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ORIGINAL ARTICLE

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

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Abstract At-sea distribution 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 also holds true for fast migrating species of international conservation concern, such as the little gull (*Larus minutus*) in the German Bight (southeastern North Sea). In this study, we used multiyear distributional data in combination with behavioural observations and food sampling to investigate spatial and temporal patterns and their possible causes during spring migration. The results show a highly focussed 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 were found either close to the mainland or close to the offshore islands. Little gulls used certain subareas 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 play an important role within the feeding sites and strongly influence 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 versus zooplankton and fish). In conclusion, the area utilisation of *L. minutus* during spring migration in the German Bight showed a clear pattern, and sites with main feeding action should be regarded as sensitive for little gulls, at least during spring migration.

Keywords Little gull · Habitat use · Behaviour · Distribution · Migration

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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 have revealed spatial patterns of many seabird species over different periods of time (e.g. Tasker et al. 1987; Camphuysen and Leopold 1994; Garthe et al. 2003). Current research focusses temporarily 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 and Webb 1999; Markones 2003; Schwemmer and Garthe 2005).

Explaining the at-sea distribution and area utilisation of endangered, migrating seabirds is particularly relevant because 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 and Spaans 1995). The little gull (*Larus minutus*) is such a migrating seabird of high conservation concern. It uses the German Bight (southeastern North Sea) intensively on its way to and from its 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 and Bauer 1982; Cramp and 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 focussed on migration patterns along the coast or over water (e.g. Camphuysen and 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. Because the spring migration of this species can take place very rapidly (Woutersen 1980; Camphuysen and 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 on the way to the breeding grounds.

Thus, at-sea observations during ship-based counts can provide a more general overview of important relationships. The simultaneous analysis of a long-term set of at-sea distributional data and behavioural observations can shade light on (1) the temporal and spatial patterns of *L. minutus*, (2) the utilisation of different areas at sea, and (3) the location of sensitive offshore sites and their 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 available only for the breeding grounds or very few resting sites on land (Glutz von Blotzheim and Bauer 1982; Cramp and Simmons 1983; Zubakin 1990; Koop 1997), while there are hardly any indications on food types taken in the marine environment during migration.

In this paper, we analysed multiple-year distributional and behavioural data of *L. minutus* as well as potential food availability. Furthermore, we assessed the different utilisation of subareas by this seabird species in order to reveal the importance of the southeastern North Sea during spring migration.

Materials and methods

At-sea distribution, behaviour, and phenology during spring migration were analysed in the German Bight, southeastern 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, but excluding the tidal flats between the islands and the mainland (Fig. 1). 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 because our study emphasised the behaviour of each individual and did not aim to estimating exact densities of birds. To correct each sighting for observer effort, which was different over the years investigated, the sum of all individuals recorded per 3′ latitude × 5′ longitude grid (grid cell size equivalent to about 30 km^2) was divided by the total kilometres travelled within that grid (hexagons in Fig. 1). Data were taken from the German seabirds at sea database (Garthe and Hüppop 2000), version 4.03 (as of June 2004).

Because distance to coast can be one major factor affecting distributions of seabirds during migration (Hutchinson and Neath 1978; Zubakin 1990; Garthe 1997) and may provide valuable information on possible mechanisms of interspecific competition and utilisation of food resources (Kubetzki and Garthe 2003; Schwemmer and Garthe 2005), this factor was investi-

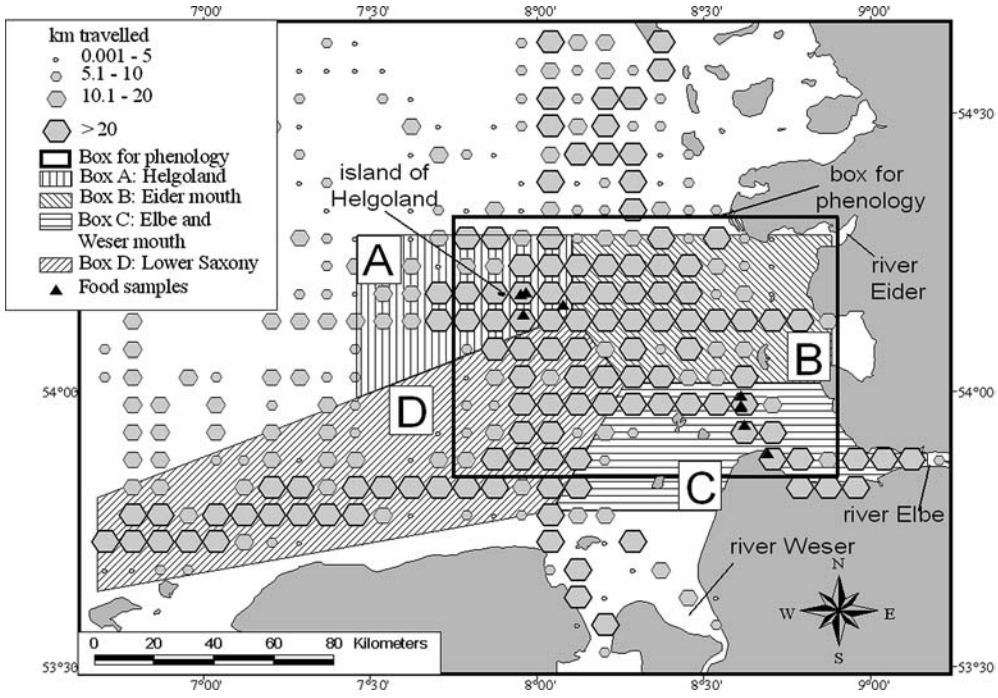

Fig. 1 Study area in the southeastern North Sea. Hexagons indicate the observer effort during April and May over the years 1991–1993, 1997–1998, and 2000–2004. The boxes A–D served for detecting differences in area utilisation by little gulls and were analysed on the basis of behaviour. *Triangles* represent locations of collection of food samples. The *bold box* was set for phenological analyses

gated for little gulls. Therefore, the distance of each centre point of each of the 3′ latitude × 5′ longitude grid cells to the closest point on land (including the Wadden Sea islands but excluding the island of Helgoland) was calculated and compared with the gull densities of the particular grid cell.

Behaviour at sea was analysed in accordance with the methods of Ashmole (1971) and Camphuysen and 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 a certain direction, (2) searching for or feeding on natural prey, (3) heading towards a certain direction while searching for or feeding on natural prey, or (4) resting (gulls that 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 and 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) aerial pursuit (hunting for prey carried by another bird). Additionally, birds associated with hydrographic fronts or with fishing vessels as well as little gulls that were involved in multispecies feeding flocks (Camphuysen and Webb 1999; Camphuysen and Garthe 2004) were recorded (574 birds in total).

For information on area utilisation by little gulls, behaviour patterns were compared between four different regions with distinct functions for a migrating seabird in the southern German Bight (boxes A–D in Fig. 1). 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,'' characterised by the influence of fresh water from the river Elbe and saline water during incoming tide; and box D is the ''Lower Saxony box,'' covering the area along the coast of Lower Saxony and south of Helgoland, the expected main migration route of little gulls in the southeastern North Sea.

Each day of observation was taken into account for statistical considerations as one when 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 one-way 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. 1). 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 adults.

For the different analyses done, the study period was altered according to the available data:

- 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).
- Behaviour was investigated from 15 April to 10 May during the years 2001–2004, as detailed observations of behaviour (Camphuysen and Garthe 2004) were not available from earlier periods.
- Phenology was investigated from 1 March to 31 May during the years 1991–1993, 1997–1998, and 2001–2004 to gain detailed information on the 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 the case with gulls (e.g. Bayer 1983; Camphuysen and 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 and Jackson 1986). Outside the breeding season and especially during migration, collection of food samples is very difficult because 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. 1). This was done with a net 60 cm in diameter with a mesh size of 0.5 mm that was towed for 5 min close to the sea surface. Samples were analysed with an 8×23 binocular, and species were determined to the lowest possible taxon. An ocular with a scale was used to measure approximate prey sizes.

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 times mentioned regarding 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. 2). At the beginning of April, only a few individuals were present; the highest numbers were found during the last 10 days of April and the first 10 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.

Whereas almost solely adults were found until mid-April, the proportions of immatures increased above all in May (Fig. 3).

Distribution

Distribution patterns revealed highest numbers close to the offshore island of Helgoland, up to 50 km from the shore (Figs. 4, 5). 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 southwest to northeast between the eastern East Frisian islands and the river Eider (Fig. 4). The offshore region, more than 50 km from shore, was hardly used by little gulls (Fig. 5).

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 feeding situation (63.9%), followed by actively searching for prey (28.3%) and surface pecking (5.6%). Only a very few gulls were recorded surface seizing (1.8%) or 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 multispecies feeding flocks, and only 0.04% joined fishing vessels (one single bird at one observation only).

Between the four spatial boxes (see above), significant differences could be detected in all but one behaviour type (resting) tested (Table 1). For individuals searching for or feeding on natural prey, the highest proportions were found in the Helgoland box and the Elbe mouth box, those two areas being significantly different from the two others (Student-Newman-Keuls post hoc test). Although the proportions of gulls heading towards a certain direction were highest in the Lower Saxony box and the Eider mouth box (Table 1), post hoc tests revealed significant differences only between the Elbe mouth box and the Eider/Lower Saxony boxes, while differences to the Helgoland box were not definite.

The highest proportions of birds associated with hydrographic fronts were found within the same boxes in which the highest feeding activity occurred (Table 1). Significant differences were revealed only between the Helgoland and the Lower Saxony boxes (Student-Newman-Keuls post hoc test).

Food availability

In most cases, food taken by little gulls at sea was too small for identification using 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 2). In the area of the outlet of the river Elbe, drowned insects—floating on

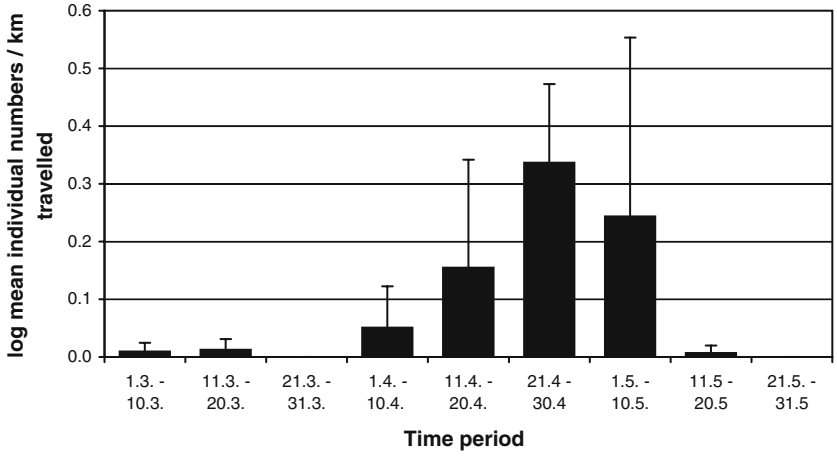

Fig. 2 Phenology of little gulls during March to May recorded within the *bold box* (Fig. 1), expressed as numbers of birds divided by observer effort (kilometres travelled). The logarithm of the original numbers was taken to match a normal distribution

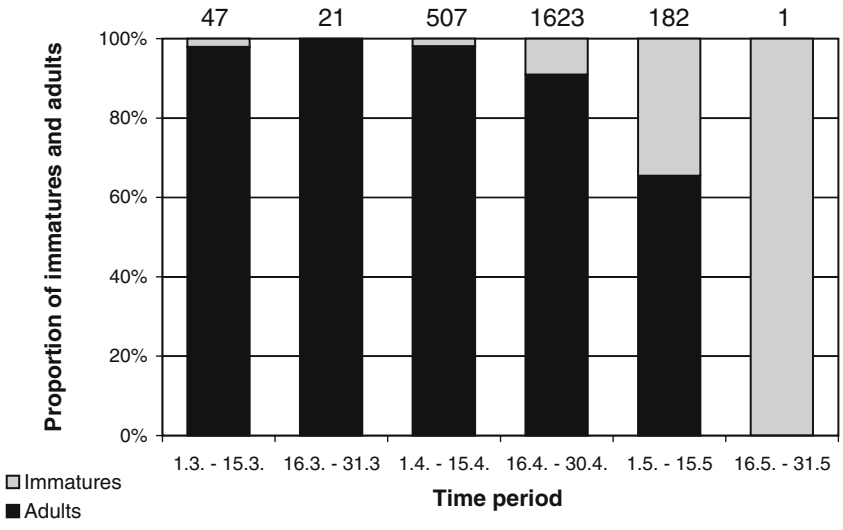

Fig. 3 Proportion of immatures and adults recorded within the *bold box* (Fig. 1)

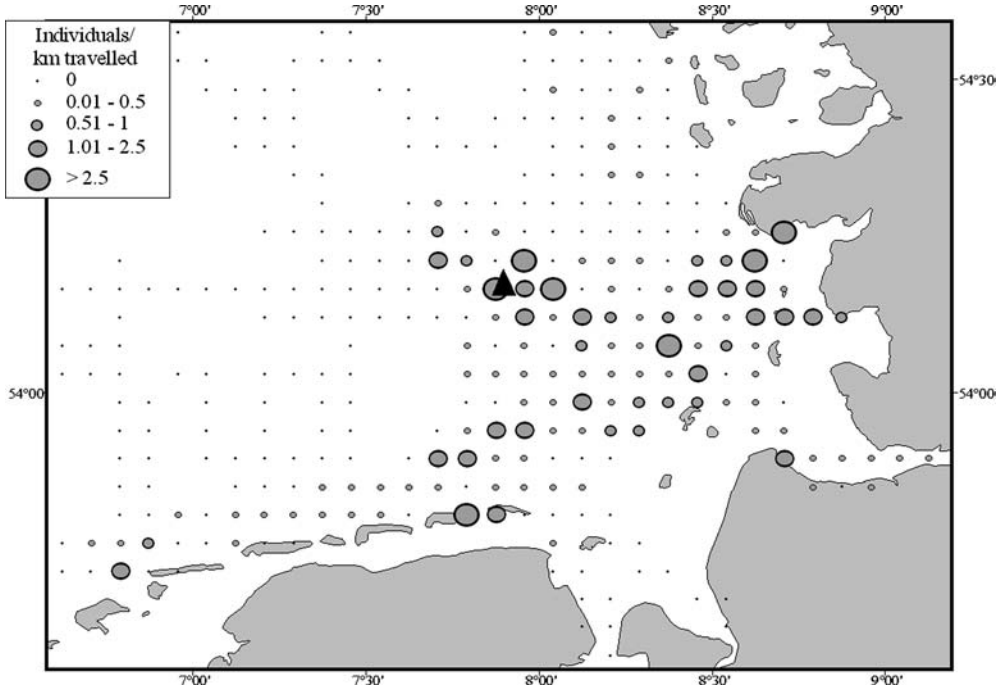

Fig. 4 Distribution of little gulls from 15 April to 10 May over the years 1991–1993, 1997–1998, and 2000–2004. Numbers of birds recorded were corrected for observer effort. The *black triangle* indicates the island of Helgoland

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 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 2).

Interspecific aggregations

Most flocks consisting of little gulls and at least one other species could be classified as feeding associations, and each appeared rather close to shore (primarily in the catchments of the river Elbe) or in the vicinity of the island of Helgoland (Fig. 6). Numbers of species associated with little gulls differed between flocks and ranged from one to six. Many of the most diverse flocks occurred in the coastal area of the river Elbe and south of the mouth of the river Eider (Fig. 6). Altogether, 14 species of birds and marine mammals were found in association with little gulls. *L. minutus* did not seem to show a preference regarding association 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. 7). All species of gulls common in the North Sea were found participating in flocks rather often, whereas the non-surface-feeding seabirds and marine mammals appeared only very rarely. Species composition in the flocks showed regional

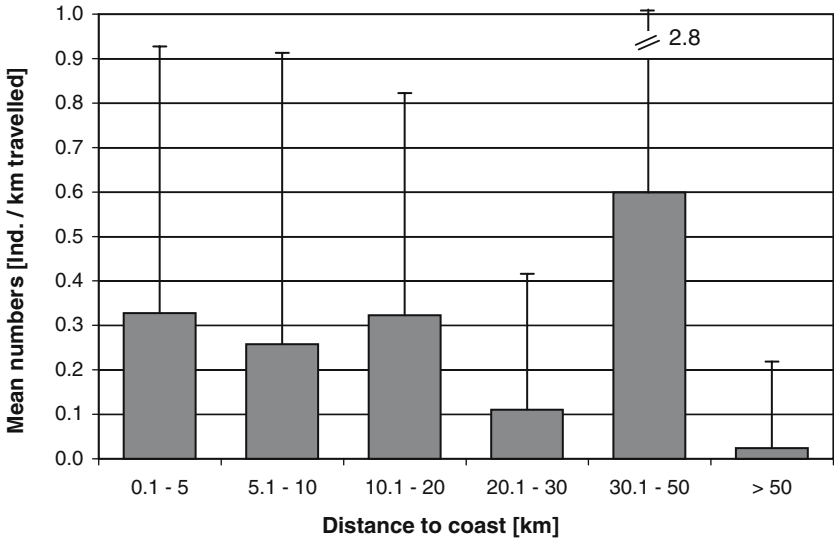

Fig. 5 Abundance of little gulls in relation to distance to the coast (including the Wadden Sea islands but excluding Helgoland)

differences on the basis of the four boxes. Common and arctic terns as well as mew 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, with each record showing different species in association with little gulls, whereas the Elbe mouth box showed the lowest species diversity, consisting mainly of gulls and terns.

Flight directions

A clear preference for northeasterly directions towards the mouth of the river Eider could be revealed for almost any observation (Fig. 8). As the only exceptions, the five individuals recorded in the inner Elbe mouth were heading northwest, and most individuals recorded north of Helgoland were heading towards the island.

Discussion

Different subareas of the German Bight seem to play an important role during spring migration of little gulls. This is particularly obvious considering both phenology and area utilisation patterns of this species.

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 with 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 and 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 the first 10 days of May. This temporal pattern matches findings of other studies very well: In many places in Britain and Ireland, the highest numbers were recorded during the end of February and the beginning of March (Lassey and Greenhalgh 1969; Hutchinson and Neath 1978; Madden and Ruttledge 1993), whereas observations from the German mainland and the Baltic reveal 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 proportion of gulls in the German Bight consists of

Table 1 Proportions of the four categories of behaviour and of gulls associated with hydrographic fronts within the four boxes (see "Materials and methods" section)

	Helgoland box	Eider mouth box	Elbe mouth box	Lower Saxony box	Significance level
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	Not significant
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	$P < 0.05$; $df = 3$

Differences between the four boxes were tested by one-way ANOVA

Table 2 Frequency and range of size of different species or groups found in fishing samples taken next to feeding little gulls at the mouth of the river Elbe ($n = 6$) and the Helgoland region ($n = 5$); for location of sample sites, see Fig. 1

Species/group	Elbe						Helgoland					Range of size (mm)
	Sample no. 1	Sample no. 2	Sample no. 3	Sample no. 4	Sample no. 5	Sample no. 6	Sample no. 1	Sample no. 2	Sample no. 3	Sample no. 4	Sample no. 5	
Ctenophora												
Pleurobrachia pileus	c	b	–	–	–	b	c	b	a	–	–	1.9–11
Cnidaria												
Tima bairda	a	–	–	–	–	a	–	–	–	–	–	4.8–6.2
Mollusa												
Bivalvia	–	a	–	a	–	a	a	–	–	–	–	1.5–10.1
Crustacea												
Dapnnia species	–	–	–	b	c	a	–	–	–	–	–	1–1.3
Copepoda	a	b	–	b	a	c	c	c	c	c	c	1.2–4
Cirripedia	–	–	c	c	b	c	–	–	–	–	a	2.3–10.3
Decapoda (Larvae)	–	–	–	–	–	–	a	–	b	b	–	1–1.5
Crangon species	–	a	–	a	–	–	–	–	–	–	–	5.8–18
Liocarcinus species	–	–	a	a	–	–	–	–	–	–	–	1.1–22.2
Carcinus maenas	–	–	a	–	–	–	–	–	–	–	–	16–34.5
Amphipoda	–	–	–	–	–	–	–	–	–	–	b	14.2
Insecta												
Hymenoptera	–	c	c	c	c	c	–	–	–	–	b	1.3–8.2
Diptera	c	a	c	b	c	c	a	a	–	–	a	1–21.1
Coleoptera	a	b	c	b	–	a	a	–	–	–	–	1–10.2
Chaetognatha												
Chaetognatha	–	–	–	–	–	–	–	–	–	–	a	14.2–17
Vertebrata												
Teleostei (eggs)	–	–	–	–	–	–	c	c	c	c	c	1.1–1.5
Teleostei (larvae)	–	–	–	–	a	a	c	a	b	b	c	5.7–12
Others												
Seeds	a	c	–	–	–	–	–	–	–	a	–	2.8–6.1

[a] 1–10 individuals in sample
[b] 11–25 individuals in sample
[c] > 25 individuals in sample

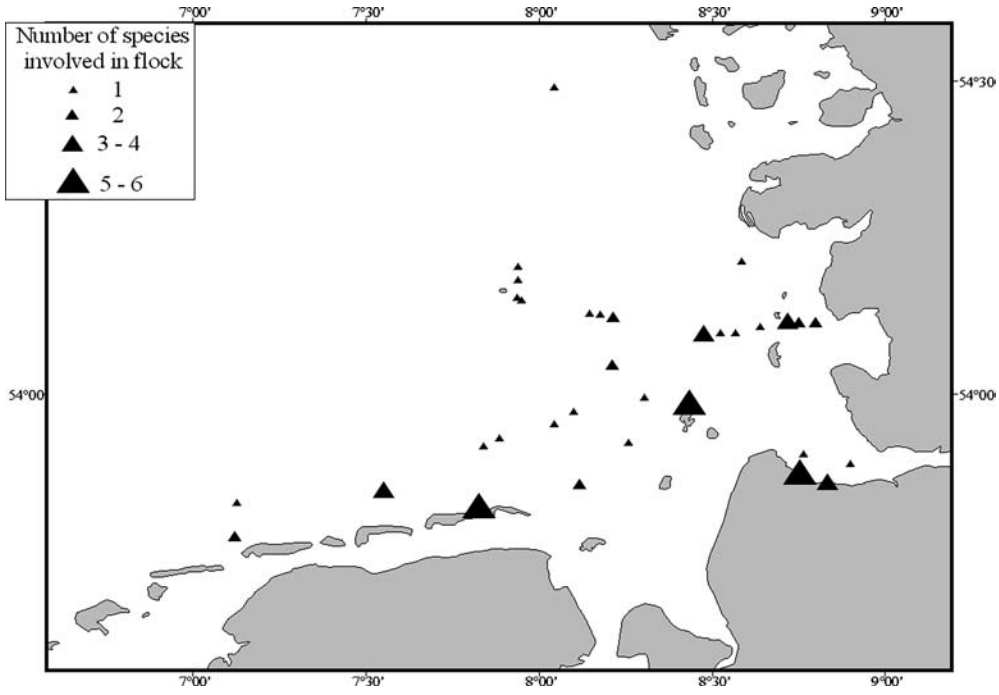

Fig. 6 Distribution of feeding flocks with little gulls involved. The size of the *triangle* indicates the number of other species participating in the flock

individuals travelling along the Dutch and French coasts as well as originating from the southern parts of Britain and Ireland, whereas a northern influx can be negated because of very low numbers of little gulls in the northern parts of Britain and Denmark during spring migration (Hutchinson and Neath 1978; Christensen et al. 1990). Several authors have pointed out the relevance of transcontinental 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, mainly strong winds (den Ouden and 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 and Greenhaigh 1969; Garthe 1993a, 1993b). It can be assumed that some individuals do not migrate as far as the breeding grounds, for some authors report long-term feeding actions and also summering at suitable sites (e.g. Hutchinson and Neath 1978; Madden and Ruttledge 1993). In the German Bight, however, numbers during summer are very low.

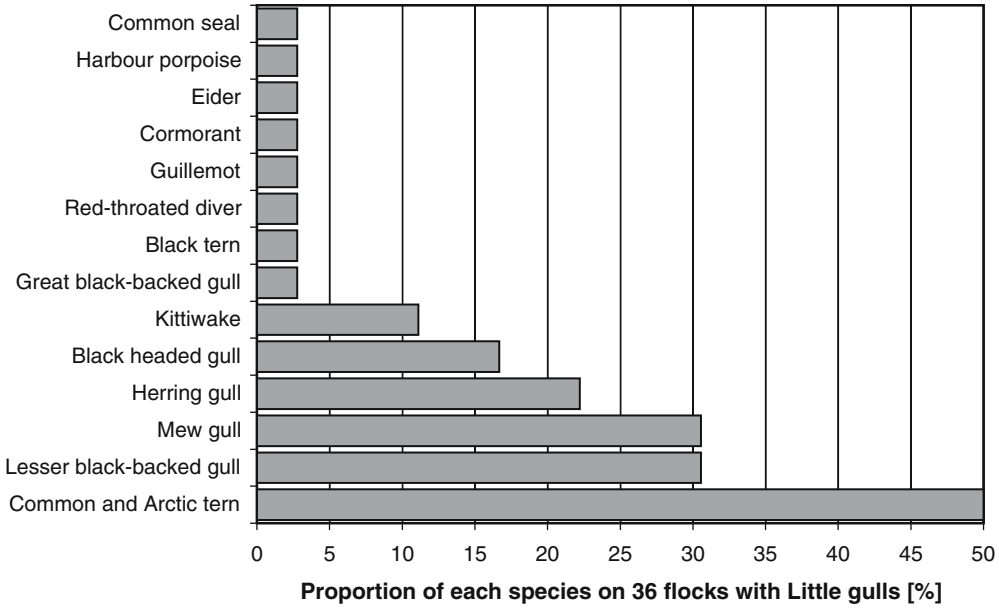

Fig. 7 Proportions of the 14 species found in 37 mixed flocks with little gulls

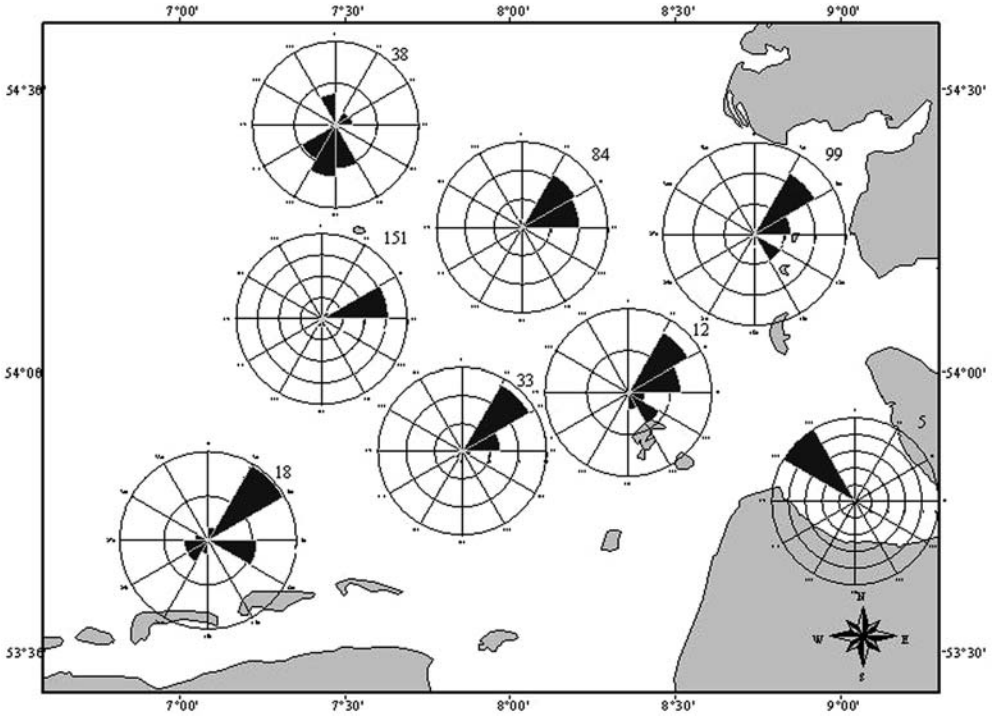

Fig. 8 Proportions of flight directions of little gulls in units of 30°. Each *circle* in flight diagram represents 20% of all gulls recorded within the spot covered by each diagram. Numbers in each diagram are absolute numbers of gulls observed. The study area was slightly reduced for a better overview

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 increased 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 indicates. Suitable feeding sites are known

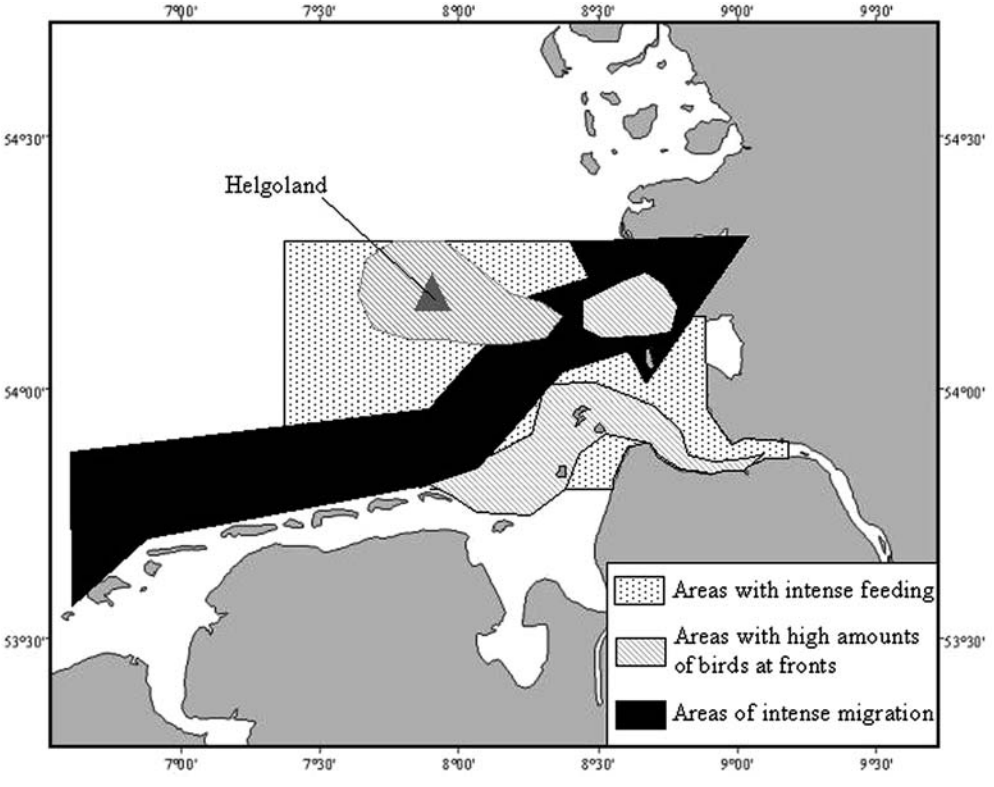

Fig. 9 Simplified scheme of area utilisation by little gulls in different regions of the southern German Bight

to attract vast numbers of little gulls and may even lead to late migration peaks because of high numbers of nonbreeders (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 that are intensely used for feeding: the area of Helgoland and the outlet of the 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). Analysis of the flight directions in this areas shows strong evidence that the river Eider was obviously used as a main migration route. This finding is supported by Gloe (1987), who observed high numbers on this river during spring. The general northeasterly direction that was visible remarkably far in the offshore area agrees very well with other land-based studies (e.g. 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 and Stougie 1990). In contrast, the river Elbe does not seem to serve as an important migration route during spring migration because only a few individuals were observed in direct flight ($n = 5$), and those were all heading down the river (Fig. 8). 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, personal communication). Taking the total numbers of individuals with flight direction towards the mainland into account, 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 the river Elbe and the area near Helgoland, both characterised 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 1; see also Fig. 9 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 with the Elbe site (Table 1), 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 that 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.

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 postglacial 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 1; Fig. 9). Krause et al. (1986) state that upwelling fronts in that region are characterised by a significantly large amount of zooplankton; food samples from this area support these findings (Table 2).

In contrast, nearly all individuals recorded in the outlet of the river Elbe were found foraging (though the overall numbers and the proportion of gulls that were actually taking up prey were lower compared with the Helgoland region), and of these, a high proportion took up prey at tidal fronts (Table 1). As fishing samples revealed, the most numerous potential prey category that little gulls were likely feeding on were drowned insects (Table 2). Fronts in this region are characterised by the convergence of coastal fresh water 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 and Frahm-Rodewald 1980; Krause and Reuter 1988). Additionally, strong tidal currents, which are commonly found in this area, can cause high prey availability, too (Eades 1982; White 1992; Keijl and Leopold 1997).

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. First, overall individual numbers of feeding gulls are lower in the Elbe region, and second,) the use of the Elbe river as a feeding and resting site seems to be much stronger during autumn migration (e.g. Albat 1993; Garthe 1993b, 1997). Here, different qualities of food might play a major role; the high amounts of zooplankton (i.e. primarily fish eggs and larvae as well as decapoda larvae and copepoda; Table 2) provides a higher energy content compared with the mainly terrestrial food (i.e. insects) in the Elbe estuary. Additionally, drowned insects might be a less predictable food source because they could be available in considerable numbers only during certain wind conditions that blew them out to the sea. This cannot be answered by the relatively small number of food samples collected. In contrast, M.F. Leopold (personal communication) reports high amounts of fish larvae used by little gulls in the Dutch offshore area. Garthe (1993b, 1997) describes the intake of small pelagic fish, mainly smelt (*Osmerus eperlanus*), in the upper part of the outlet of the Elbe during autumn, which could not be observed during spring. According to Möller (1984), smelt is a very frequent pelagic fish of the Elbe river and is abundant throughout the year. The proportion of small 0-group smelt, which—according to

its length—is suited best as prey for little gulls, is available from June onwards but seems to be superabundant during August and September. According to Garthe (1993b), this is the main autumn migration period of *L. 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 insects and zooplankton as well as small fish are the most likely food used during spring migration. First, according to our behavioural observations, most feeding little gulls were recorded dipping or surface pecking (Ashmole 1971). This is a typical behaviour for intake of small organisms, which float close to the water surface. Second, although investigations of stomach contents are very rare and available only 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 and Simmons 1983; Zubakin 1990). Finally, 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). Our 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 food choice of little gulls seem to lead to an avoidance of competition with other gulls or terns. *L. minutus* can be classified as a typical social feeder, and it can be assumed that this species benefits from foraging in interspecific groups, for terns and larger gull species that occur most frequently in such associations (Fig. 6) tend to feed on a different range of food. 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 are associated with hunting auks during winter, a phenomenon that we could observe frequently (unpublishing 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, our study revealed different area utilisation patterns of 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. These 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.

Zusammenfassung

Räumliche Verhaltensmuster von Zwergmöwen (*Larus minutus*) auf See während des Frühjahrszuges in der südöstlichen Nordsee

Die Verbreitung von Seevögeln auf See ist in der Vergangenheit auf unterschiedlichen geografischen Ebenen und unter verschiedensten Fragestellungen in vielen Teilen der Welt beschrieben worden. Das Auffinden einzelner Parameter bzw. die Erklärung von Prozessen, welche Verbreitungsmuster definieren, ist jedoch oft nicht einfach und in den meisten Fällen bisher nur wenig untersucht. Dies gilt um so mehr auch für schnell ziehende Seevogelarten, die durch ihre vergleichsweise kurze Anwesenheit und hohe Dynamik auf dem Zug nur schwer erfasst werden können. Die Zwergmöwe (*L. minutus*) in der Deutschen Bucht (südöstliche Nordsee) ist ein solcher Seevogel, der darüber hinaus international Schutzbemühungen unterliegt. In dieser Studie werden anhand langjähriger Verbreitungsdaten in Verbindung mit detaillierten Verhaltensbeobachtungen (nach einem neu entwickelten Klassifizierungskatalog) und der Beprobung von Nahrungsverfügbarkeit räumliche und zeitliche Muster im Frühjahrszug der Zwergmöwe untersucht. Darüber hinaus wird eine Einschätzung der Bedeutung bzw. der Qualität unterschiedlicher Seegebiete für diese Art unternommen. Die Ergebnisse zeigen einen auf die letzten Wochen des April und die ersten Wochen des Mai stark fokussierten Frühjahrszug. Dabei scheint dem Fluss Eider eine übergeordnete Rolle als Hauptzugroute zuzukommen, da schon früh im offenen Seegebiet bei offensichtlich ziehenden Individuen zu einem hohen Anteil die Flugrichtung eindeutig zur Eider hinwies. Die höchsten Zahlen von Zwergmöwen konnte entweder nahe dem Binnenland oder nahe den vorgelagerten Inseln erfasst werden. Der Region um Helgoland schien dabei eine besondere Bedeutung zuzukommen. Hier trat nicht nur eine erhöhte Zahl von Zwergmöwen auf, sondern diese Region gehörte neben dem Elbmündungsbereich zu jenen, in denen Zwergmöwen in hohem Maße Nahrung suchten bzw. aufnahmen. Im Gegensatz dazu fand in anderen Bereichen (nördlich Niedersachsen und nahe der Eidermündung) verstärkt reiner Zug statt. Hydrografische Phänomene wie Fronten oder Schaumstreifen spielten eine wichtige Rolle innerhalb der Regionen mit starker Nahrungsaufnahme und schienen Verbreitung und Verhalten deutlich zu beeinflussen. Der Energiegehalt der verfügbaren Nahrung und das Fressverhalten in verschiedenen Regionen des Untersuchungsgebietes lässt den Schluss zu, dass es Unterschiede in der Qualität der Hauptfressgebiete der Zwergmöwe während des Frühjahrszuges geben dürfte: Im Bereich der Elbmündung traten weniger Nahrung suchende Individuen auf als in der Region nahe Helgoland. Die Nahrungsproben im Elbmündungsgebiet wiesen einen hohen Anteil von energieärmeren ertrunkenen Insekten auf, während nahe

Helgoland die Verfügbarkeit von energetisch günstigeren Zooplankton-Organismen und Fisch höher war. Allerdings gibt es deutliche Anhaltspunkte dafür, dass der Bereich der Elbmündung eine wichtigere Rolle im Herbstzug dieser Art spielt. Zusammenfassend lässt sich sagen, dass die Raumnutzung von *L. minutus* während des Frühjahrszuges in der Deutschen Bucht ein klares Muster aufweist. Die Bereiche mit starker Nahrungsaufnahme sollten als besonders wichtig für den Heimzug der Zwergmöwe eingestuft werden.

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