences of surface-feeding and how strong is the competition between the species investigated in the coastal zone?
- (4) Which future scenarios for the species investigated may take place if anthropogenic activities or natural processes in the coastal zone would change?

(1) What are the overall patterns of habitat use by the investigated species within the coastal zone of the German North Sea coast?

Within the five chapters presented in this thesis, I have focussed on a variety of important surface-feeding species and on detailed parts of the complex coastal zone of the German North Sea coast. Habitat use of species that are very common in all coastal landscape types, like the black-headed gull (Chapter I), was analysed for the whole coastal zone. In contrast, e.g. little gulls and Arctic terns (Chapters III and V) that are known to show a smaller foraging niche and mainly concentrate on the pelagic zone (offshore or Wadden Sea) of the coastal system, were studied within their main foraging habitats. In order to judge the importance of the three landscape types of the whole coastal zone for all species investigated, it is thus necessary to summarize the results found within this study and to add additional information from the literature (Table 21).

Table 21: Simplified summary of the significance of the three coastal landscape types for the species investigated within this thesis. As not all combinations of species and landscape types were analysed in detail within Chapters I-V, some information was taken from the literature (BHG = black-headed gull; CG = common gull; HG = herring gull; LBBG = lesser black-backed gull; LG = little gull; AT = Arctic tern).

	Pelagic offshore zone	Wadden Sea (tidal streams and tidal flats)	Nearshore mainland	Source
BHG	Minor importance throughout the year. In the adjacent area to the Wadden Sea, moderate importance of Brown Shrimp trawlers.	Tidal flats have moderate to high importance particularly during chick-rearing and autumn. Strong site-dependant differences are likely.	High importance particularly during migration and early breeding. Strong associations with agricultural activities.	this study; Garthe & Hüppop (1994); Dervedde (1994); Walter & Becker (1994; 1997)
CG	Highest importance during winter. Compared to black-headed gulls minor foraging success in association with fisheries.	Site-dependent importance of the tidal flats mainly during breeding time.	Pastures have a significant function during winter. Habitat mosaic of the nearshore mainland is likely to enable coexistence particularly with black-headed gulls. Less association with agricultural activities.	this study; Dervedde (1994); Walter & Becker (1997); Mitschke et al. (2001); Kubetzki & Garthe (2003)
HG	The offshore zone far away from the coast is used particularly during the winter months. In the adjacent area to the Wadden Sea, moderate importance of Brown Shrimp trawlers.	High association with tidal flats particularly during the breeding time.	Generally low numbers within the agricultural mainland. Slightly higher importance during spring migration. Frequently used for resting purposes.	this study; Tasker et al. (1987); Noordhuis & Spaans (1992); Dervedde (1994); Walter & Becker (1994; 1997)
LBBG	High importance of different parts of the offshore zone for foraging. High affinity to purely marine prey. Moderate importance of shrimp fishery. After breeding time high importance of beam trawl fisheries further offshore.	Minor use of tidal channels, very low numbers on tidal flats. Then, most frequently resting.	Very low importance of the mainland as revealed by direct observations. However, increasing amount of terrestrial components of food indicate possible foraging habitat change during recent years.	this study; Garthe & Hüppop (1994); Kubetzki & Garthe (2003)
LG	Small-scale differences in habitat use and behaviour within different offshore zones during spring migration. High association with natural hydrographic phenomena. More offshore winter distribution.	No use of tidal flats. Tidal streams as well as estuaries used during migration.	Low significance of terrestrial sites, but important staging sites located within freshwater areas.	this study; Koop (1985); (1997); Gloe (1987); Garthe (1993b)
AT	During breeding time important foraging sites located at the boarder to the Wadden Sea. After breeding moderate importance of offshore sites.	Tidal flats are only used for resting. Small tidal creeks and larger tidal streams provide highly important foraging sites. Prey availability and diet choice is highly influenced by the tidal cycle.	Terrestrial mainland habitats are not of any importance. Freshwater habitats near the coast are likely to play a moderate role for habitat switch during times of reduced prey availability in the marine area.	this study; Frick & Becker (1995); Camphuysen & Winter (1996)

It is important to bare in mind that analyses of habitat use of seabirds are always a matter of scale (Hunt & Schneider 1987). The scale of the investigations carried out within the dedicated chapters were chosen according to the special questions raised as well as according to the species investigated. Thus, for instance, it was necessary to focus on a broader spatial scale for the widely distributed lesser black-backed gull (Chapter II) while habitat use of little gulls was analysed at a smaller spatial scale (Chapter III). Particularly the findings of niche segregation patterns of the four gull species on the nearshore mainland show, however, that some important processes of habitat utilisation patterns ultimately take place within the smallest habitat mosaic (Chapter IV). In contrast to the studies conducted within the pelagic offshore zone or the Wadden Sea area, for those investigations made on land it is much more easy to characterise the (more static) terrestrial habitat types. Patterns of habitat use within the marine environment are much more difficult to identify due to their variable nature. Long-term data sets such as the German Seabirds at Sea database are highly valuable to obtain reliable results.

The present study has stated the overall importance of the coastal zone as foraging habitat for all species investigated. For most of the species, the opportunity to use a variety of smaller and larger habitat patches and to switch between sites during times of reduced prey availability might play the most important role (Chapter I; Sibly & McCleery 1983; Anett & Pierotti 1989). The switch between the three landscape types of the coastal zone was only analysed for black-headed gulls, but it might also be an important strategy for the less opportunistic species, including Arctic terns, which might benefit from freshwater habitats in the mainland close to the coast (Frick & Becker 1995). Combining direct observations of habitat use with recordings of behaviour and of prey taken by the respective species, the integrative approach of this study, led to a deeper insight into the functions of habitats for seabirds in the coastal zone. In the following section, the use of seabirds as indicators for the functions and for the quality of these sites is discussed.

(2) How powerful is the bioindicator approach?

Seabirds have been used as indicators for changes in the marine environment for several years (e.g. Cairns 1987; Montevecchi 1993; Monaghan 1996; Monaghan et al. 1996; Furness & Camphuysen 1997). In general, there are three basic approaches to use seabirds as bioindicators: (1) Most studies aim to utilise observations of prey intake by seabirds as an indication of the status of prey stocks (such as commercially harvested fish species) which can provide a useful tool to replace expensive fishery surveys (Cairns 1987; Montevecchi 1993). As this approach will only be possible with monophagous species (Montevecchi 1993; Monaghan 1996), it was not considered the main aim of the bioindication approach within the present study. (2) One more application of bioindication is to conduct long-term data analyses of prey taken by seabirds in order to detect shifts

in the marine food web (e.g. Montevercchi & Myers 1996). (3) The third approach is to use patterns of habitat utilisation and behaviour as well as prey choice of seabirds at different temporal and spatial scales as an indication of site quality and its ecological function for seabirds. The last two applications were used within the scope of the present study and subsequently will be discussed in more detail.

Particularly the Chapters I and II prove the high potential of opportunistic surface-feeding seabirds to indicate profound changes in the coastal food web dynamic by monitoring (historical) changes in prey choice and in temporal and spatial habitat utilisation patterns. Using opportunistic seabird species for this approach provides an excellent method to detect changes in the food web dynamics of the whole coastal system. Cairns (1987) states that monophagous species quantify prey availability most reliably. Opportunistic species might not be able to provide such exact sampling of single prey species, however, they are particularly well-suited to evaluate prey availability in different habitat types of the coastal zone. Particularly opportunistic surface-feeding species are likely to mainly reflect prey which is (super)abundant (Chapter I) and thus provide an excellent source of information on temporal and spatial patterns of changes of the prey supply (Monaghan 1996). In order to conduct a reliable monitoring of the whole coastal zone, it is however necessary to have long-term data sets available. For the distribution at sea, the German Seabirds at Sea database provides such a highly valuable source of information (Garthe & Hüppop 2000). It would be most preferable to conduct additional, methodological consistent long-term sampling schemes of food choice of surface-feeding seabirds. As such long-term data sets were not available for the present study, in many cases a comparison with available results from literature had to be carried out (besides the sampling of my own, more recent data). Due to different methods and sample sites used, the conclusions received from that comparison will certainly be biased to a certain extent. However, even this approach was able to reveal distinct changes of the coastal food web and of basic changes of habitat use.

It is very important to consider that surface-feeding seabirds in the pelagic zone are only able to “sample” the upper part of the water column. Thus, these species are only suited to reveal interactions with marine organisms that can be exploited by this limited foraging technique. Furthermore, the present study showed that it is necessary to utilise a variety of species for the purpose of monitoring of habitats, because, as a consequence of niche segregation, the species have their core-distribution in different parts of the coastal system. Thus, it is important to choose species that may reflect the respective part of the coastal zone by their foraging ecology. In order to cross-validate the indications of prey availability received by observations of seabirds, it would be desirable to collect independent data of the prey source itself by fishing and other means (Monaghan 1996). This was not possible for each of the special studies conducted within this work due to logistic limitations. However, in several cases missing data of the status of the prey species could be compensated by information from the literature for closely related sciences.

The use of behavioural observations in order to judge the ecological functions of habitats for the investigated species is highly recommendable. The results of the present study demonstrate that simple direct observations of the behaviour of seabirds within their habitats have a strong power to classify sites according to their significance for the respective species. The results of Chapters II, III and V clearly show that it was possible to reveal distinct sites (at various spatial scales) that were highly important for foraging purposes of seabirds while others were used more intensively for resting or migration or for commuting to foraging sites and breeding colonies. When management decisions in the coastal zone have to be taken, the ecological functions of sites for seabirds is a decisive factor. Habitats need to be treated differently when only used for transfer purposes instead of being important moulting, resting or foraging sites of seabirds (ICES 2006; Louzao et al. 2006). Due to their highly visible lifestyle, surface-feeding seabirds are certainly suited best for this kind of analyses, but all other group of seabirds can principally be treated the same way.

In conclusion, the approach to merge the temporal and spatial patterns of habitat use, behaviour and prey taken by seabirds in order to gain information on ecological function of the sites is highly valuable and can provide an important step towards the management of the whole coastal zone.

(3) What are the consequences of surface-feeding and how strong is the competition between the species investigated in the coastal zone?

The majority of the seabirds species living today use pursuit diving as foraging technique to exploit prey (Brooke 2002; Shealer 2002). Although this foraging method seems to be highly efficient, it is very energy-demanding and (at least at a larger spatial scale) can only support high numbers of individuals within very productive marine regions (Brooke 2002). Montevecchi (1993) states that surface-feeding seabird species frequently need to utilise a larger sea area to encounter their less predictable prey compared with sub-surface-feeders. Consequently, particularly during breeding time surface-feeders often have less buffer time to enhance foraging activity during times of reduced prey availability (Monaghan 1996). However, besides these negative components of surface-feeding, there are several characteristics that make this foraging technique valuable:

(1) Although surface-feeding may be less effective in terms of prey intake per unit foraging time, it requires no special adaptations of diving and no morphological alterations of the body for underwater locomotion. (2) Consequently, the wings of many species are still adapted for long foraging flights and thus the utilisation of sites far offshore. Consequently, this species group is the only one that is able to dwell within areas of lower productivity, such as the tropics (Brooke 2002). (3) Moreover, many species (including most of those investigated within the present study) are still able to use the coastal mainland and tidal flats and are thus highly adapted for foraging in a coastal zone. (4) Most surface-feeding species are feeding generalists (Montevecchi

1993). This seems to be an adaptation necessary to cope with the unpredictable, patchy and ephemeral availability of their prey. Furthermore, the present study was able to show the high importance of the close temporal and spatial overlap between surface-feeders and their prey (Chapters I, II and V; compare e.g. with Sjöberg 1989). (5) The distinct foraging techniques of different species of surface-feeders are very different (Shealer 2002; Fig. 1). This enables niche segregation among the diversity of species utilizing this foraging behaviour.

Particularly the five gull species investigated within the scope of the present study do not differ significantly in terms of their foraging technique. However, it was possible to show that the closely related gull species nevertheless revealed distinct patterns of temporal, spatial and behavioural niche segregation within the German coastal zone of the North Sea. Basic patterns of niche segregation are certainly primarily due to large scale differences of habitat use of the three major landscape types of the German coastal zone (see Table 21). As the findings of Chapter IV show, there are likely many patterns of niche segregations that take place at a much smaller spatial (microhabitat) scale. As can be assumed by the core-distribution of the respective species as well as by taking into account their basic foraging ecology (e.g. Kubetzki & Garthe 2003), the general competition between the four gull species seems to be moderate at present (for detailed discussions on this issue see the discussions of Chapters II and IV). Mainly black-headed gulls seem to compete with common gulls at least within the mainland region during certain times of the year (Chapter IV) and lesser black-backed gulls seem to moderately compete with herring gulls particularly in the nearshore part of the offshore zone (Chapter II).

Hunt & Hunt (1973) were able to show that the high numbers and species diversity of gulls in Europe, in contrast to those of North America, could be explained by intensive anthropogenic activities. The present study indeed revealed various indications for the high importance of both fishing and agricultural activities for the benefit of gulls. Particularly black-headed and lesser black-backed gulls seem to be positively related to anthropogenic activities in the whole coastal zone (Chapters I, II and IV). The positive development of breeding pair numbers of most of the species investigated (Fig. 3) indicate a sufficient food basis that in turn is strongly enhanced by anthropogenic activities and the comparatively low intensity of competition among most species in the coastal zone. Each of the special chapters revealed the significance of different coastal landscape types for the respective species investigated as well as the significance of anthropogenic activities. Thus it is possible to develop scenarios for possible implications with breeding pair numbers, foraging opportunities and competition (among) several species in case that natural or anthropogenic processes in the coastal zone would change within the near future (see below).

(4) Which future scenarios for the species investigated might take place if anthropogenic activities or natural processes in the coastal zone would change?

The future development of the species investigated in the German coastal zone of the North Sea are likely to be strongly dependent on changes of both natural and anthropogenic processes. In contrast to natural processes, anthropogenic activities may change more rapidly, leaving little time for the species to evolve responses such as the exploitation of new foraging opportunities. There are many examples from literature for significant changes of habitat use and foraging ecology of seabirds as a consequence of altering anthropogenic activities, notably changes of fisheries (Oro 1996; Arcos & Oro 1996; Hüppop & Wurm 2000). This indicates that also opportunistic species may strongly rely on anthropogenic activities. At present, fundamental changes of fishing intensity and technique – which can be a decisive factor for providing discards for scavengers – in the German Bight are not likely. The effort of the German Brown Shrimp fishery was on a constant level during recent years (Ehrich et al. 2006). This fishery type is likely to be the most crucial one for most of the species investigated, as it is taking place close to the shore, and many different surface-feeding species utilise this food source (e.g. Walter & Becker 1994; 1997). The present study did not primarily focus on effects of fishery on surface-feeding species. However, Chapter II indicates that fishery in the offshore zone has a strong significance for lesser black-backed gulls at least during the post-breeding period (see also Camphuysen 1995). The findings of the present study also indicate that natural food (particularly swimming crabs) is of major importance during recent years and can be assumed to compensate for possible reduced utilisation of fishing discards without that (at least certain colonies of) this species would suffer from strong reductions in prey availability. It is important to emphasize that no particular investigations have been carried out within the scope of that study that focussed on the significance of the Brown Shrimp fisheries. Unpublished data strongly indicate that this fishery type is still highly significant primarily for herring gulls (and to a minor extent also for black-headed gulls) and that during the recent years also lesser black-backed gulls seem to follow fishing vessels in higher numbers compared to several years ago. This emphasizes the findings of changing distributions patterns (i.e. more coastal distribution) of this species during recent years (Chapter II) and might indicate a lower significance of different fishery types in the offshore zone that were still of major importance for this species several years ago (e.g. Garthe & Hüppop 1994). In conclusion, it is very likely that major changes of particularly Brown Shrimp fisheries would indeed affect several species investigated. However, many of them seem to have different feeding opportunities to compensate such possible major changes. A detailed analysis of this issue would be required in order to judge detailed effects of changing fishing intensity on the species investigated.

The second important anthropogenic activity in the coastal zone is certainly farming at coastal mainland areas. There are much fewer studies available for this topic compared to studies on influences of fishery. The investigation carried out within this

thesis is one of the first approaches to shed light on this problem with respect to niche segregation of the species concerned. Black-headed and common gulls are certainly the species that are strongest related to changes in agricultural practices. Chapter IV could clearly show that black-headed gulls benefit most from recent agricultural intensifications. As several studies pointed out it is very likely that the mechanisation and overall intensification of the European agriculture will further increase (Chamberlain et al. 2000; Vickery et al. 2001; Buckwell & Armstrong-Brown 2004). This seems to be most beneficial for black-headed gulls, while the reductions of grassland is very likely to pose future threats particularly to common gulls. Furthermore, since 2006 most of the German rubbish tips are closed which have been a major important food source particularly for herring gulls (R Rehm pers. comm.). It would be highly important to repeat a similar study of analysis of competition among gulls in the coastal mainland after this fundamental change, as additional competitive pressure from herring gulls, having lost a major food source, are to be expected. In conclusion, the recent tendency of agricultural intensification appears to be at present most beneficial for black-headed gulls which is certainly ultimately reflected in the positive development of their breeding population trend (Fig. 3).

Besides the effects of these anthropogenic activities the integrative approach of bioindication used within this study was able to detect profound historical changes of habitat use of black-headed gulls in the whole coastal zone, indicating a reduced quality of the tidal flats of the Wadden Sea area (Chapter I). This effect is accompanied with a recent decline of breeding pair numbers of important characteristic tidal species breeding along the North Sea coast (Koffijberg et al. 2006) as well as with declines of migrating bird species such as Arctic (wading) birds (e.g. Blew et al. 2005a; Colijn & Garthe 2006). It is certainly too early to judge the quality of the tidal flats of the whole Wadden Sea area by these indications. However, future studies should aim to analyse the benthic community of the German tidal flats in order to evaluate reasons for the reduced utilisation of this foraging habitat during recent years. The significant decline of breeding pair numbers of herring gulls (Koffijberg et al. 2006; Fig. 3) might similarly reflect major changes in the Wadden Sea zone.

In contrast, diet analysis, foraging success and foraging habitat use as well as breeding pair trend (Fig. 3) of the Arctic tern in the Wadden Sea (Chapter V) strongly indicated an acceptable food source for piscivorous surface-feeders in the coastal zone of the German North Sea. As already discussed within Chapter II, the good availability of fish suitable for predators such as terns or for the widely distributed lesser black-backed gull may also result from indirect effects such as overfishing of predatory fish species which causes higher abundance of smaller (suitable) fish. However, at least the findings of Arctic tern diet and foraging behaviour seem to indicate that the pelagic zone of the Wadden Sea and the estuaries are still able to maintain their important function as fish nursery (e.g. Thiel 1995; Vorberg & Breckling 1999; Thiel & Potter 2001). Fish richness within the pelagic zone of the Wadden Sea and the adjacent offshore region is not likely

to serve all surface-feeding species that were investigated within the present study. Particularly the herring gull will depend on the tidal flats of the Wadden Sea, while common gulls are likely to depend on carefully managed pastures in the coastal mainland.

Outlook and future perspectives

The integrative approach used in this study was able to reveal habitat use by surface-feeding seabirds in all important parts of the coastal system as well as to elucidate their function and quality. The findings of this thesis clearly indicate the importance to conduct spatially extended analyses of habitat use in the whole coastal zone if the aim is to evaluate important mechanisms of niche segregation and temporal and spatial changes in habitat use. This study demonstrates the highly useful approach of combined analyses of distribution, behaviour and prey used by seabirds in order to reveal the overall quality and ecological function of different sites within the different landscape types of the coastal zone. To further improve the applicability of this approach and to confirm the results received from direct observations on distribution and behaviour, it would be highly preferable to use data loggers attached to the birds. A combination of an observational and data logger approach might serve best to elucidate the location of sites used for different purposes. In addition, direct studies on prey availability should be carried out to confirm the findings of prey choice by the birds. In general, the approach used within the present study is highly useful to identify sensible sites for management purposes.

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Publikationen

Schwemmer P, Garthe S (2006) Spatial patterns in at-sea behaviour during spring migration by little gulls (*Larus minutus*) in the south-eastern North Sea. *Journal of Ornithology* 147: 354-366

Schwemmer P, Garthe S (2006) Sea ducks and impacts of ship traffic in the Baltic Sea. *Journal of Ornithology suppl* 147: 249

Garthe S, Schwemmer P (2005) Seabirds at Sea – Untersuchungen in den deutschen Meeresgebieten. *Vogelwelt* 126: 67-74

Schwemmer P, Garthe S (2005) At-sea distribution and behaviour of a surface-feeding seabird, the lesser black backed gull (*Larus fuscus*), and its association with different prey. *Marine Ecology Progress Series* 285: 245-258

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

The chapters of this thesis are partly published (Chapter II and III) or submitted (Chapter I and IV) or prepared for submission to peer reviewed journals (Chapter V). The following list provides an overview about my personal contributions on each of the publications:

Chapter I:

Regular habitat switch as an important feeding strategy of an opportunistic seabird species

Authors: Philipp Schwemmer; Stefan Garthe

Research and Technology Centre Büsum, University of Kiel, Germany

Submitted to *Journal of Animal Ecology*

Contributions: SG and PS developed the ideas of this study. PS conducted most of the field work, PS conducted the data analysis. PS and SG discussed the results, PS wrote the manuscript.

Chapter II:

At-sea distribution and behaviour of a surface-feeding seabird, the lesser black-backed gull (*Larus fuscus*), and its association with different prey

Authors: Philipp Schwemmer; Stefan Garthe

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Published in *Marine Ecology Progress Series* (2005) 285: 245-258

Contributions: This chapter is based on results of my Diploma thesis "Verbreitung und Aktivitätsmuster der Heringsmöwe (*Larus fuscus*) in der Deutschen Bucht". It has been extended by analysing new data and thus contains additional results and literature. SG developed the idea of this study. PS conducted most of the field work, PS conducted the data analysis. PS and SG discussed the results, PS wrote the manuscript.

Chapter III:

Spatial patterns in at-sea behaviour during spring migration by little gulls (*Larus minutus*) in the south-eastern North Sea

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Published in *Journal of Ornithology* (2006) 147: 354-366

Contributions: PS and SG developed the ideas of this study. PS conducted most of the field work, PS conducted the data analysis. PS and SG discussed the results, PS wrote the manuscript.

Chapter IV:

Area utilisation of gulls in a coastal farmland landscape: Habitat mosaic supports niche segregation of opportunistic species

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Submitted to *Landscape Ecology*

Contributions: SG developed the ideas of this study. PS conducted the field work, PS and RM conducted the data analysis. PS, SG and RM discussed the results, PS wrote the manuscript.

Chapter V:

Influence of water flow velocity and water depth on distribution and foraging patterns of a surface-feeding seabird in the German Wadden Sea

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Contributions: PS, NG, NM and SG developed the ideas of this study. PS, NG and NM conducted the field work, PS conducted the data analysis. PS, NG, NM and SG discussed the results, PS wrote the manuscript.

Erklärung

Hiermit erkläre ich, dass die vorliegende Arbeit selbständig von mir angefertigt wurde und dass sie – abgesehen von der Beratung durch meinen Betreuer – nach Inhalt und Form meine eigene Arbeit ist. Sie wurde keiner anderen Stelle ganz oder zum Teil im Rahmen eines Prüfungsverfahrens vorgelegt. Kapitel II baut jedoch auf Ergebnissen meiner Diplomarbeit auf. Die Arbeit ist unter Einhaltung der Regeln guter wissenschaftlicher Praxis entstanden. Dies ist mein einziges und bisher erstes Promotionsverfahren. Die Promotion soll im Fach Biologische Meereskunde erfolgen. Des Weiteren erkläre ich, dass ich Zuhörer bei der Disputation zulasse.

Kiel,.....

Philipp Schwemmer