INTRODUCTION

Large-scale variations in seabird distributions are mainly caused by environmental heterogeneity resulting from physical oceanographic processes (Haney 1987) and pervasive anthropogenic disturbance (Jackson et al. 2001, Camphuysen 2005). However, patchiness in seabird distribution may also occur at smaller scales due to species-specific responses to the environment (e.g. Garthe 1997, Wanless et al. 1997, Boyd et al. 2006). Likewise, the presence of surface features (e.g. floating wood, debris, seaweed, buoys, and fronts) may determine seabird distribution as they provide resting places and can temporarily increase available food sources, to which seabirds can quickly respond. Haney (1987), for example, described patchiness due to the visible surface manifestations (slicks alternating with ripples of rough water) of internal waves. The seabird patchiness was probably due to qualitative differences in prey composition as most birds were actively foraging or feeding. Similar observations were done at fronts (e.g. Haney 1985, Balance & Pitman 1999, Vandendriessche et al. 2007).
Spear et al. 2001), due to the locally elevated level of prey biomass. Especially the distribution of phalaropes (mostly feeding or resting) has been linked to the presence of large and persistent oceanic fronts and other oceanographic features that concentrate zooplankton at the surface (e.g. Haney 1985 & 1986, Lee 1987, Brown & Gaskin 1988).

On an even smaller scale, a wide variety of floating objects have been reported to attract seabirds: Cadée (2002) reports on peckmarks on and ingestion of debris like plastic, styrofoam and cuttlebones in the North Sea; Arcos (2000) observed an alternative feeding strategy of Balearinic Shearwaters Puffinus mauretanicus involving capture of fish under floating objects; and floating seaweeds in the Bay of Fundy (Canada) are shown to attract seabirds such as phalaropes, gulls and terns (Parsons 1986, Huettmann pers. comm.).

The influence of floating seaweed patches on the distribution and behaviour of seabirds formed the key issue of the present study. Floating seaweeds, both the permanently floating Sargassum and ephemeral patches composed of different species, are shown to teem with small marine animals seeking food and refuge, including crustaceans and fish (e.g. Fine 1970, Tully & O’Ceidigh 1986, Coston-Clements et al. 1991, Ingolfsson 1995, Kingsford 1995, Vandendriessche et al. 2006a, Vandendriessche et al., 2007). The increased biomass in invertebrates and fish compared to the surrounding water column may constitute an important, more or less predictable source of extra food, although probably exploited in an opportunistic way (Arcos 2000). In the Sea of Okhotsk, for example, Dunlins Calidris alpina were seen feeding on rafts of floating seaweed, probably taking snails and insects (Huettmann pers. comm.). Furthermore, floating seaweeds could play an important role by signalling suitable feeding areas to birds since they tend to accumulate in biologically rich water masses (Arcos 2000).

From the observations listed above, it is clear that seabirds are attracted to surface phenomena like floating seaweeds. Other than a few studies concerning Sargassum and some sporadic notes, however, few investigations have been done on the topic of seabirds associated with floating seaweeds. As a result, the present study aims to examine the seaweed’s possible attractions for seabirds in Northeast Atlantic waters, based on the European Seabirds At Sea database (ESAS). The main research questions of this study are: “Are there seabirds that are frequently seen associated with ephemeral patches of floating seaweed?”, and “Are these associations feeding mode-dependent?”.

**MATERIALS AND METHODS**

The seabird data used in the analyses were extracted from the European Seabirds At Sea database, which is composed of seabird observations collected and coded using standardised survey techniques (Tasker et al. 1984, Camphuysen et al. 2004). The database was established in the early 1980s and contains results of ship-based and aerial seabird surveys in Northwest European waters (Camphuysen & Garthe 2004). Of special interest for this study is the use of standardised coding of behaviour types in the database. The coding system, for example, introduced specific coding of associations of birds with certain surface phenomena and emphasises on feeding behaviour and foraging interactions. Codes have been devised for birds associating with near-surface fish shoals or marine mammals, with floating objects such as wood, rubbish, oil slicks and seaweeds, and with fronts, buoys, markers, vessels, offshore installations, sea-ice or land. The birds are further described according to behaviour, such as flying towards the surface phenomenon, scavenging, searching for prey, feeding, or resting. Furthermore, the description of the foraging behaviour is detailed and distinguishes between 20 behavioural codes like holding fish, aerial pursuit, scavenging at fishing vessel, surface pecking, and actively searching. The great benefit of detailed behavioural coding is that it provides insight in potential correlations between seabird presence and oceanographic or other factors driving prey, and that it allows discrimination between real associations and coincidental observations (Camphuysen & Garthe 2004).
The used data originated from the period 1979–2000. Detailed association codes were only recorded in <1% of all records. Because the coding system was not always used at the same level of detail (e.g. a large proportion of the records only distinguished between ‘associated with fish shoals’, ‘approaching observation base’ and ‘patterning’), a quantitative analysis of the importance of floating seaweeds was biased. The lack of metadata concerning the level of detail in the use of the coding system prohibited a straightforward restriction of the data. However, as the bias depended on the observers and circumstances per trip, it was assumed that the bias was straightforwardly applied to the entire dataset, enabling comparisons between species. Consequently, the numbers resulting from the analyses can be used for interspecies comparison, but they do not give reliable estimates of real seaweed-associated densities.

Although the database contained data about all Northwest European waters, the data about seaweed-associations in seabirds were concentrated in the North Sea. Therefore, only the seabird data from that region (59°17’–51°26’N and 2°47’W–6°58’E, see Fig. 1) were extracted and used in the analyses. Only data of common seabirds were included; rare seabird species (less than 300 records) and terrestrial birds were excluded. All abundances of seabirds were expressed as frequencies of occurrences to correct for aggregation behaviour.

Seabird species were grouped a priori according to foraging behaviour based on literature (Cramp et al. 1978–1997). The non-parametric Kruskal-Wallis test was applied to test for differences between multiple independent groups. Pairwise tests were done using the multiple comparisons procedure (Conover 1971).

RESULTS

Floating seaweed accounted for 2% of all observations of surface phenomena (Fig. 2A; large man-made objects like buoys, platforms and vessels not taken into account) and for 4% of all seabird counts in association with these phenomena. These percentages, however, are likely to be underestimated because floating seaweed is often an important constituent of patches of floating matter and lines in sea, and because floating seaweeds often converge at fronts.

The most common visitors of floating seaweed patches were Guillemots Uria aalge, Common Scoters Melanitta nigra, Lesser Black-backed Gulls Larus fuscus and Kittiwakes Rissa tridactyla, Gannets Sula bassana, Razorbills Alca torda, Eiders Somateria mollisima, Sandwich Terns Sterna sandvicensis and Common Terns Sterna hirundo (Fig. 2B). Occasional visitors included other gulls (Herring Gulls L. argentatus, Common Gulls L. canus, Greater Black-backed Gulls L. marinus, Black-headed Gulls L. ridibundus) and Arctic Terns S. paradisaea, Fulmars Fulmarus glacialis, Greater Skuas Stercorarius skua, Cormorants Phalacrocorax carbo and Red-breasted Mergansers Mergus serrator.
In order to quantify the importance of floating seaweeds to seabirds, the percentages of observations that seabirds were observed with floating seaweed were calculated per species (Fig. 3). These percentages differed among species, depending on the mode of foraging (groups indicated in Fig. 3). The results indicate that surface feeding species that make shallow dives (terns and...
Red-breasted Mergansers) benefit most from the presence of floating seaweeds and their associated macro- and ichthyofauna (on average 0.49% of occurrences associated with seaweed). Species hunting for pelagic and bottom-dwelling prey (divers, Guillemots, Razorbills, Puffins Pratercula arctica, Gannets and Cormorants; together 0.03%), and especially benthos feeders (Common Scoters and Eiders; 0.21%) were frequently seen in association with floating seaweeds, while opportunists and scavengers like gulls and skuas were recorded on few occasions (0.02%). Finally, petrels and shearwaters (surface-seizing, pursuit-plunging, pursuit-diving) were seldomly seen in association with floating seaweeds (<0.001%).

The most common behavioural activities of the birds associated with floating seaweed were found to be surface pecking and actively searching (mainly gulls and terns), and pursuit plunging (mainly Cormorants) (Table 1). At the few occasions that activities of Razorbills, Fulmars, seaducks and Guillemots were recorded, they were mostly pursuit-plunging or actively searching.

Because foraging behaviour in terns was regularly described, we compared their behaviour around seaweeds to their behaviour outside seaweed patches (Fig. 4). The three tern species were most commonly associated with fish shoals (up to 20%) and their top-3 foraging activities varied when comparing seaweed-associated birds with the rest of the observed birds. Arctic Tern was mainly seen dipping and surface pecking in the vicinity of floating seaweeds, which is similar to other cases, in which they were mainly seen surface pecking, actively searching and dipping. Foraging behaviour was quite similar in Sandwich Tern as well: in both cases the main activities were actively searching and deep plunging. Considerable differences, however, could be observed in Common Tern, which was mainly seen surface pecking and dipping around floating seaweeds, but was actively searching, pursuit diving or scavenging in most other cases. These results indicate that, especially in the case of Common Tern, the presence of floating seaweed patches may influence foraging behaviour and therefore also prey choice.

Table 1. Behavioural activities of birds associated with floating seaweeds, expressed as percentage of total observations per species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Actively searching</th>
<th>Scavenging</th>
<th>Surface pecking</th>
<th>Surface seizing</th>
<th>Dipping</th>
<th>Deep plunging</th>
<th>Pursuit plunging</th>
<th>No description</th>
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<td>0</td>
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<td>0</td>
<td>0</td>
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DISCUSSION

Seaweed-associated birds and their foraging behaviour

The results of the present study indicate that some seabird species are attracted to floating seaweeds and that the affinity for these seaweeds is correlated with feeding habit. Of a few of the species that were (occasionally) found associated with floating seaweeds, some reports already exist in literature concerning association of conspecifics or congeners with floating seaweeds. Of other species, only sporadic notes about behaviour or diet indicate a possible interest for floating objects as foraging grounds. Finally, for some species, there are no indications other than the association percentages in the present study for attraction to floating seaweed patches.

As could be expected from their foraging habits (parasitism, scavenging, and opportunistic surface feeding), gulls and skuas were only occasionally observed in the vicinity of floating seaweeds. Only Herring Gull, Lesser Black-backed Gull and Kittiwake were observed while surface pecking or surface seizing (Table 1). Skuas and gulls also appeared in low numbers around Sargassum mats, where they only occasionally fed (Haney 1986).

In the present study, shearwaters, Fulmars and Storm Petrels Hydrobates pelagicus showed little or no affinity for floating seaweeds, although their foraging behaviour includes surface-seizing. In the Mediterranean, however, Arcos (2000) reported on an alternative feeding strategy of Balearic Shearwaters (usually plunge-diving, pursuit-diving and surface-seizing of small fish; or interaction with subsurface predators), involving capture of fish under floating objects, both biotic and abiotic. Stomach analysis from Manx Shearwaters Puffinus puffinus off the south-eastern coast of the USA suggested foraging around floating Sargassum mats (Lee 1995), a feeding behaviour also commonly exhibited by Audubon’s Shearwaters P. lherminieri (Haney 1986). Similar behaviour or evidence from stomach contents have not yet been reported for shearwaters in the North Sea. Fulmars were in a few cases seen while actively searching in the vicinity of floating seaweeds. Although Cadée (2002) reports on peckmarks on and ingestion of debris in the North Sea, and Zaitsev (1971) described surface-feeding on neustonic invertebrates, the only evidence that Fulmars feed on floating-object-associated fauna is the presence of the isopod Idotea metallica in their diet (Furness &
Todd 1984) as this isopod exclusively establishes populations on objects drifting on the sea surface (Gutow 2003).

The group of surface feeding, shallow divers (terns and Red-breasted Mergansers) showed the highest association percentages with floating seaweeds. Furthermore, the feeding behaviour of Common Tern showed a shift from actively searching, pursuit diving or scavenging to surface pecking and dipping in the vicinity of floating seaweeds. This shift indicates that this species feeds on the invertebrates and/or small fish that are associated with the seaweeds. The interest of terns (species not specified) for seaweed-associated fauna was observed in Canada as well, where they were seen plunge-diving in the immediate vicinity of floating seaweed patches (Parsons 1986). Another observation of seaweed-association was done in South Africa, where Antarctic Terns Sterna vittata frequently roosted at sea on floating wood or floating kelp stipes (Tree & Klages 2004). Similarly, Bridled Terns S. anaethetus and Black Terns Chlidonias niger frequently used floating Sargassum as roost sites and foraging habitat in Haney (1986).

The association of Red-breasted Mergansers with floating seaweed has not been reported before, but is not surprising given its diet and method of feeding: primarily fish obtained by foraging from the surface with head and eyes immersed and subsequent diving. Next to fish, seaweed-associated invertebrates like Idotea, Palaeamon and Gammarus have been described as prey (Cramp et al. 1978–1997).

Of the group consisting of deep-diving, pelagic and bottom feeding species, Razorbills, Gannets, Cormorants and Guillemots were occasionally observed in association with floating seaweeds. The behaviour of these species was only recorded in a few cases, in which they were mostly pursuit-plunging. Especially Gannets and Cormorants are known to pick up floating debris from the sea surface, which they use as nesting material together with, or instead of seaweed (Podolsky & Kress 1989, Tasker et al. 2000). Gannets and Cormorants are mainly piscivores feeding on a variety of pelagic and benthic species (e.g. gadoids, herring, eel, labrids, flatfishes), but some records also mention the ingestion of the pelagic/neustonic Lump-sucker Cyclopterus lumpus (Burton 1980, Lillien-dahl & Solmundsson 2006). The juveniles of this fish species are known associates of floating seaweeds in north-western Europe (Davenport & Rees 1993, Ingólfsson & Kristjánsson 2001, Vandendriessche et al. 2007). Their occurrence in cormorant and gannet stomachs may indicate the use of floating seaweeds as foraging grounds.

An unexpected outcome of this study was that Common Scoters and Eiders showed relatively high association percentages (mean 0.21% in group 5, Fig. 3). These species are mainly benthos feeders (primarily molluscs; Cramp et al. 1978–1997), although Eiders have been reported foraging around attached seaweed at high tide, and feed on invertebrates associated with the algae (e.g. Hamilton & Nudds 2003). Consequently, it is likely that they are attracted to high densities of seaweed-associated fauna.

**Advantages of floating seaweed for seabirds**

The association of seabirds with floating seaweeds indicates that birds are attracted by the increased prey concentration. Given the seasonal and ephemeral character of such patches in the study area (contrary to the permanently floating Sargassum), the seaweed-associated fauna can only be exploited in an opportunistic way. Still, they can temporarily constitute an important and predictable source of extra food. At the same time, floating seaweeds and other floating objects can signal suitable feeding areas, since they tend to accumulate in biologically rich waters such as convergence fronts (Arcos 2000). Another use of floating seaweed patches was mainly described in Sargassum patches, were tern and phalarope species often roost on the semi-solid surface, probably allowing them to conserve energy when not foraging (Haney 1986, pers. obs.). Similar behaviour was however not described in the study area. To summarise, it can be stated that the increased structural complexity and food supply in ephemeral floating seaweed patches may enhance
foraging conditions for some seabird species depending on their preferred prey and foraging strategy, which consequently increases small-scale patchiness in seabird distribution.

Methodology and research outlook
The bias in the used database does not allow us to make reliable quantifications of seaweed-assocation in seabirds. Furthermore, the description of seabird behaviour in the vicinity of floating seaweeds was not straightforwardly recorded with the same level of detail, and some entries of behavioural codes seem unlikely (e.g. pursuit diving in terns). These factors call for caution in interpreting the data. However, the general message of the present study is not affected by this bias: the results indicate that some seabirds show an interest in floating seaweeds as foraging or resting grounds. Consequently, it would be worthwhile to focus on the association between seabirds and seaweeds in the future, recording behaviour with much detail. Additionally, the effects of seasonal variation and variation in size of floating seaweed patches on seabird behaviour should be investigated.

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This study would have been impossible without the consent to use the European Seabirds At Sea database. Therefore, the authors would like to thank all ESAS-partners for approving to the use of the data for this research topic. The first author acknowledges a specialisation grant from the ‘Institute for the Promotion of Innovation through Science and Technology in Flanders’ (IWT). The study was conducted within the framework of GOA 1205398 and GOA-BBSea 01GZ0705 (Ghent University), and the European networks MarBEF and ENCORA. Dr. G. Van Hoey, the editor and two anonymous referees are acknowledged for their constructive comments on earlier versions of the manuscript.

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SAMENVATTING

Drijvende wierpakketten zijn meestal rijk aan dierenle-
ven, van kleine planktonische crustaceëen tot juveniele
vissen. Omdat de aanwezigheid van dergelijke pakketten
voor zeevogels een signaal kan zijn dat er veel voedsel
gewonden kan worden gevonden, veronderstelden we dat
het voorkomen van drijvende wierpakketten leidt tot een
kleinschalige, patchy verdeling van zeevogels. De invloed
van drijvende wierpakketten op de verspreiding en het
gedrag van zeevogels kan worden gemeten, afhankelijk van de manier waarop ze voedsel zoeken. De
resultaten tonen aan dat vooral soorten die voedsel zoeken aan het wateroppervlak en oppervlakkig duiken (sterns en de Middelste Zaagbek Mergus serrator) vaak voorkomen bij drijvende wierpakketten. Soorten die zoeken naar prooien in de waterkolom of vlak boven de zeebodem (duikers, Zeekoeten Uria aalge, Alken Alca torda, Papegaaiduikers Fratercula arctica, Jan-van-Genten Sula bassana en Aalscholvers Phalacrocorax carbo), en vooral benthoseters (Zwarte Zee-eenden Melanitta nigra en Eidereenden Somateria mollissima) werden geregeld waargenomen bij drijvende wierpakketten, terwijl dat bij opportunistische soorten en aaseters zoals meeuwen en jagers veel minder vaak werd vastgesteld. Stormvogels en pijlstormvogels, die hun prooi aan het wateroppervlak grijpen of erachteraan duiken, werden weinig gezien in de omgeving van drijvend zeewier. Het meest voorkomende gedrag van zeevogels bij drijvend zeewier was pikken aan het wateroppervlak, actief zoeken en achtervolgend duiken.

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