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Investigating a seabird hotspot: factors influencing the distribution of birds in the southern Baltic Sea

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to my parents

Contents

Chapters

Summary

The southern Baltic Sea in northeastern Europe has been described as one of the most important areas for seabirds in the Western Palaearctic, based on extraordinary high numbers of birds occurring in the area particularly during the winter half-year. Most studies, however, only comprise information about the distribution of birds, while the factors and mechanisms causing the observed distribution patterns are only seldom addressed. Prey distribution and abundance and foraging strategies are certainly the most decisive factors determining the distribution and habitat choice of seabirds at sea, but diet preferences are unknown for many species. However, an extensive understanding of the functionality between seabirds and their marine environment is essential not only to be able to assess natural changes in numbers and distribution, but to evaluate the risks posed by anthropogenic activities as human pressure on marine ecosystems has increased enormously over the last decades. This thesis overcomes the lack of comprehensive knowledge about the ecology of birds in the brackish environment of the southern Baltic Sea and provides basic information on bird-habitat-relationships, on interspecific interactions and on diet preferences of selected species. Furthermore, set net fisheries as a particularly high threat to birds in the southern Baltic Sea are exemplarily outlined in this thesis. The methods to address the study objectives comprise ship-based *Seabirds at Sea* surveys to reveal spatial and temporal distribution patterns, mathematical modelling to analyse these patterns with regard to habitat parameters and species' interactions, analyses of stomach contents for dietary studies and the development of an approach to evaluate the conflict between birds and human impacts.

The avifauna of the brackish Baltic Sea strongly differs from truly marine systems: while pelagic species are only represented by auks, the bird community is dominated by species that breed in (arctic) freshwater habitats and occur in the southern Baltic Sea only during winter and migration. The different species are not evenly distributed, but show clear preferences for certain areas and habitats, depending on their diet and foraging strategies. Birds feeding on or near the sea bottom, like sea ducks and grebes, are restricted to areas with low water depth and, according to the substrate preference of their main prey species, occur in waters over specific bottom sediment types. Species that mainly forage on pelagic fishes, like auks, are not restricted to shallow waters but also occur in deeper offshore areas. Surface feeding species are mainly represented by gulls. Especially the large *Larus*-species have strongly adapted to the use of discards and offal from fishing vessels and distribution patterns are influenced by the occurrence of human fishing activities accordingly.

Detailed ecological questions are addressed in two case studies on grebes that are represented in the study area by three species and more than 10 000 wintering birds. The habitat choice of Slavonian Grebes is influenced by water depth and bottom sediment type: they prefer shallow waters of 4 to 14 m depth and occur only over sandy sediments. Both habitat factors can be linked to diet preferences: while the diving depth of endothermic animals is limited due to energetic constraints and thermoregulation, sediment type is regarded to be a proxy for food choice. The diet of Slavonian Grebes mainly consists of gobies that frequently occur over sandy bottom substrates. Great Crested and Red-necked Grebes prefer waters up to 26 m and 30 m, respectively. Within the areas suitable with regard to water depth, the three grebe species exhibit distinctive distribution patterns with only low spatial overlap. Furthermore, with increasing abundance of one grebe species, the abundance of the others significantly decreases. As the diet of the three grebe species differs only slightly, they seem to enable coexistence by spatial segregation rather than by ecological separation via different dietary niches. This indicates that interspecific competition, well known to influence seabird communities during the breeding season, can also act as structuring mechanism in densely populated wintering areas.

The most prominent threat to the highly abundant diving bird species are set net fisheries, extensively carried out in the southern Baltic Sea and leading to the entanglement and drowning of birds foraging underwater. Two indices are developed to overcome the lack of comprehensive knowledge on bird bycatch: a spatial overlap approach indicates the potential of conflict for diving birds in relation to set net fisheries, based on data of bird abundance and fishing activities, while a vulnerability index based on relative bird abundance indicates the maximum susceptibility of birds towards drowning mortality. Vulnerability and potential conflict exhibit spatial and temporal variations and are particularly high in coastal areas and on shallow offshore grounds during winter and spring. Large areas of the German Baltic Sea have been designated as protected areas and the implementation of management objectives is currently under process. The presented approach involving an improved understanding of the spatio-temporal occurrence of potential bycatch events and the assessment of bird vulnerability towards the impact provides a valuable tool for such management purposes.

By addressing various aspects of the ecology of birds at sea, this thesis fills considerable gaps in the knowledge about one of the most important areas for seabirds and waterbirds in the Western Palaearctic. It provides basic information on the relationship between birds and their biological and physical environment, which is fundamental to evaluate the consequences of human impacts and to set up appropriate conservation measures.

Zusammenfassung

Seevögel verbringen einen Großteil des Jahres auf dem offenen Meer und halten sich meist nur während der Kükenaufzucht kurzzeitig an Land auf. Dies macht sie zu einem der schwierigsten Studienobjekte innerhalb der Gruppe der Vögel. Untersuchungen konzentrierten sich daher lange Zeit ausschließlich auf das Brutgeschehen, während über das Vorkommen und Verhalten von Seevögeln in ihrem marinen Lebensraum nur wenige Informationen vorhanden waren. Erst im Laufe der letzten Jahrzehnte führten technische und methodische Weiterentwicklungen, insbesondere die Etablierung von Schiffs- und Flugzeug-gestützten Erfassungen und die Anwendung von Satellitentelemetrie und Datenloggern an Vögeln, zu immer umfassenderen Kenntnissen über das Leben von Seevögeln auf dem offenen Meer. Insbesondere durch die Durchführung von Schiffs- und Flugzeugzählungen konnte die südliche Ostsee als eines der bedeutendsten Gebiete für See- und Wasservögel in der Westpaläarktis beschrieben werden. Mehr als 38 Arten halten sich regelmäßig in den Küstengewässern und auf hoher See auf, die meisten davon unterliegen internationalen Naturschutzabkommen und Konventionen. In einigen Gebieten treten beträchtliche Konzentrationen auf, die auch im internationalen Kontext von großer Bedeutung sind. Untersuchungen an Vögeln in der südlichen Ostsee beschränkten sich bisher meist auf die Beschreibung von Verbreitungsmustern, insbesondere während des Winterhalbjahres, in dem die höchsten Anzahlen im Jahresverlauf auftreten. Teilweise wurde auch auf die Funktionalität verschiedener Gebiete und die Nahrungswahl einzelner Arten eingegangen. Über die Zusammenhänge zwischen Vögeln und ihrem Habitat und die Faktoren und Prozesse, die die beobachteten Verbreitungsmuster bedingen, liegen jedoch kaum Informationen vor. Umfassende Kenntnisse dieser Mechanismen sind jedoch essentiell für ein grundlegendes Verständnis der ökologischen Funktion von Vögeln in ihrem marinen Lebensraum. Nur dadurch ist es möglich, Veränderungen in Verbreitung und Abundanz zu bewerten oder Verteilungsmuster vorherzusagen. Die Ostsee ist aufgrund des stark eingeschränkten Wasseraustausches mit dem offenen Ozean, der permanenten Schichtung und der durch Schwellen geprägten Beckenstruktur besonders empfindlich gegenüber natürlichen und anthropogenen Einwirkungen. Andererseits ist sie Gegenstand intensiver menschlicher Nutzung, beispielsweise durch Schiffsverkehr, Fischerei, Abbau von Rohstoffen, die geplante Errichtung von Windenergieanlagen und touristischen Aktivitäten entlang der Küste. Nur durch ein umfassendes Verständnis der Habitatnutzung verschiedener Arten und der zugrunde liegenden Faktoren können die Auswirkungen dieser Aktivitäten auf die Vogelwelt bewertet und entsprechende Schutzmaßnahmen getroffen werden.

Die vorliegende Arbeit trägt wesentlich zu einem besseren Verständnis der Vogel-Habitat-Beziehungen und damit der Rolle von Seevögeln in ihrem natürlichen, aber auch vom Menschen beeinflussten Lebensraum in der südlichen Ostsee bei. In einem anfänglichen Übersichtskapitel wird ein aktueller Überblick über die Verbreitungsmuster der wichtigsten Arten im Jahresverlauf und über grundlegende Prinzipen der Habitatwahl gegeben. Die Avifauna der südlichen Ostsee wird von Arten dominiert, die meist in limnischen Lebensräumen in den nördlichen und östlichen Tundra- und Arktisgebieten oder entlang der Ostseeküste brüten und nur zum Überwintern in brackische oder marine Gebiete ziehen, wie beispielsweise Meeresenten, Lappentaucher und Seetaucher. Typische Hochseevögel sind nur durch die Gruppe der Alken vertreten, während Eissturmvögel, Basstölpel und Dreizehenmöwen, charakteristische Vertreter der Vogelwelt der benachbarten Nordsee, nur seltene Gäste sind. Die verschiedenen Arten weisen charakteristische Verbreitungsmuster auf, die meist in Zusammenhang mit der bevorzugten Nahrung und der Ernährungsstrategie stehen. Arten, die sich von benthischen oder benthopelagischen Beutetieren ernähren, wie Meeresenten und Lappentaucher, sind überwiegend auf Gebiete mit geringer Wassertiefe beschränkt und kommen daher nur in den flachen Küstengewässern oder auf Flachgründen im Offshore-Bereich vor. Je nach Substratpräferenz der Beutetierarten halten sich die Vögel dabei bevorzugt über verschiedenen Oberflächensedimenten auf. Arten, deren Nahrungsspektrum aus pelagischen Beutearten besteht, wie z.B. Trottellummen, werden dagegen auch in tieferen Gebieten angetroffen. Möwen hingegen sind als Oberflächenfresser weder an Wassertiefe noch an bestimmte Sedimenttypen gebunden. Die Verbreitung der verschiedenen Arten erstreckt sich über weite Teile der südlichen Ostsee. Insbesondere die großen *Larus*-Arten nutzen jedoch in hohem Maße ungenutzten Beifang und Abfall aus der Fischerei, weshalb ihre Verteilungsmuster durch das Vorkommen von Fischereifahrzeugen beeinflusst werden.

In zwei Spezialkapiteln werden anhand der Lappentaucher (Fam. Podicipedidae), die im Winterhalbjahr mit drei Arten und mehr als 10 000 Individuen im Untersuchungsgebiet vertreten sind, detaillierte ökologische Fragestellungen bearbeitet. Anhand von Habitatmodellen werden die wichtigsten Einflussfaktoren auf die Verteilungsmuster beschrieben, Nahrungsuntersuchungen ermöglichen Rückschlüsse auf die Zusammenhänge zwischen den Arten und ihren Habitatpräferenzen. Zudem werden die Wechselwirkungen zwischen den einzelnen Arten untersucht, um die Rolle von interspezifischer Konkurrenz auf die Verbreitung von Lappentauchern im Wintergebiet zu bewerten. Für die Habitatwahl des Ohrentauchers sind Wassertiefe und Oberflächensediment entscheidende Faktoren. Wassertiefe wirkt dabei über die maximal mögliche Tauchtiefe: Ohrentaucher tauchen bei der Nahrungssuche bis zum Grund, wobei die energetischen Kosten für den Tauchvorgang und für die Aufrechterhaltung der Körpertemperatur mit zunehmender Tauchtiefe ansteigen. Insbesondere für kleine Arten wie den Ohrentaucher ist eine Minimierung des Energieverbrauches daher von entscheidender Bedeutung für die Verbreitung innerhalb der marinen Überwinterungsgebiete. Die Bindung an einen bestimmten Sedimenttyp liegt in der bevorzugten Beuteart begründet: Ohrentaucher ernähren sich in der südlichen Ostsee zu einem großen Teil von Grundeln (Fam. Gobiidae), einer Fischart, die häufig auf Sandböden anzutreffen ist. Dementsprechend kommen Ohrentaucher überwiegend in Gebieten mit sandigen Sedimenten vor. Auch Haubentaucher und Rothalstaucher ernähren sich zu einem großen Teil von benthischen oder benthopelagischen Fischarten und halten sich daher bevorzugt in Gebieten mit geringeren Wassertiefen auf. Innerhalb der geeigneten Gebiete weisen die drei Lappentaucherarten unterschiedliche Verbreitungen mit nur geringen räumlichen Überschneidungen auf. Zudem beeinflussen sie sich direkt in ihren Verteilungsmustern: Mit zunehmender Anzahl einer Art nehmen die anderen Arten in diesen Gebieten jeweils signifikant in ihrer Anzahl ab. Interspezifische Konkurrenz wird als Ursache für diese Ergebnisse vermutet und diskutiert. Aufgrund der nur geringen Unterschiede im Beutespektrum der drei Arten wird ein gleichzeitiges Vorkommen im Überwinterungsgebiet unter Ausschluss von Konkurrenz offenbar nicht durch die Besetzung unterschiedlicher Nahrungsnischen, sondern durch eine kleinräumige Trennung der Verbreitungsgebiete ermöglicht.

Abschließend wird exemplarisch für die zahlreichen anthropogenen Aktivitäten in der südlichen Ostsee der Konflikt zwischen Seevögeln und der Stellnetzfischerei dargestellt. Fischerei mit Stellnetzen wird in großem Umfang praktiziert und ist eine starke Bedrohung für die zahlreichen Arten, die ihre Nahrung tauchend erbeuten und sich dabei in den kaum sichtbaren Netzen verfangen und ertrinken. Zwei Ansätze werden verfolgt, um die Wissenslücken über den Beifang von Vögeln in Stellnetzen zu schließen: Zum Einen wird anhand von Verbreitungskarten, die auf den relativen Abundanzwerten aller tauchenden Vogelarten basieren, deren grundsätzliche Empfindlichkeit gegenüber Stellnetzfischerei abgeleitet. Zum Anderen wird durch die räumliche Verschneidung von Daten zur relativen Vogelabundanz und zur Fischereiaktivität das Konfliktpotential zwischen beiden dargestellt. Empfindlichkeit und Konfliktpotential weisen große räumliche und zeitliche Unterschiede auf und erreichen die höchsten Werte in den Küstengebieten und auf Offshore-Flachgründen im Winter und Frühjahr. Große Bereiche der südlichen Ostsee wurden als Vogelschutzgebiete ausgewiesen, entsprechende Managementmaßnahmen zur Erreichung der Schutzziele werden derzeit erarbeitet. Der in dieser Arbeit präsentierte Ansatz, der einerseits zu einem besseren Verständnis der Empfindlichkeit betroffener Arten gegenüber dem Eingriff beiträgt, andererseits aber auch konkrete Konfliktbereiche aufzeigt, stellt ein hilfreiches Instrument für die Entwicklung von Schutzmaßnahmen in diesem Zusammenhang dar.

General introduction

Scientific background

The habit of spending long periods at sea, out of the sight of land, has made seabirds one of the most difficult and challenging groups of birds to study and to understand. For long times, information on the life of seabirds was only available from investigations carried out during the short time they spend on land to breed and raise their chicks. Therefore, it was mostly related to breeding ecology and behaviour (Schreiber and Burger, 2002). Advances in methods and technology, however, offered the opportunity to study seabirds in their marine environment, where they spend the vast majority of their time. The implementation of ship and aerial surveys enabled scientists to describe at-sea distribution patterns, community structures and interspecific interactions of bird species on a large and medium scale (e.g. Brown, 1986; Tasker et al., 1987; Ballance, 2007), while the development of satellite transmitters and data logger offered the opportunity to study seabirds in inaccessible areas and shed new light on strategies of individual birds (e.g. Wanless et al., 1985; Jouventin and Weimerskirch, 1990; Wilson et al., 2002; Schreiber and Burger, 2002). The first step into a new understanding of the life of birds in their marine environment consisted in the description of basic distribution patterns and the identification of key areas at sea and their functionality for different species, e.g. as foraging and feeding grounds. Hereby, spatial and temporal variations in bird distribution patterns were found at various scales (e.g. Hunt, 1990; Harrison et al., 1994; Stone et al., 1995; Garthe, 1997; Schwemmer and Garthe, 2006). The most important task, however, is a comprehensive understanding of the factors and processes driving the observed patterns, i.e. the revealment and evaluation of the relationship between bird distribution and physical and biological characteristics of the ocean (e.g. Hunt, 1990; Shealer, 2002; Ballance, 2007).

The distribution of birds at sea is not homogeneous. It is strongly influenced by a variety of different mechanisms, including geographic, atmospheric, hydrographic and temporal parameters as well as various fixed habitat factors (Fig. GI-1). In the German Bight in the North Sea, hydrographic processes have been proved to be a key determinant of seabird distribution (e.g. Garthe, 1997; Markones et al., 2008; Garthe et al., 2009). Besides, morphological and physiological capacities and constraints (e.g. flight and diving abilities) as well as intra- and interspecific interactions affect seabird occurrence and behaviour (e.g. Ashmole, 1963; Furness and Monaghan, 1987; Lewis et al., 2001; Shealer, 2002). Underlying all these aspects is the need of seabirds to find enough food for themselves and, during the breeding season, for their offspring. Prey distribution and abundance on one hand and foraging strategies on the other hand are certainly the most decisive factors determining the distribution and habitat choice of seabirds at sea (Schneider and Piatt, 1986; Hunt et al., 1990; Shealer, 2002). In the vast expanses of the open oceans, prey is patchy in space and time and its availability varies on various scales (e.g. Piersma et al., 1988; Haney and Solow, 1992; Ballance et al., 1997). This consequently influences the occurrence of predators and makes the prediction of seabird distribution patterns more difficult.

Apart from physical and biological parameters that set the conditions for the occurrence of seabirds in the marine environment, anthropogenic activities may cause irregularities in the distribution and abundance of birds at sea (Garthe, 2005; Kaiser et al., 2006). Marine areas are nowadays intensively used, and seabirds have been described to react to anthropogenic activities in various ways, depending on the kind of impact and on species' sensitivities (e.g. Vauk et al., 1989; Leopold, 1993; Tasker et al., 2000; Furness, 2003; Garthe and Hüppop, 2004; Dierschke et al., 2006; Kaiser et al., 2006; Mendel et al., 2008). Hereby, human pressures can originate from sea or from land and can act directly or indirectly on seabirds (Fig. GI-2). Direct influences are e.g. disturbance (ship traffic, wind farms), deterioration of body condition (pollution) or mortality (collision with technical constructions, entanglement in fishing gear). Indirect influences mainly act via effects on habitat conditions and prey availability, like eutrophication, fishing activities or habitat destruction (e.g. exploration or extraction of resources, technical constructions).

Detailed knowledge about the influence of both natural and anthropogenic factors is essential for a comprehensive understanding of the distribution and behaviour of birds at sea. It provides the basis for the evaluation and prediction of spatio-temporal occurrence patterns and enables the assessment of changes in numbers and distribution. Based on such information, the consequences of human activities on seabirds can be assessed and appropriate measures for their protection and the conservation of their marine environment can be derived (Ballance, 2007; Markones, 2007).

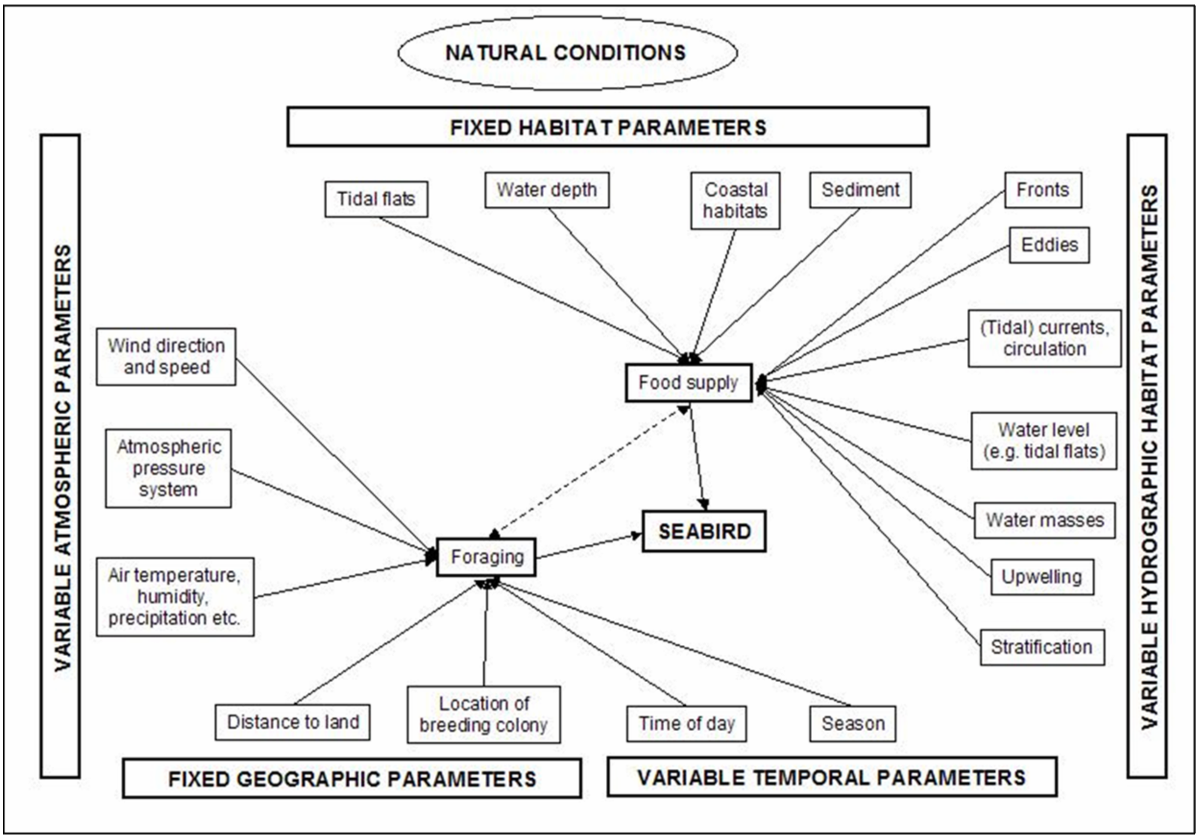

Fig. GI-1. Natural conditions influencing the distribution and behaviour of seabirds. Only the most relevant factors are shown. Taken from Garthe (2005).

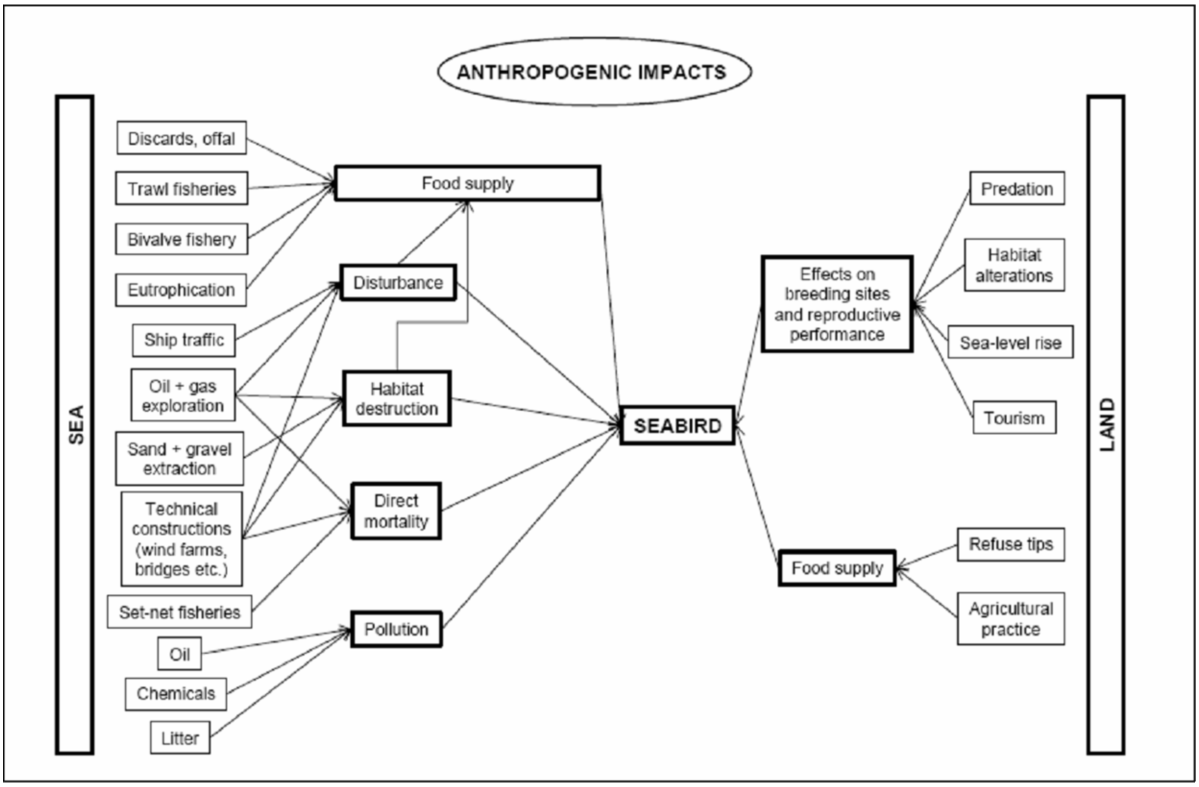

Fig. GI-2. Human impacts influencing the distribution, behaviour and life history of seabirds. Only the most relevant factors are shown. Taken from Garthe (2005).

Rationale of the thesis and chapter outline

This thesis focuses on the ecology of birds in the southern Baltic Sea in northeastern Europe, which is one of the most important areas for seabirds and waterbirds in the Western Palaearctic. Many birds that breed in northern Europe and Siberia use the Baltic coasts and the open sea for resting, wintering and moulting. The survival of several species depends on the conditions they encounter in the Baltic Sea (e.g. Durinck et al., 1994). The Baltic avifauna is dominated by sea ducks, grebes, divers, auks and gulls. Many of these species are rather “waterbirds”, breeding in freshwater habitats and becoming “seabirds” only during the non-breeding season when they winter in marine or brackish areas.

During the last two decades, high at-sea effort by ship and aircraft based surveys has led to comprehensive knowledge about the distribution of birds in the southern Baltic Sea, primarily for the winter season (Durinck et al., 1994; Skov et al., 2000; Garthe et al., 2003). Year-round spatial and temporal distribution patterns have been described for the first time by Sonntag et al. (2006). Few studies, however, have been conducted yet to reveal the relationships between birds and their habitats. The most characteristic and most numerous birds in the (southern) Baltic Sea are sea ducks, and thus most ecological studies in the area focused on them (e.g. Kirchhoff, 1979; Meissner and Bräger, 1990; Bräger et al., 1995; Kube and Skov, 1996). As benthivorous feeders, sea ducks are concentrated above patches of suitable mussel stocks in areas where low water depth enables them to forage in the most energy efficient way. If such suitable areas are known, distribution patterns of sea ducks are rather predictable. Less attention has been paid to fish-eating bird species. As they forage on highly mobile prey whose distribution itself depends on a variety of variable factors, the occurrence and habitat selection of piscivorous seabird species is much more difficult to study and to describe. The hydrographic characteristics of the southern Baltic Sea are mainly influenced by its basin structure and a strong salinity gradient from west to east (see below). They significantly influence the occurrence of all organisms, in particular the distribution of fishes and thus of birds as their predators.

To obtain their (fish) prey, seabirds use a variety of feeding methods, such as diving from the surface and pursuing prey while swimming under water (pursuit diving), picking prey from the surface while swimming (surface pecking) or flying (dipping), or plunge diving into the water column from high in the air (Nelson, 1979; Shealer, 2002). The majority of piscivorous birds in the southern Baltic Sea are pursuit divers, but information on their diet is scarce for most species.

This thesis aims at filling important gaps in the knowledge about the ecology of birds in one of the most important sea areas in the Western Palaearctic. It updates information on the spatial and temporal variation in the distribution of birds in the southern Baltic Sea given by Sonntag et al. (2006) and describes the basic principles of their habitat selection. Detailed ecological analyses focus on the group of grebes (family Podicipedidae), which are specialised divers and the only birds that are able to spend their entire lifecycle in water (Fjeldså, 2004). They are represented in the southern Baltic Sea by three different species comprising a high number of individuals and have not been the object of ecological studies so far. The main objective is to identify the factors influencing the habitat selection of grebes, taking into account fixed habitat parameters and the role of interspecific interactions. As habitat use is primarily linked to prey availability and feeding techniques, diet studies are carried out to evaluate the revealed mechanisms of habitat selection. Such fundamental ecological knowledge provides the basis for a comprehensive understanding of the role of birds in the brackish environment of the southern Baltic Sea and is essential for the evaluation of changes in distribution patterns and abundance. The Baltic Sea is particularly sensitive to natural and anthropogenic impacts (Matthäus, 1996). It is strongly influenced by a variety of human activities that affect different seabird species to various extents (e.g. Garthe et al., 2003; Mendel et al., 2008). The consequences of such impacts on seabirds can only be assessed on the basis of detailed information on the natural factors influencing their distribution. The most important threats to birds in the Baltic Sea are oil pollution, ship traffic, resource extraction, the intended construction of wind farms and fisheries. The latter is mainly represented by an intensive use of static fishing gear, particularly bottom-set gill nets (set nets), which bear a high potential for accidental bird bycatch. Because of the very high number of birds in the southern Baltic Sea that obtain their prey by diving and are thus particularly sensitive to entanglement in under-water nets, one chapter of this thesis focuses on the conflict between diving birds and set net fisheries and the vulnerability of birds towards drowning mortality.

The high and often internationally important numbers of birds in the southern Baltic Sea and their specific habitat requirements define a wide array of tasks for nature conservation in general and bird conservation in particular (Garthe, 2005). Comprehensive ecological knowledge about seabirds required for these tasks is provided by this thesis. It is divided into four independent chapters addressing the following study objectives:

Chapter I: Characterisation of the seabird fauna of the southern Baltic Sea: spatio-temporal distribution and basic habitat selection patterns

This introductory characterisation of the avifauna of the southern Baltic Sea provides comprehensive information on the occurrence of the most common species and reveals basic principles of the bird-habitat-relationships. It thus establishes the baseline for more detailed analyses of selected species (**Chapter II** and **III**) and for an evaluation of the sensitivity of birds to human activities (**Chapter IV**).

Chapter II: A freshwater species wintering in a brackish environment: habitat selection and diet of Slavonian Grebes in the southern Baltic Sea

In this chapter, a habitat model is developed to analyse the functionality of the distribution patterns of a key bird species with regard to two selected habitat parameters, water depth and bottom sediment type. Diet studies are carried out to evaluate the results of the habitat analysis with information on dietary preferences.

Chapter III: Can competition explain distribution patterns of grebes wintering in the southern Baltic Sea?

The effect of interspecific relationships on the at-sea distribution of different grebe species wintering in the southern Baltic Sea is analysed based on data on distribution, habitat requirements and diet. The occurrence of separation strategies of grebes via spatial segregation or dietary specialisation is investigated to evaluate the role of competition in birds outside the breeding season.

Chapter IV: Seabirds and set nets: assessment of conflict potential and vulnerability of birds to bycatch in gillnets in the southern Baltic Sea as tools for conservation management

Based on data of bird distribution and fishing effort, methods to assess the conflict between birds and set net fisheries and to describe the vulnerability of birds towards this impact are developed and evaluated with respect to their appropriateness to derive conservation measures.

Study area

The work described in this thesis has been conducted in the southern Baltic Sea in north-eastern Europe, defined here as the area between 53.9° to 55.0° N and 9.5° to 15.0° E. The Baltic Sea is a rather shallow sea, geologically young and dominated by a continental climate with warm summers and cold winters with extended ice cover. It is one of the largest brackish water areas in the world (Matthäus, 1996). The hydrographic and ecological characteristics of the Baltic Sea are strongly related to its basin structure and a pronounced salinity gradient from west to east. Temperature and salinity conditions and thus all density related processes are influenced by the narrow and shallow Kattegat and by a freshwater influx of about 440 km^3 per year from large riverine systems. The Kattegat is the only connection to the adjacent North Sea and the Atlantic Ocean beyond and an effective barrier preventing the ocean water from freely flowing into the Baltic Sea (Matthäus, 1996; Telkänranta, 2006). Vertical circulation is limited by a strong year-round density stratification and the exchange of energy and nutrients is restricted by the permanent pycnocline. Water masses from the deep areas can only be exchanged via horizontal influx from the North Sea, which is, however, impeded by the narrow connection and the cascading basin structure. This results in periodical stagnating conditions on the sea bottom, which can lead to oxygen depletion and the formation of hydrogen sulphide. Due to these conditions, the Baltic Sea is a highly sensitive ecosystem and very susceptible to natural and anthropogenic impacts (Matthäus, 1996).

Due to the young age and the continuously decreasing salt concentration from west to east, the total number of species in the Baltic Sea is low compared to fully marine systems. Marine species strongly decrease in numbers from the Danish straits to the Baltic proper in the central part and further to the Gulf of Finland and the Bothnian Bay in the east, while the occurrence of freshwater species that can tolerate brackish conditions increase along this gradient. Furthermore, temperature also has an impact on life in the Baltic Sea because of extensive ice cover especially in the northeastern part (Arndt, 1996). The distinct gradients in environmental variables result in a well-defined division of the biocoenosis in the (southern) Baltic Sea (Arndt, 1996; Kube and Skov, 1996).

Fish fauna of the study area

Most bird species in the southern Baltic Sea are piscivorous. For this reason, a short description of the fish fauna in the study area is subsequently provided.

The characteristic hydrographic features of the Baltic Sea, especially the salinity regime, strongly influence the fish community in the southern Baltic Sea and result in the occurrence of marine and freshwater fish species. Variations in the influx of salt water from the adjacent North Sea or of freshwater from the rivers discharging into the Baltic Sea via lagoons cause shifts in the occurrence and distribution of marine or freshwater species sporadically or regularly migrating into the Baltic Sea (Winkler and Schröder, 2003). In general, the number of marine fish species decreases from west to east and from north to south (Thiel et al., 1996).

The Baltic fish fauna is quite diverse. Presently, it is dominated by planktivorous species, especially clupeids (Döring et al., 2006). In the pelagic or benthopelagic zone, Atlantic Herring, European Sprat and Atlantic Cod are the dominating species, accounting for more than 90% of the total fish stock (Schnack, 2003). Other characteristic pelagic species are e.g. Atlantic Salmon, Sea Trout, Garpike and European Smelt. Atlantic Herring and European Sprat play the central role within the Baltic Sea ecosystem and build up most of the total fish biomass. In the Pomeranian Bight are important spawning sites of the western Baltic spring spawning stock of Atlantic Herring (Gröhsler, 2003). However, complex relationships between abiotic factors (temperature, salinity, oxygen), inter- and intraspecific interactions (predation, food competition, cannibalism) and fisheries (target species, effort) result in fluctuations between a cod- or clupeid dominated system (see Schnack, 2003; Döring et al., 2006).

Characteristic representatives of the benthic community in the southern Baltic Sea are several species of flatfish, in particular Flounder, European Plaice, Dab and Turbot. Furthermore, there are various commercially unimportant, small-sized species that play an important role in the benthic ecosystem, like gobies (mainly Common Goby and Sand Goby), sticklebacks (mainly Three-spined Stickleback) and sandeels (Lesser Sandeel, Great Sandeel). In the sea weed belt along the coast, pipefishes (Broad-nosed Pipefish, Nilsson’s Pipefish, Straightnose Pipefish) occur frequently (Thiel et al., 1996; Winkler and Schröder, 2003).

In the Pomeranian Bight with its high riverine influx, both freshwater and marine species can be found. Frequently occurring freshwater species are Pike-perch, which has important spawning sites in rivers and lagoons connected to the bight (Hahlbeck and Müller, 2003), European Perch, Ruffe and Roach (Thiel et al., 2007). Compared to other regions of the German Baltic Sea, the Pomeranian Bight and its adjacent waters host many rare species like Twaite Shad or European River Lamprey (Thiel et al., 2007). Due to its importance for various fish species, the area comprises the largest proportion of proposed and already established marine reserves in the German Baltic Sea (EU Directive 92/43/EEC, Annex II).

Thus, a diverse fish fauna with various small-sized and schooling species constitutes the food base for the high number of piscivorous birds in the southern Baltic Sea.

1 Characterisation of the seabird fauna of the southern Baltic Sea: spatio-temporal distribution and basic habitat selection patterns

Abstract

The avifauna of the southern Baltic Sea is dominated by the occurrence of divers, grebes, sea ducks and gulls, while pelagic species are only represented by auks. Distribution patterns were studied by ship-based transect counts and were shown to undergo spatial and temporal variations. Most species occurred in the study area during the winter half-year, while comparably few species were present during summer or year-round. Basic principles of the habitat selection were analysed by carrying out a canonical correspondence analysis, using longitude, distance to the nearest coast, water depth and bottom sediment type as environmental variables. All factors significantly influenced the community structure of wintering birds, with longitude and distance to coast exhibiting the highest effects. They were mostly related to food availability and foraging techniques, either via an effect on prey size (longitude as a proxy for salinity), via substrate preferences of benthic or demersal prey species (sediment type) or due to the energetic constraints of diving for food (water depth), and thus influenced the various bird species in different ways, according to their respective diet preferences and feeding strategies. The habitat selection of gulls which exploit only the upper layers of the water surface was hardly affected by these factors. Especially the large *Larus*-species have strongly adapted to the use of discards and offal from fishing vessels and distribution patterns were influenced by the occurrence of fishing activities accordingly.

Introduction

The Baltic Sea is one of the most important areas for seabirds and waterbirds in the Western Palaearctic. The first comprehensive surveys to provide basic knowledge of the Baltic avifauna were carried out in the winter periods from 1987 to 1993 and resulted in an average of nine million birds that occurred in the investigated parts each winter (Durinck et al., 1994). A more comprehensive data set on waterbirds along the Baltic coasts and an extended data set for the offshore areas were analysed with regard to Important Bird Areas (IBAs) by Skov et al. (2000).

In the German (southern) parts of the Baltic Sea, 38 species occur regularly in the nearshore and offshore areas, aside the proximate coastal zone. Concentrations are highest during winter, when up to one million individuals use the area for resting and feeding (Mendel et al., 2008). Numbers are often internationally important (e.g. Prokosch and Kirchhoff, 1983; Durinck et al., 1994; Scheller et al., 2002), and most species are subject to various international conservation-related conventions and directives, in particular the EU Birds Directive and the African-Eurasian Waterbird Agreement (AEWA).

From the year 2000 onwards, several ship- and plane-based research projects were dedicated to describe and analyse the distribution and abundance of seabirds in the German Baltic Sea, mainly in the offshore area, at high spatial and temporal resolutions. Most of these projects stood in the context of the intended construction of offshore wind farms as well as the demarcation and designation of Special Protection Areas (SPAs) required under the EU Birds Directive. This has resulted in new reports which confirmed and supplemented the high importance of these waters for seabirds and waterbirds in winter and spring (Garthe et al., 2003) and for some species also in summer (Sonntag et al., 2004). Based on the data collected within these research projects, the EU Commission has designated a 2010 km²-sized SPA in the offshore area of the Pomeranian Bight (eastern part of the German Baltic Sea) in 2004, covering the most important concentrations of seabirds in the German Exclusive Economic Zone (EEZ; BMU, 2004; Garthe, 2006). In 2005, the SPA has been adopted as protected area by the German national legislation (BMU, 2005).

The following study provides a comprehensive overview of the occurrence of the most important seabird and waterbird species in the southern Baltic Sea, based on eight years of ship-based seabird surveys. In terms of bird distribution, it constitutes an update of the publication of Sonntag et al. (2006), the first description of seasonal bird occurrence in this area. Beside comprehensive distribution information, the study comprises an analysis of the basic principles of the habitat choice of selected species to reveal some of the environmental factors and processes that cause the observed distribution patterns and their spatial and temporal variability.

Methodology

Recording of birds at sea

The occurrence of seabirds at sea was studied by ship-based transect counts, following an internationally standardised method for northwest European waters (e.g. Tasker et al., 1984; Garthe et al., 2002; Camphuysen and Garthe, 2004). From the top deck or bridge-wing of the research vessel, two or three observers recorded all flying and swimming individuals within a 300 m wide band transect running parallel to the ship's track on one or both sides in successive 1-minute intervals (default within the German *Seabirds at Sea* programme). The length of the transect segments ahead was the distance the ship covered in successive 1-minute counting intervals and therefore depended on ship speed. From the transect length and the transect width (300 m) the surveyed area could be calculated.

Birds swimming within the transect band were recorded continuously along the survey line. To flying individuals, the *snapshot method* according to Tasker et al. (1984) was applied. Only birds flying at full minute (per convention) over the transect band were labelled "in transect". This correction prevented an overestimation of frequently and/or fast flying birds. All birds swimming beyond 300 m and all flying birds which were not inside the 300 m at full minute were additionally recorded as "outside transect" for further information (e.g. on behaviour), but they were not included in density calculations. Following Tasker et al. (1984), birds were usually searched for with naked eyes. With binoculars, determinations of species, age, sex or behaviour were confirmed or carried out. For the recording of divers, grebes and sea ducks, however, the area in front of the vessel had to be regularly – sometimes even continuously – scanned with binoculars by an additional observer. These species have very high flushing distances in front of approaching ships (often > 1 km) and are thus very likely to be overlooked with naked eyes (Garthe et al., 2002).

Geographic positions were recorded in 1-minute intervals with a portable GPS to link all observations to their respective position at sea. In the period 2000 to 2008, more than 30 000 ship kilometres have been travelled within the German Baltic Sea, with seasonally and interannually variations in survey effort (Fig. 1.1).

From 2002 onwards, standardised aerial transect surveys have been carried out in the German Baltic Sea to study the distribution of seabirds synchronous over large areas. Birds were recorded from a 2-propelled aircraft (Partenavia P-68) with bubble windows at a constant height of 250 feet (78 m) and with a speed of 90 - 100 knots (180 km/h). However, the present study is based on the analysis of ship counts only (except of one analysis of gulls and fishing activities, see below), as these comprise a much better seasonal coverage of the study area and thus allow for a better resolution of seasonal bird distribution. Moreover, species identification is difficult from plane due to the high speed of the observation platform, especially of similar looking species like divers, terns and auks, or in large aggregations of birds. Finally, small species like Slavonian Grebes are frequently overlooked during aerial surveys, particularly in areas with high overall bird density (FTZ, unpubl. data). For a more detailed description of the method, see Diederichs et al. (2002). Advantages and disadvantages of both methods are compiled in Garthe et al. (2004).

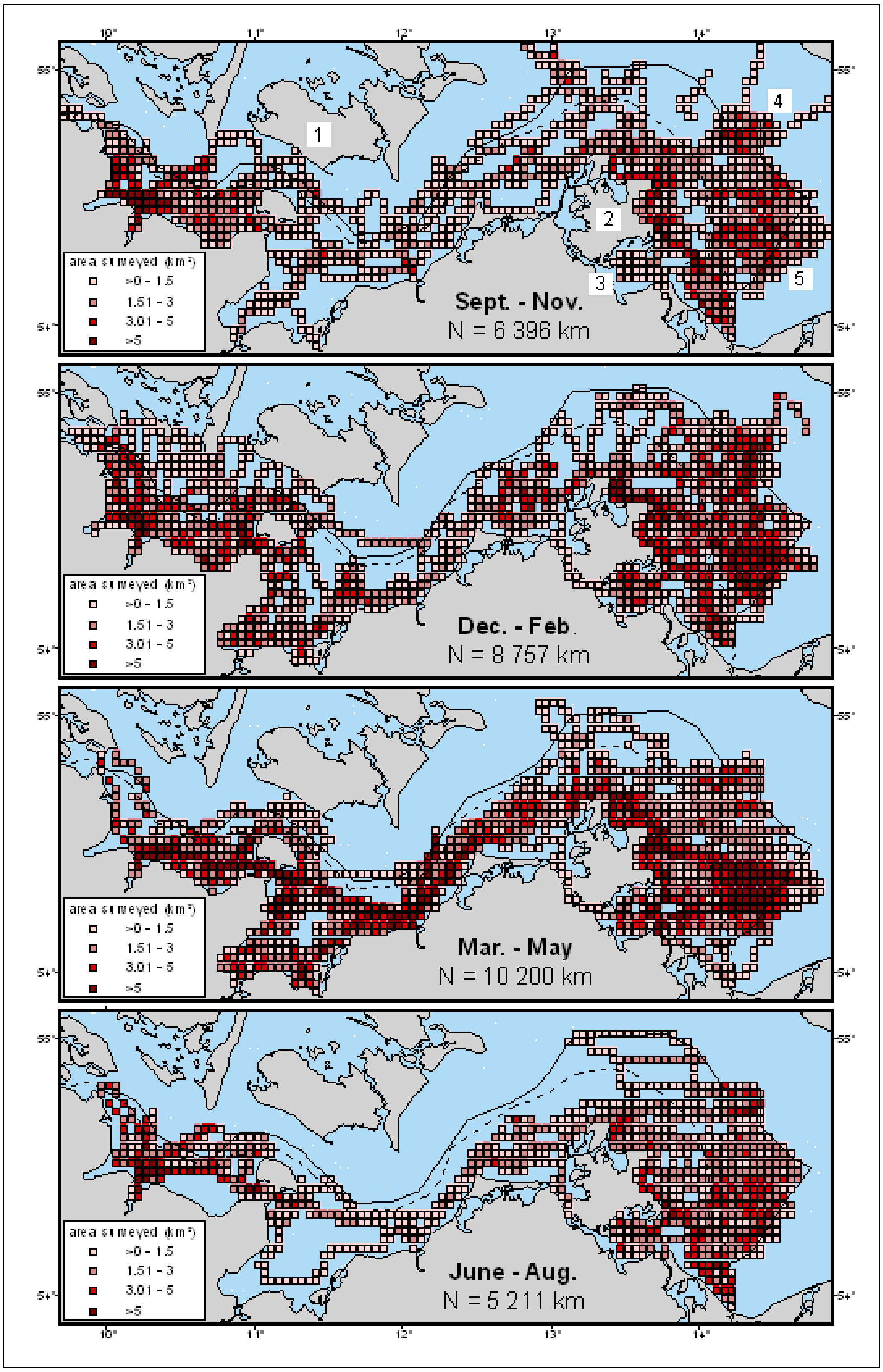

Fig. 1.1. Seasonal effort of ship-based bird surveys in the study area of the southern Baltic Sea 2000-2008, based on 2’ latitude x 3’ longitude grid cells (total grid size ca. 12 km²). Dashed line: German 12 nautical mile boundary; continuous line: boundary of the German Exclusive Economic Zone. 1) Danish isles, 2) Rügen, 3) Greifswald Lagoon, 4) Adlergrund, 5) Odra Bank (in the Pomeranian Bight).

Selection of species considered

This study comprises species that occur in the coastal and in the offshore areas of the southern Baltic Sea. However, only species that have been recorded in numbers of at least 100 individuals aside the proximate coastal zone (i.e. more than 1 km distant from the shore) have been considered.

Some species, e.g. Mute Swans, Greater Scaups, Common Goldeneyes and Goosanders, as well as various species of dabbling ducks and geese, also occur in the southern Baltic Sea, but their distribution is strongly restricted to (inner) coastal waters and lagoons that are not accessible with larger survey vessels. These species are thus only insufficiently recorded during ship-based surveys and consequently are not included in this study. However, they are covered by counts carried out from land within the framework of the annual midwinter Waterbird Census organised by the Dachverband Deutscher Avifaunisten (DDA). Results have been published e.g. by Skov et al. (2000) and Struwe-Juhl (2000).

Distribution maps

The occurrence of bird species is presented in four seasonal distribution maps based on the species-specific definition of seasons according to Garthe et al. (2007). The periods are specified in the maps. Maps were created using version 5.12 of the German *Seabirds at Sea* database (June 2008; Garthe et al., 2007), comprising data for the study area for the period 2000 to 2008. They are based on abundances, i.e. number of individuals per area surveyed, per 3’ latitude x 5’ longitude grid cells (grid size ca. 30 km²). Exceptions are marked in the figure captions. For each grid cell and species, the total number of individuals recorded was divided by the total area surveyed within that grid. Thus, the data are mean values of all surveys included and corrected for counting effort, which was unequal across the study area.

Because some swimming birds, particularly those in the more distant parts of the transect bands or in high-density areas, have likely been overlooked, the number of swimming birds was multiplied by species-specific correction factors adopted from Garthe (2003). These factors were calculated by using the *distance-sampling* method developed by Buckland et al. (1993) and by applying functions available in the DISTANCE software package (Laake et al., 1993). Numbers of flying birds were not corrected. For divers, grebes, sea ducks, mergansers, cormorants and auks, counting intervals with a sea state higher than four (according to *Beaufort* scale; Dietrich et al., 1975) were excluded from the analysis as such conditions prevent a thorough recording of these species.

Habitat analysis of wintering birds

For the community of birds occurring in the southern Baltic Sea in winter (December to February), the most important season in this area for many species, basic principles of the habitat selection were studied by carrying out a canonical correspondence analysis (CCA), using the *vegan* package in version 2.8.1 of R (R Development Core Team, 2008). CCA is a multivariate method to reveal the relationships between biological assemblages of species and their environment (ter Braak and Verdonschot, 1995). The four environmental (explanatory) variables longitude (as a proxy for salinity gradients), distance to the nearest coast, water depth and bottom sediment type were analysed in terms of their influence on the community of wintering birds, comprising of 17 species (see Table 1.1). These factors were considered to have a potential effect on the habitat selection of birds at sea, either direct, e.g. by means of the maximum possible diving depth during foraging dives, or indirect, e.g. via an influence on prey organisms.

Data on longitude were recorded during ship-based surveys with a portable GPS (see above) and were queried from the German *Seabirds at Sea* database. The distance to the nearest coast was calculated by assigning the respective bird positions to the coastline using the *geoprocessing wizard* in ArcView GIS 3.2. Data on water depth, classified into 1-metre categories, were obtained from the Danish Hydraulic Institute (DHI). Sediment data were provided by the Geological Survey of Denmark and Greenland (GEUS; Hermansen and Jensen, 2000). They were classified into six different sediment types based on grain size and content of organic material (type 1: mud, <0.04 mm, >10% organic matter; type 2: sandy mud to muddy sand, <0.04 mm, 1-10% organic matter; type 3: sand, locally with gravel and stones, 0.04-2.0 mm; type 4-6: lag sediment of different origins). Water depths and sediment types were allocated to bird data using the *geoprocessing wiz*ard in ArcView GIS 3.2. Thereby, log10 values of water depth were used. The influence of the four habitat factors on the whole winter community was analysed with the function *envit* in R, using 1000 permutations of the CCA. The habitat preferences of the respective species were visualised in and derived from an ordination diagram. Basically, the following principles can be applied to the interpretation of the diagram:

- the higher the value for longitude, the more easterly is the distribution of a given species
- the higher the distance value, the more offshore occurs the species
- the higher the value for water depth, the deeper are the waters where the species occurs
- the higher the sediment value, the more coarse is the sediment type in areas where the species occurs

Not all results of the CCA can be explained and accounted for without further, comprehensive habitat analyses. As the present study only intends to provide an overview of the basic principles of the habitat selection of wintering birds, the findings are mainly interpreted in relation to the distribution maps (Figs. 1.2 - 1.24) and supplemented by some information from the literature. Most knowledge exists for sea ducks, the most characteristic and most intensively studied group in the southern Baltic Sea so far. For this reason, a more detailed analysis of their habitat selection in terms of water depth was conducted in the present analysis and compared to other studies. Thereby, the abundances of sea ducks recorded within the observation transect were assigned to the respective depth values in ArcView GIS 3.2. Subsequently, the percentage of birds occurring in different depth classes was calculated for each species separately. The habitat selection of grebes is described in **Chapter II** and **Chapter III** of this thesis and thus not further addressed at this point.

Influence of fishing activities on the distribution of gulls

Some bird species are known to attend fishing vessels to feed on discards and offal. During the ship-based seabird surveys described above, associations of birds with human fishing activities are recorded by default. For gull species, the proportion of birds associated with fishing vessels within the observation transect was calculated for different time periods. Additionally, an aerial survey conducted in August and September 2004 was analysed to study the influence of human fishing activities on the distribution patterns of Herring and Greater Black-backed Gulls. Maps are based on bird abundances, i.e. numbers of individuals per area surveyed, for each 1-second counting interval. This way, data are corrected for counting effort. Fishing activities are visualised in the maps as the number of fishing boats recorded per counting interval at the position of the observation platform.

Results and Discussion

Distribution patterns of characteristic species

The avifauna of the southern Baltic Sea is characterised by the occurrence of various waterbird species (most notably sea ducks, grebes and divers), auks and gulls. Beside auks, truly pelagic species like Northern Fulmars, Northern Gannets or Black-legged Kittiwakes are only rare visitors from the adjacent North Sea. The various species in the southern Baltic Sea exhibit distinctive spatial and temporal distribution patterns. For localities referred to in the following text, see Fig. 1.1.

The most characteristic and most abundant birds are four species of sea ducks, which occur in coastal waters and on shallow offshore grounds. They exhibit strong aggregation behaviour and mainly occur in large flocks, sometimes up to several thousand individuals. **Common Eiders** are mainly restricted to the western part of the study area (Fig. 1.2), while **Velvet Scoters** predominantly occur in the Pomeranian Bight in the east (Fig. 1.3). **Common Scoters** (Fig. 1.4) and **Long-tailed Ducks** (Fig. 1.5) are widely distributed throughout the southern Baltic Sea, with the latter being the most numerous of all sea duck species.

Mergansers are represented in the study area by **Red-breasted Mergansers**, which occur in locally large numbers in the coastal zones of the southern Balitc Sea (Fig. 1.6).

Grebes are represented in the study area by three species. **Great Crested Grebes** and **Red-necked Grebes** are widespread throughout the study area, but Great Crested Grebes are restricted to coastal waters (Fig. 1.7), while Red-necked Grebes can be found in coastal and offshore waters (Fig. 1.8). **Slavonian Grebes** mainly occur in the eastern part of the study area, especially on the Odra Bank in the Pomeranian Bight. The distribution is predominantly offshore, but there are some local hotspots in coastal areas (Fig. 1.9).

From the group of divers, **Red-throated Divers** (Fig. 1.10) and **Black-throated Divers** (Fig. 1.11) occur regularly in the southern Baltic Sea. They are widely distributed within the study area, but the two species exhibit different hotspots. Their numbers are rather equal in winter but differ considerably during migration periods.

Great Cormorants, the only cormorant species in the southern Baltic Sea, occur in many coastal zones of the study area, with a hotspot around the Greifswald Lagoon in the east, where large breeding colonies are located. The distribution only seldom expands into the offshore areas (Fig. 1.12). Great Cormorants often occur as single birds or in small flocks, but they also forage in groups, depending on prey availability. Larger fishes are usually caught singly, while small shoaling fish are often hunted in large flocks that could comprise several hundred individuals (see Garthe et al., 2008; Mendel et al., 2008).

Auks are the only truly pelagic species in the southern Baltic Sea. **Razorbills** (Fig. 1.13) and **Common Guillemots** (Fig. 1.14) are widely distributed within the study area and often occur offshore in deeper waters. **Black Guillemots** exhibit a distribution hotspot around the offshore bank Adlergrund, but local concentrations could also be found in some coastal areas (Fig. 1.15).

Six species of regularly occurring gulls belong to the avifauna of the southern Baltic Sea. **Herring Gulls** (Fig. 1.16), **Greater Black-backed Gulls** (Fig. 1.17) and **Common Gulls** (Fig. 1.18) are most abundant and widespread and can be found in nearly all coastal and offshore areas. **Common Black-headed Gulls** occur in comparably low numbers mainly in the coastal zones (Fig. 1.19), and only few **Lesser Black-backed Gulls** are present in the study area (Fig. 1.20). **Little Gulls** exhibit a distinct distribution hotspot in the eastern part of the study area during autumn migration, where they aggregate in large feeding flocks in the coastal zones of the Pomeranian Bight and in the Greifswald Lagoon (Fig. 1.21).

Terns occur only in low abundances within the study area. The feeding grounds for **Sandwich Terns**, **Common Terns** and **Arctic Terns** breeding along the southern Baltic Sea coast are mainly in inner coastal waters, lagoons or inland lakes (Klafs and Stübs, 1987; Scheller et al., 2002). Therefore, only few individuals of these species can be found in the coastal parts of the study area in summer (Fig. 1.22), but numbers are higher during migration periods (Fig. 1.23). **Black Terns** occur in the study area in locally high concentrations during autumn migration (Fig. 1.24). They aggregate in large feeding flocks in the coastal areas of the Pomeranian Bight and in the Greifswald Lagoon, often together with Little Gulls.

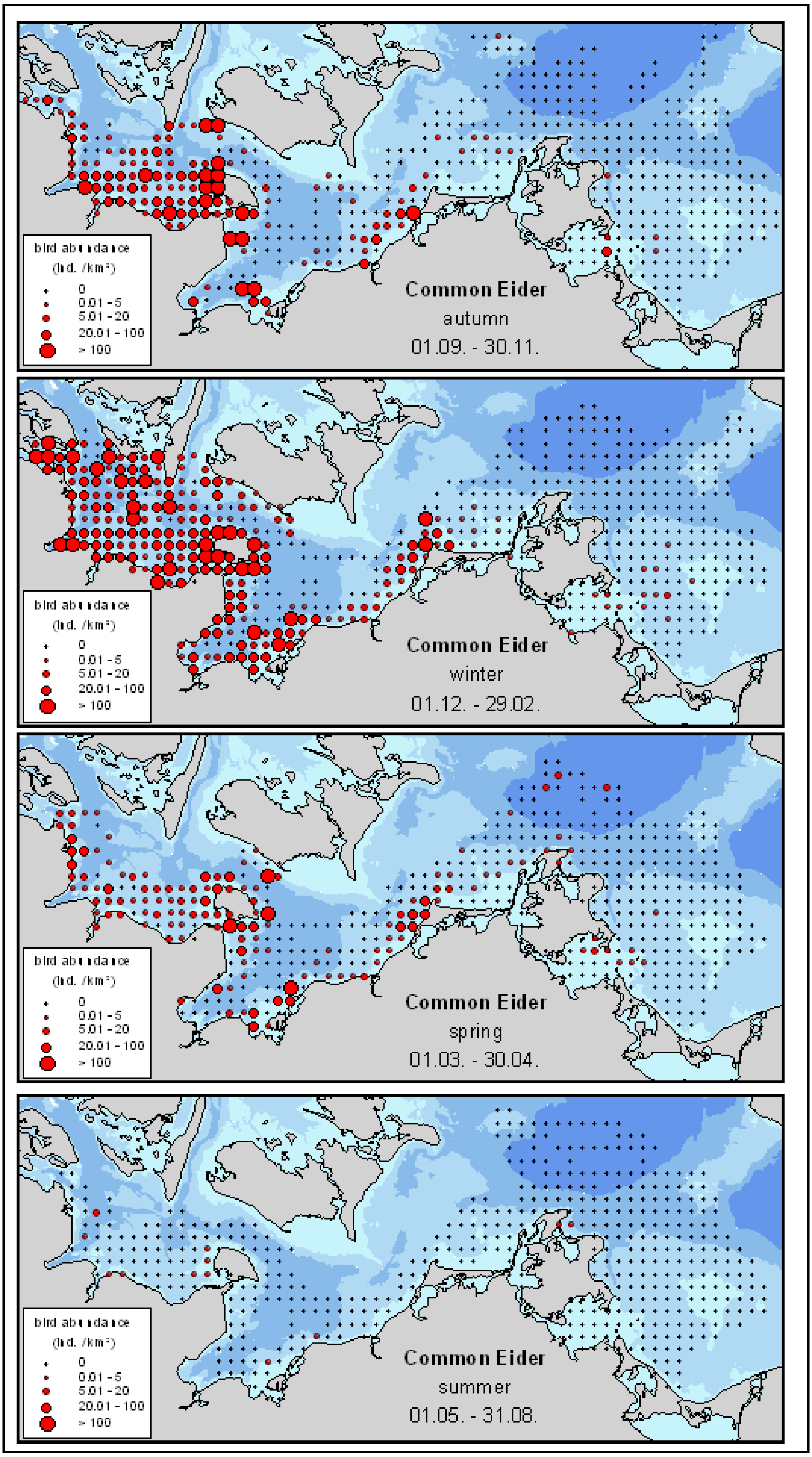

Fig. 1.2. Seasonal distribution of Common Eiders, 2000-2008.

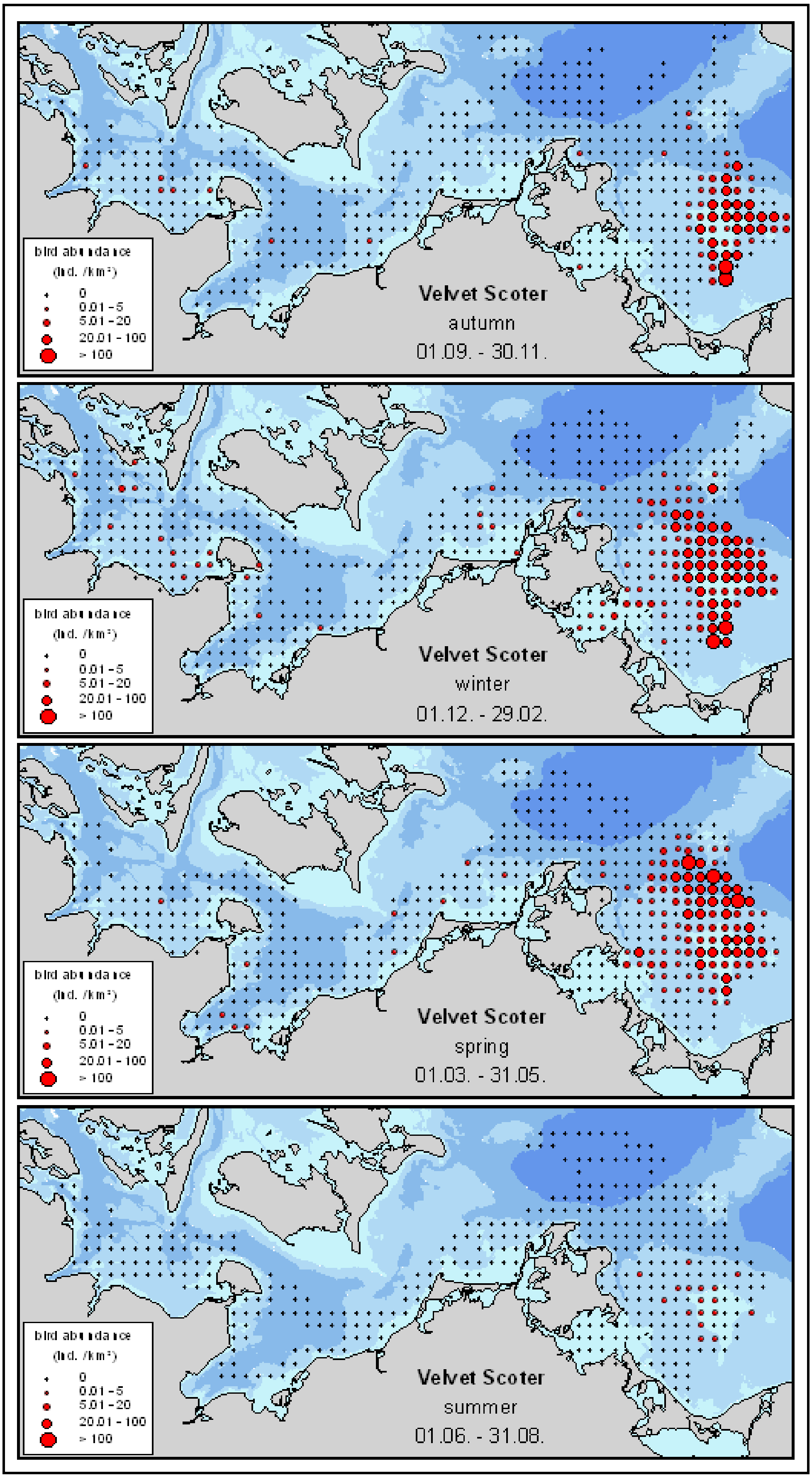

Fig. 1.3. Seasonal distribution of Velvet Scoters, 2000-2008.

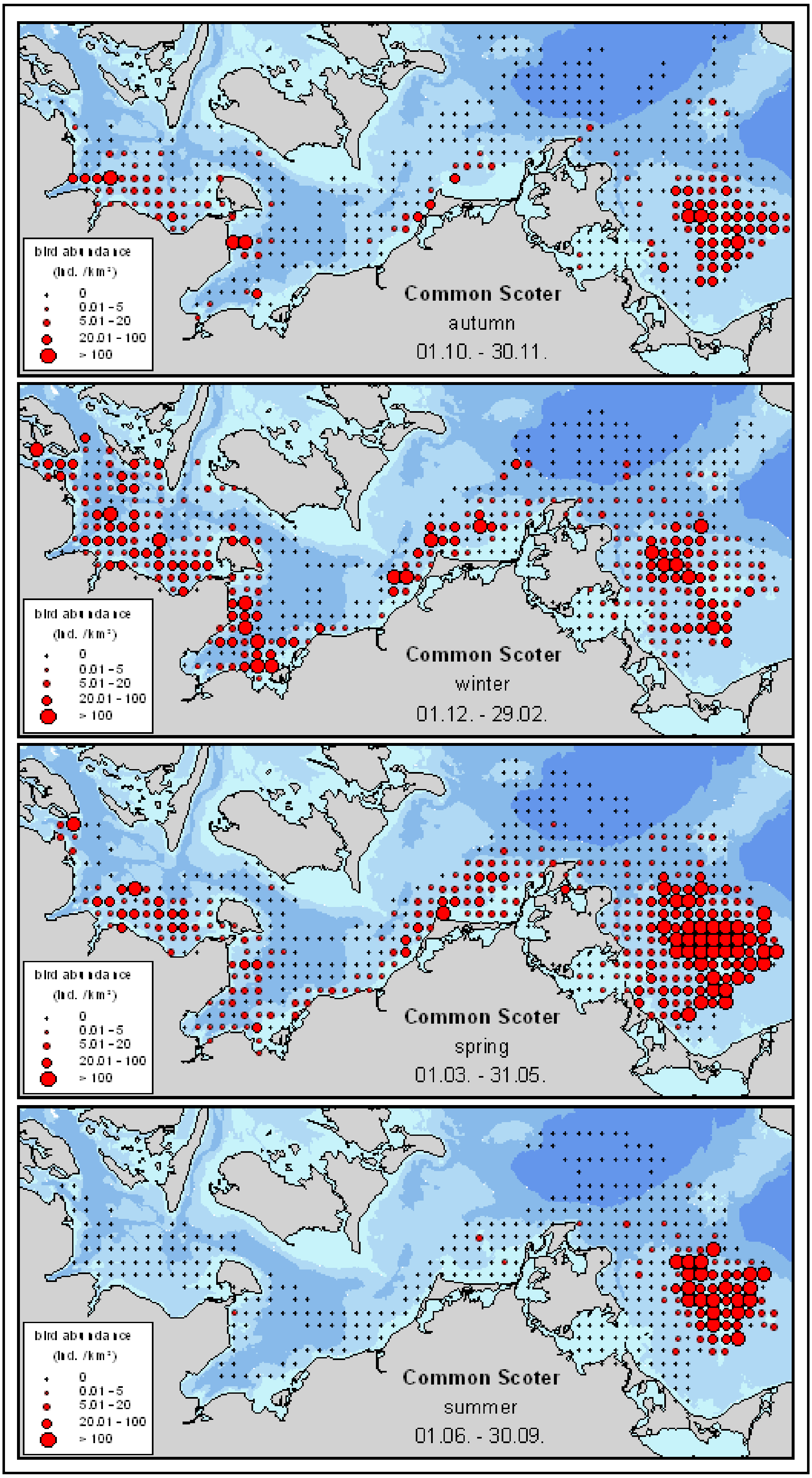

Fig. 1.4. Seasonal distribution of Common Scoters, 2000-2008.

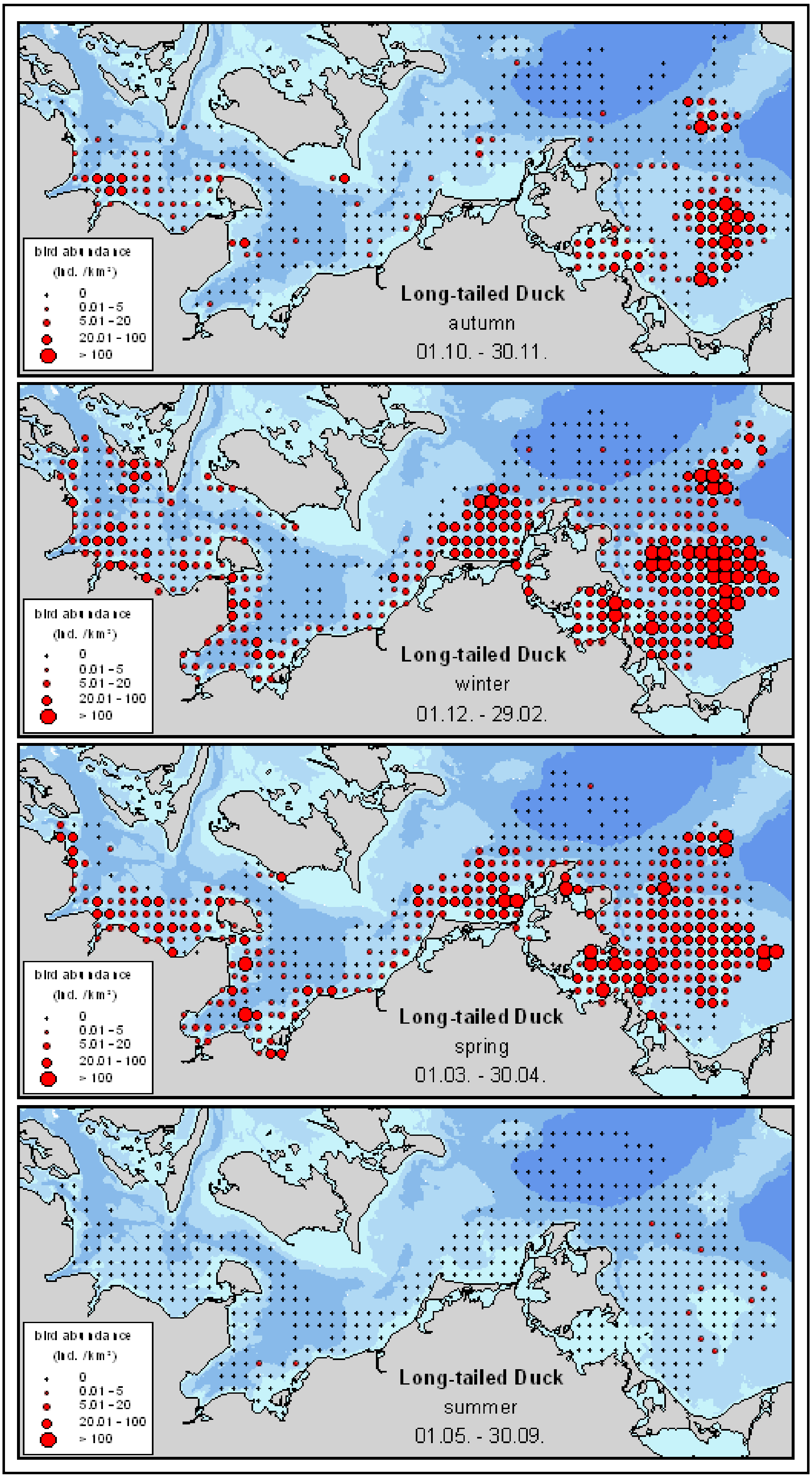

Fig. 1.5. Seasonal distribution of Long-tailed Ducks, 2000-2008.

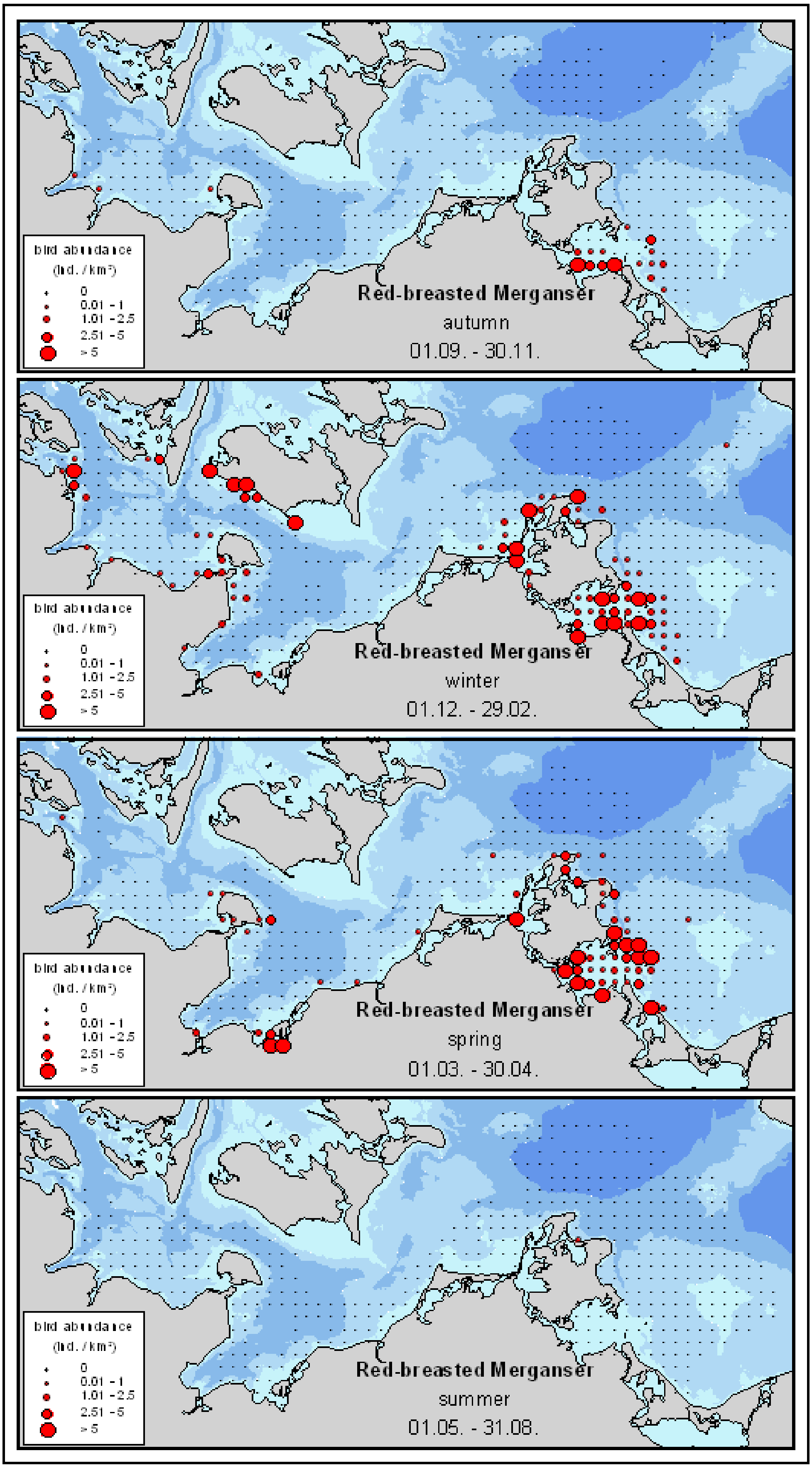

Fig. 1.6. Seasonal distribution of Red-breasted Mergansers, 2000-2008.

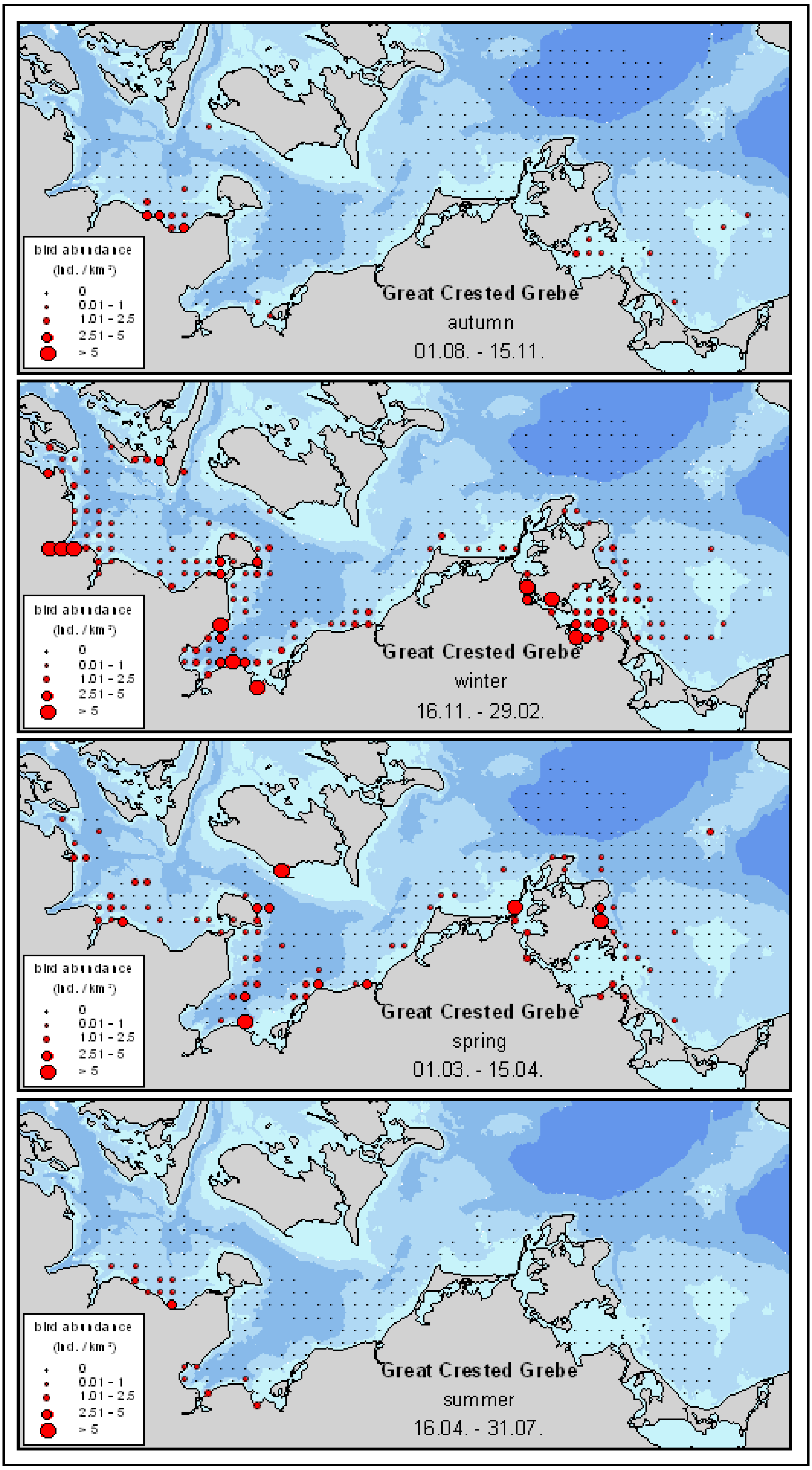

Fig. 1.7. Seasonal distribution of Great Crested Grebes, 2000-2008.

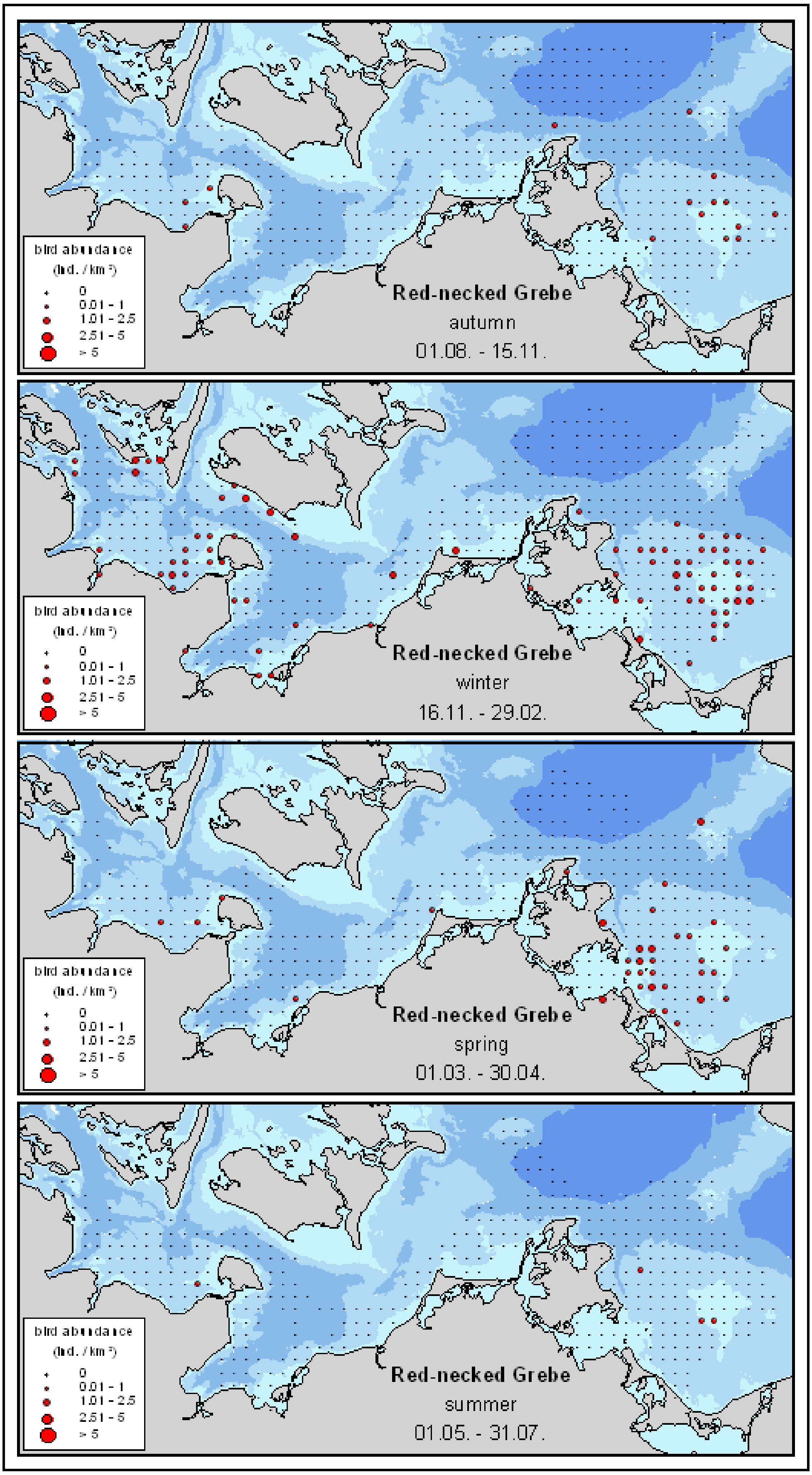

Fig. 1.8. Seasonal distribution of Red-necked Grebes, 2000-2008.

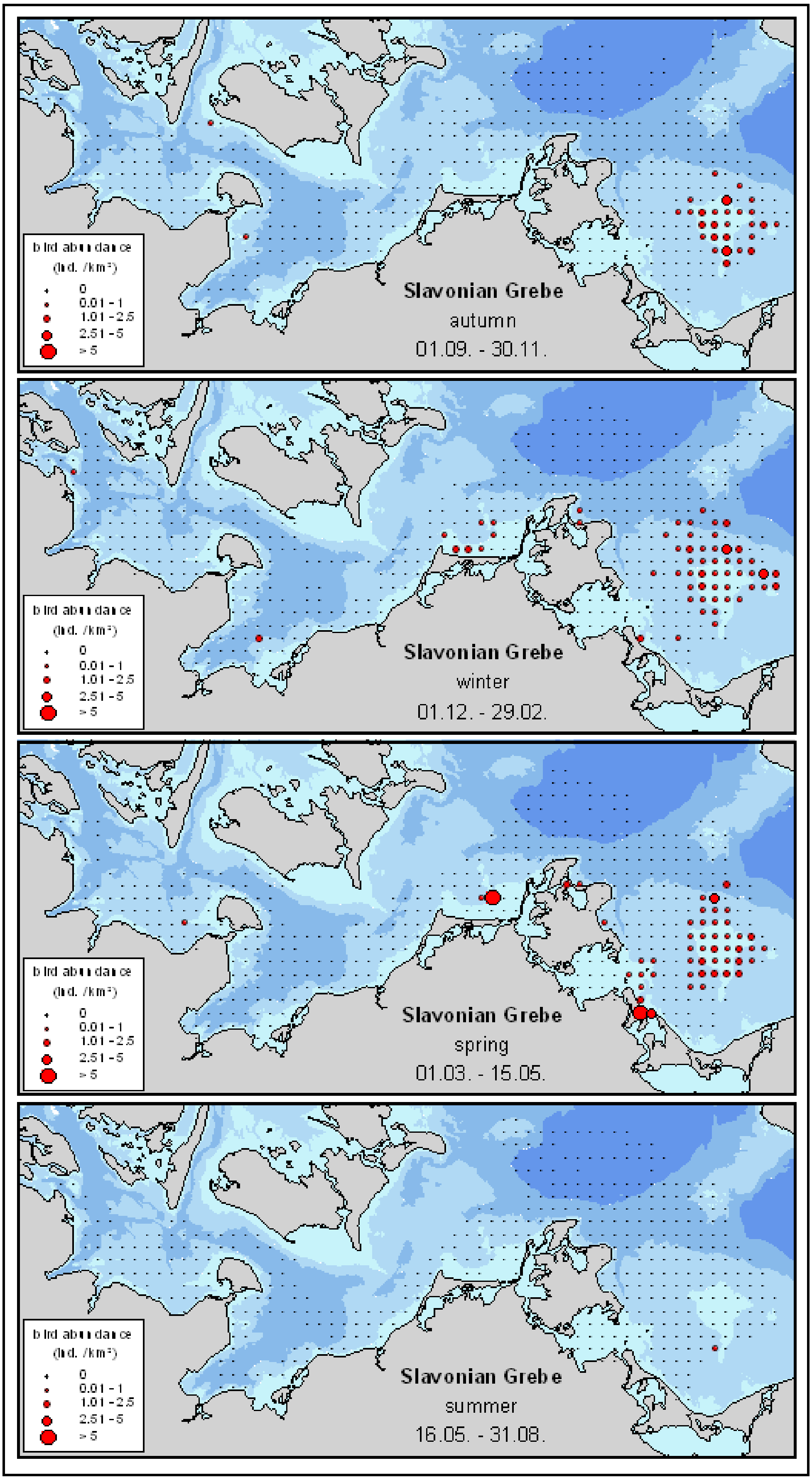

Fig. 1.9. Seasonal distribution of Slavonian Grebes, 2000-2008.

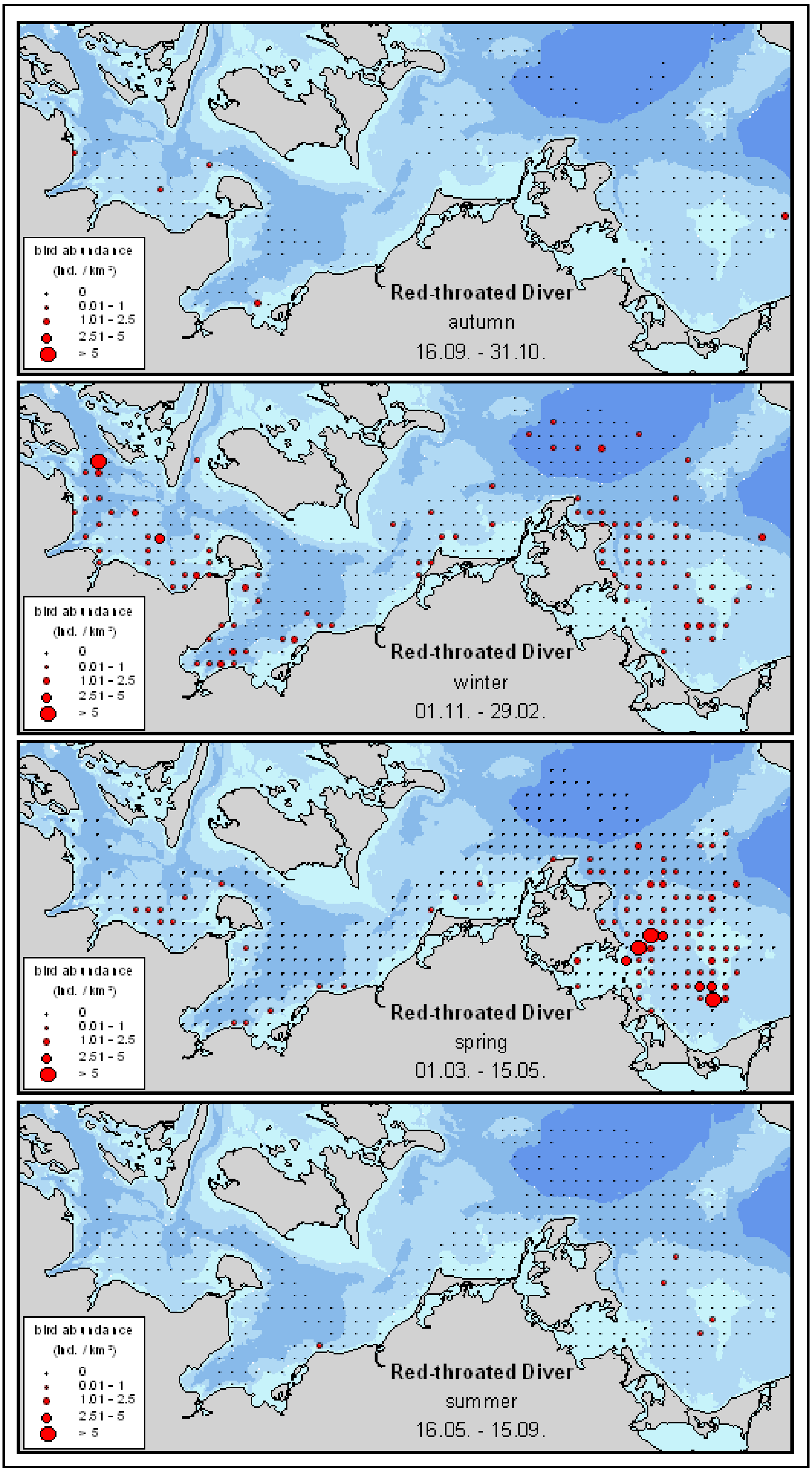

Fig. 1.10. Seasonal distribution of Red-throated Divers, 2000-2008.

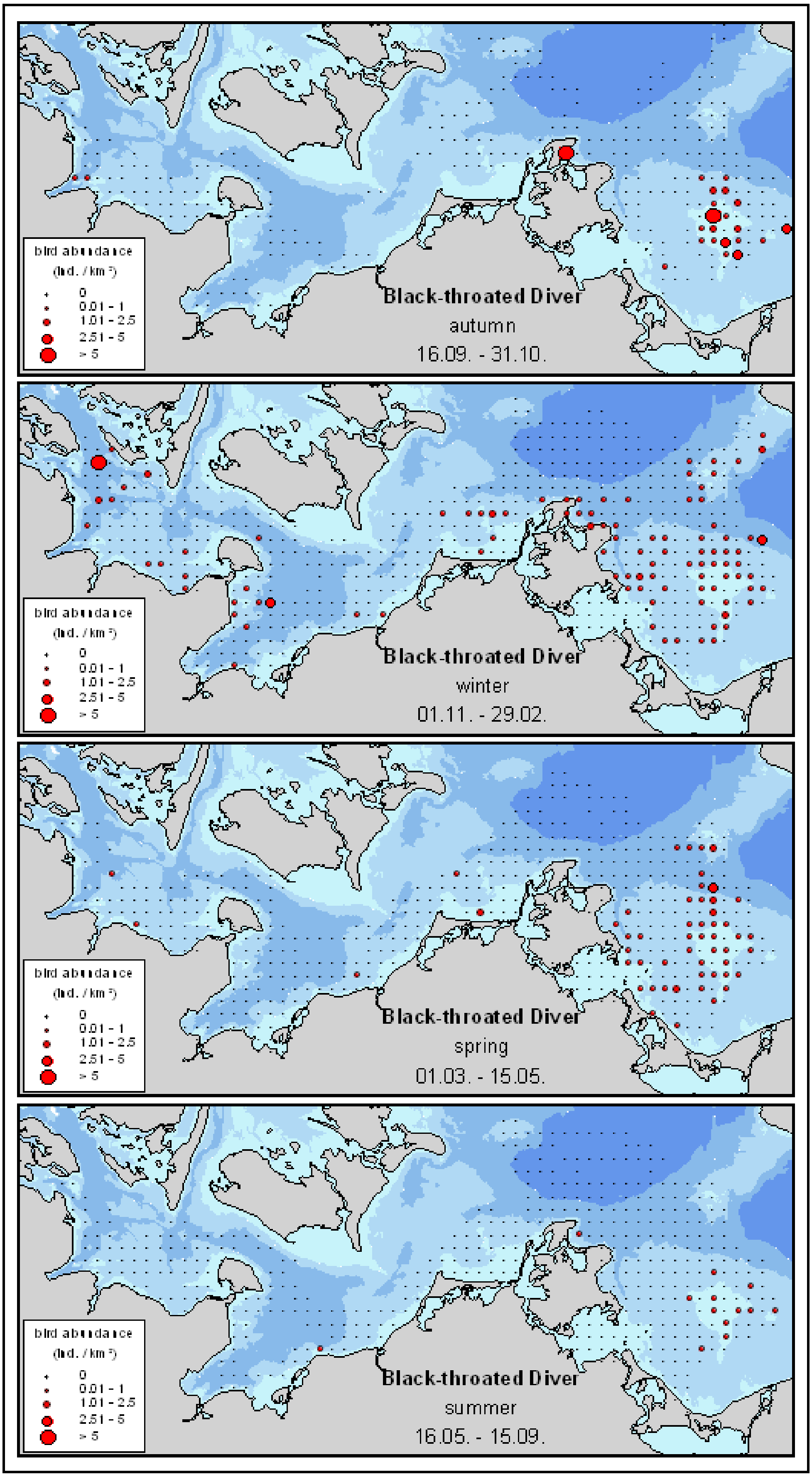

Fig. 1.11. Seasonal distribution of Black-throated Divers, 2000-2008.

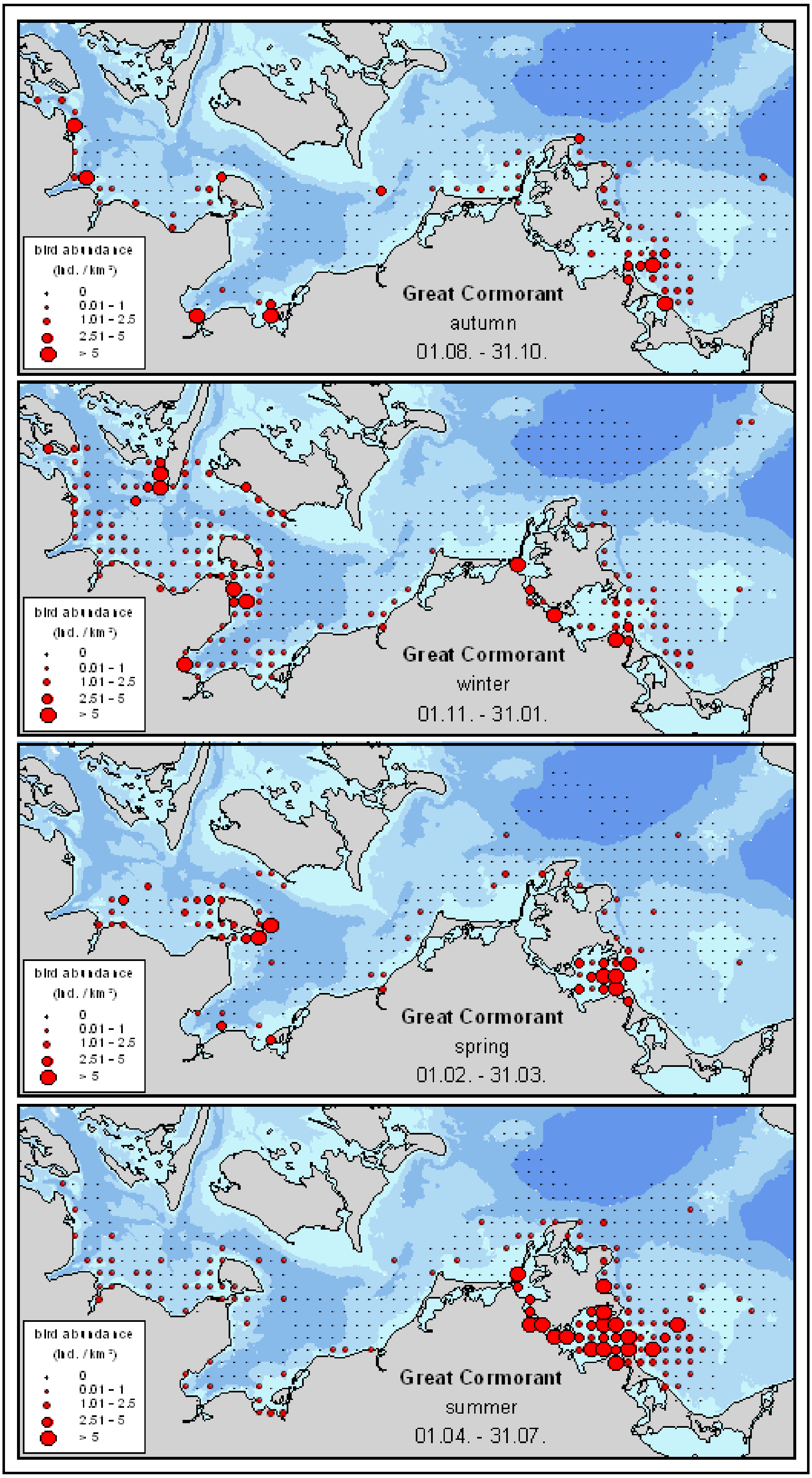

Fig. 1.12. Seasonal distribution of Great Cormorants, 2000-2008.

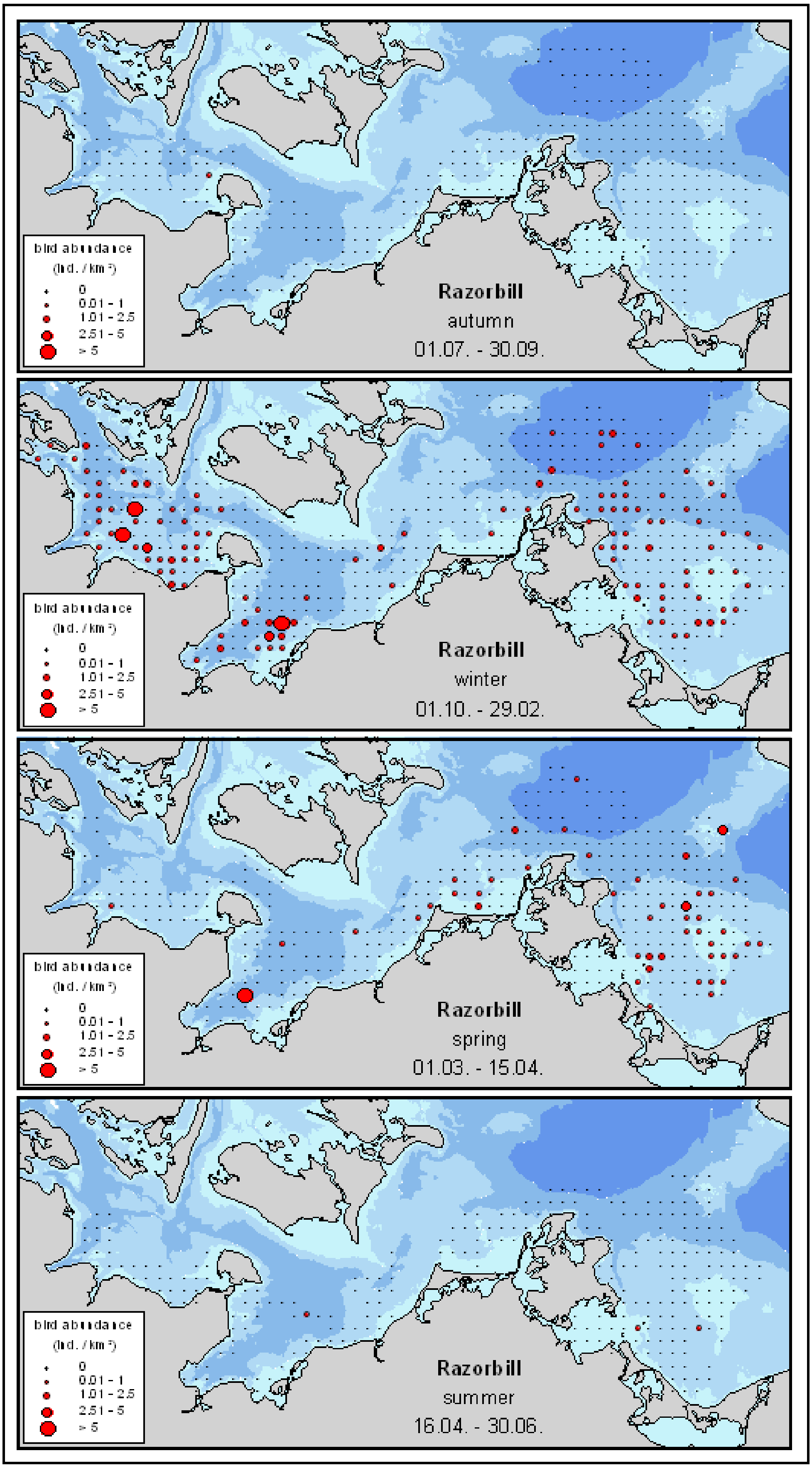

Fig. 1.13. Seasonal distribution of Razorbills, 2000-2008.

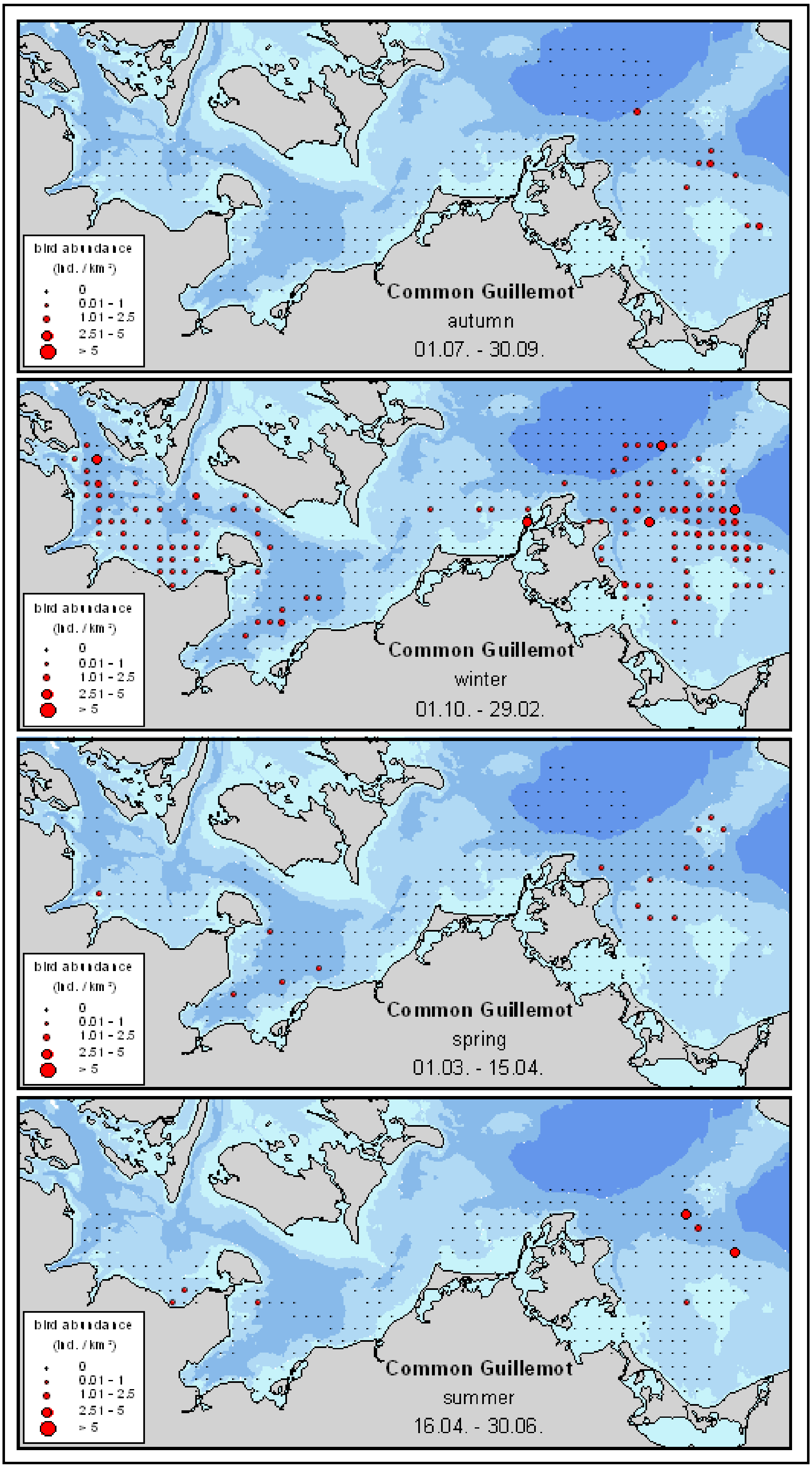

Fig. 1.14. Seasonal distribution of Common Guillemots, 2000-2008.

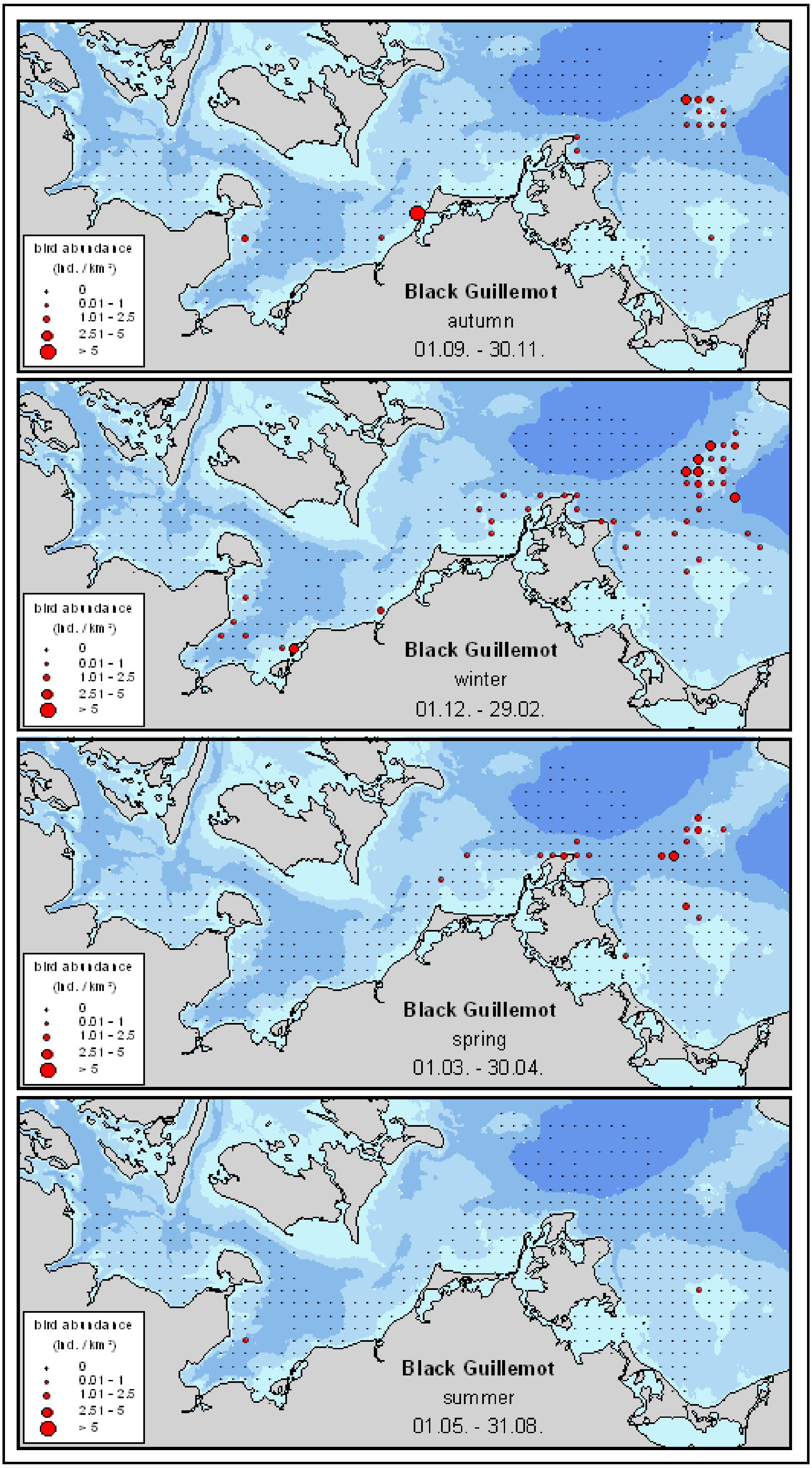

Fig. 1.15. Seasonal distribution of Black Guillemots, 2000-2008.

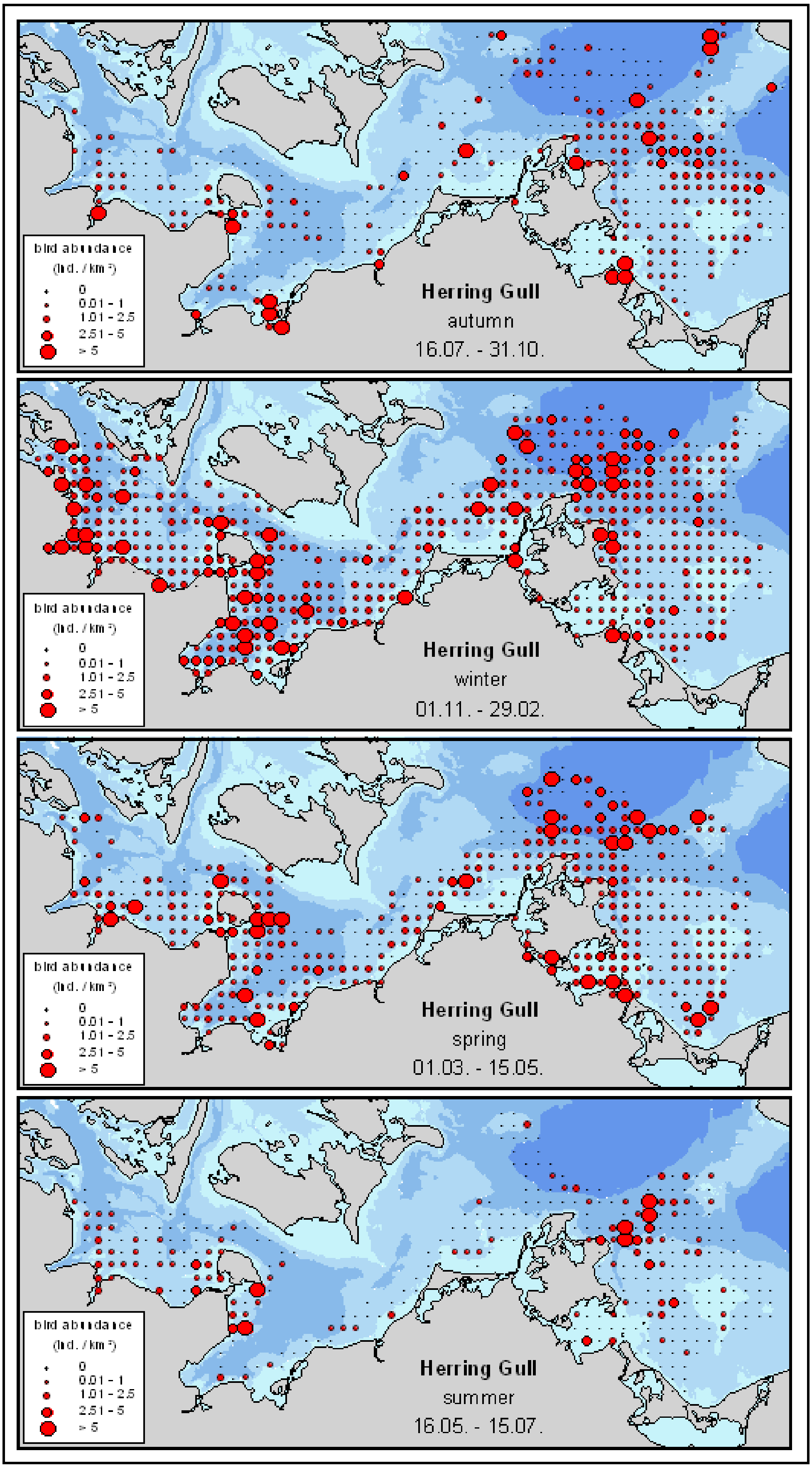

Fig. 1.16. Seasonal distribution of Herring Gulls, 2000-2008.

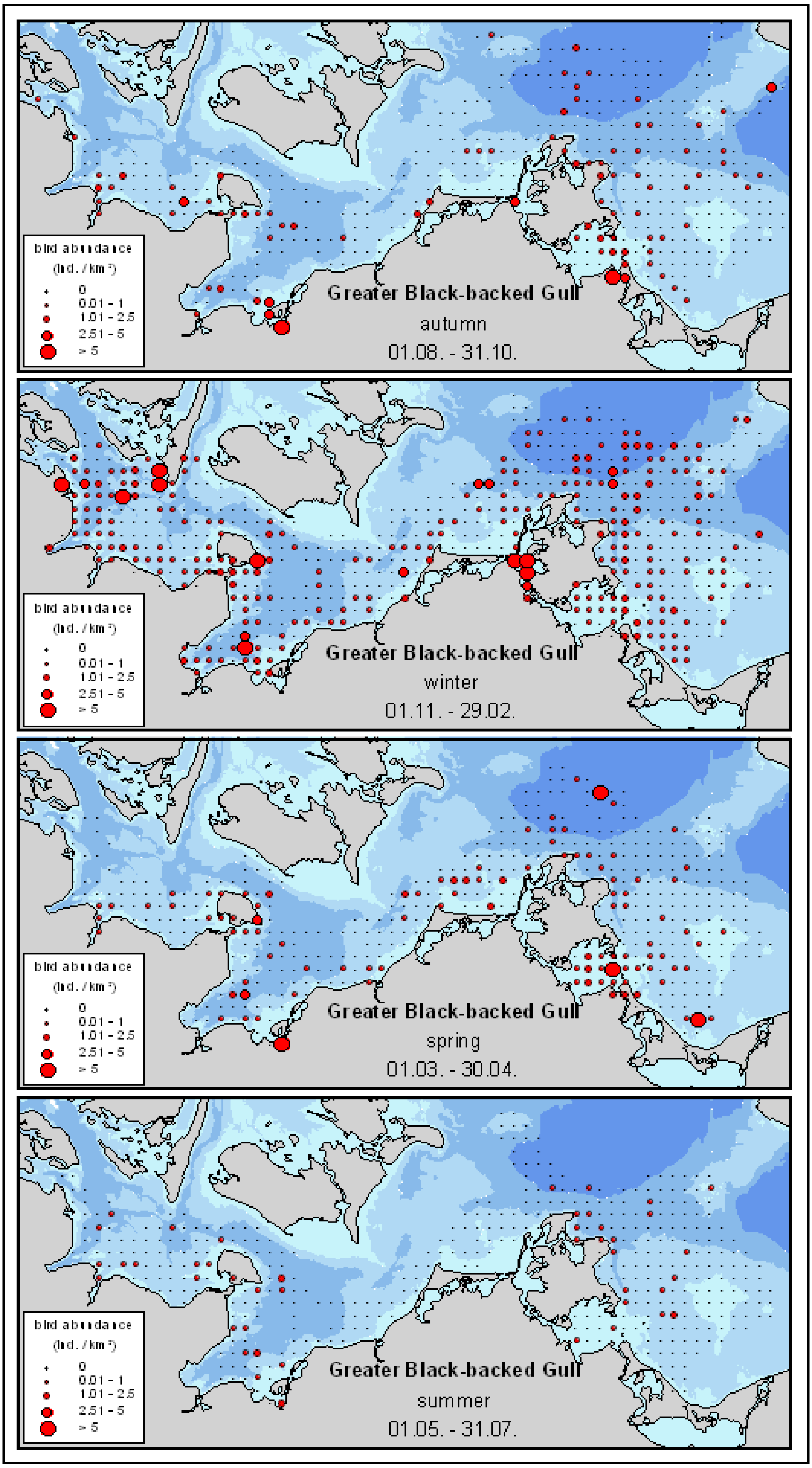

Fig. 1.17. Seasonal distribution of Greater Black-backed Gulls, 2000-2008.

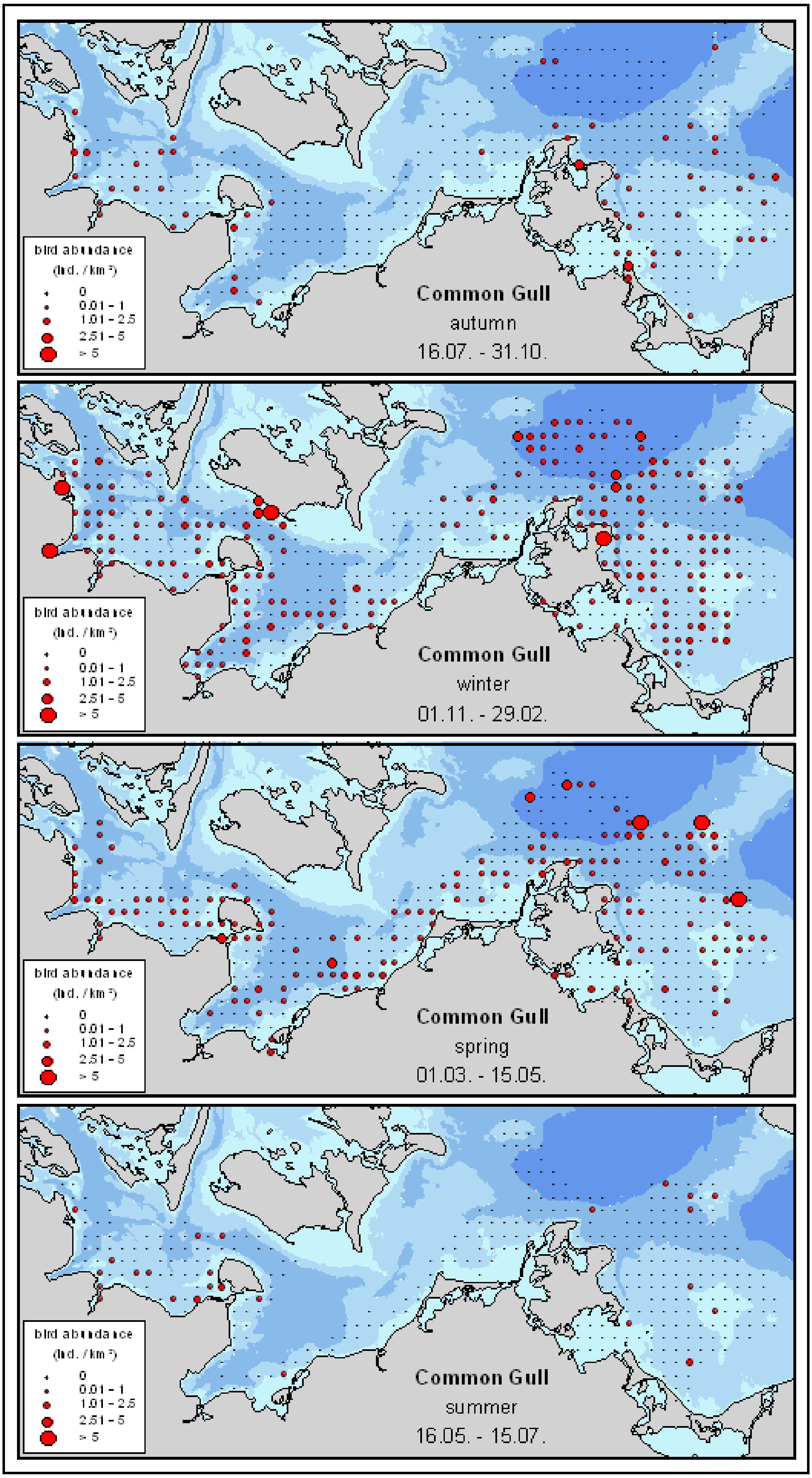

Fig. 1.18. Seasonal distribution of Common Gulls, 2000-2008.

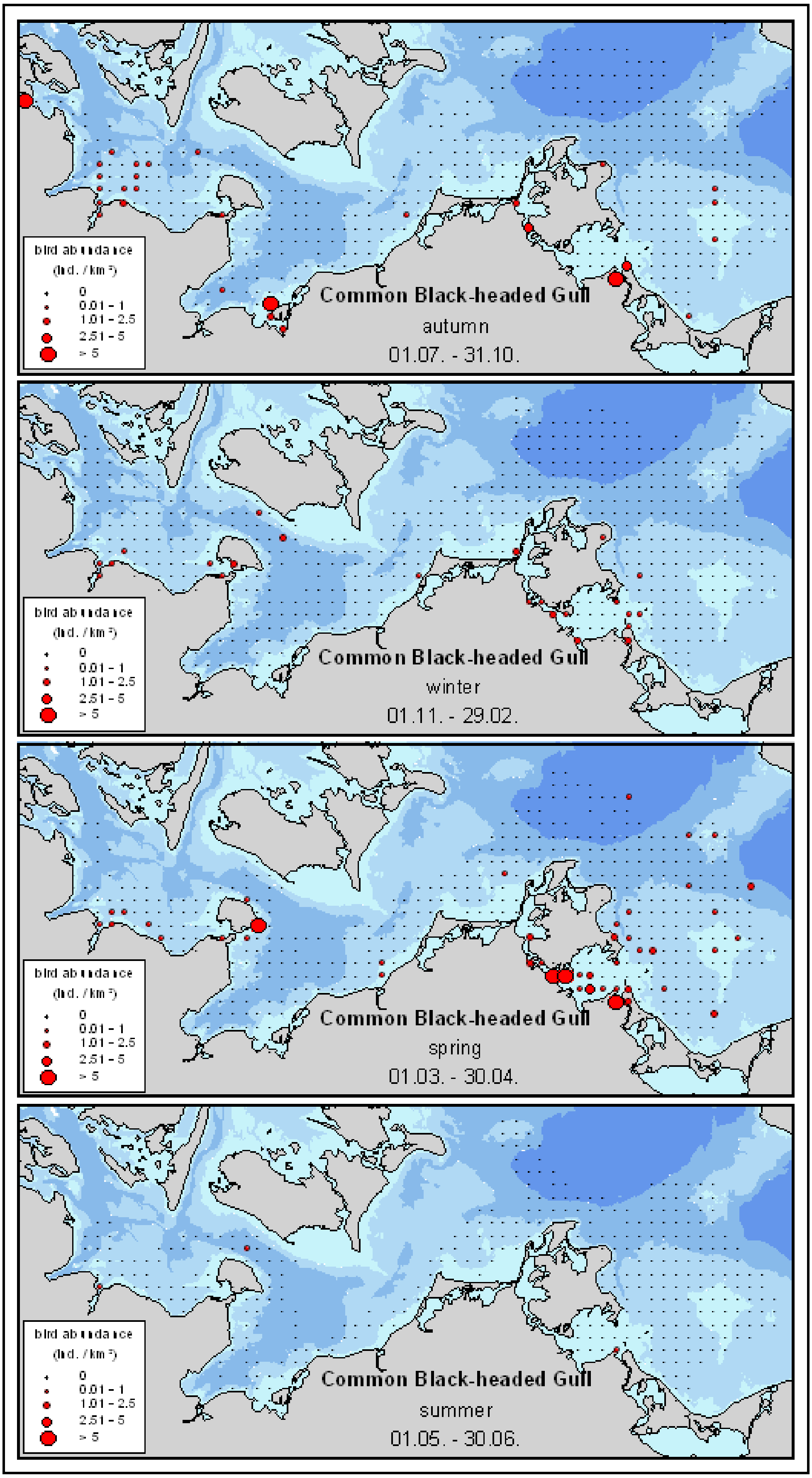

Fig. 1.19. Seasonal distribution of Common Black-headed Gulls, 2000-2008.

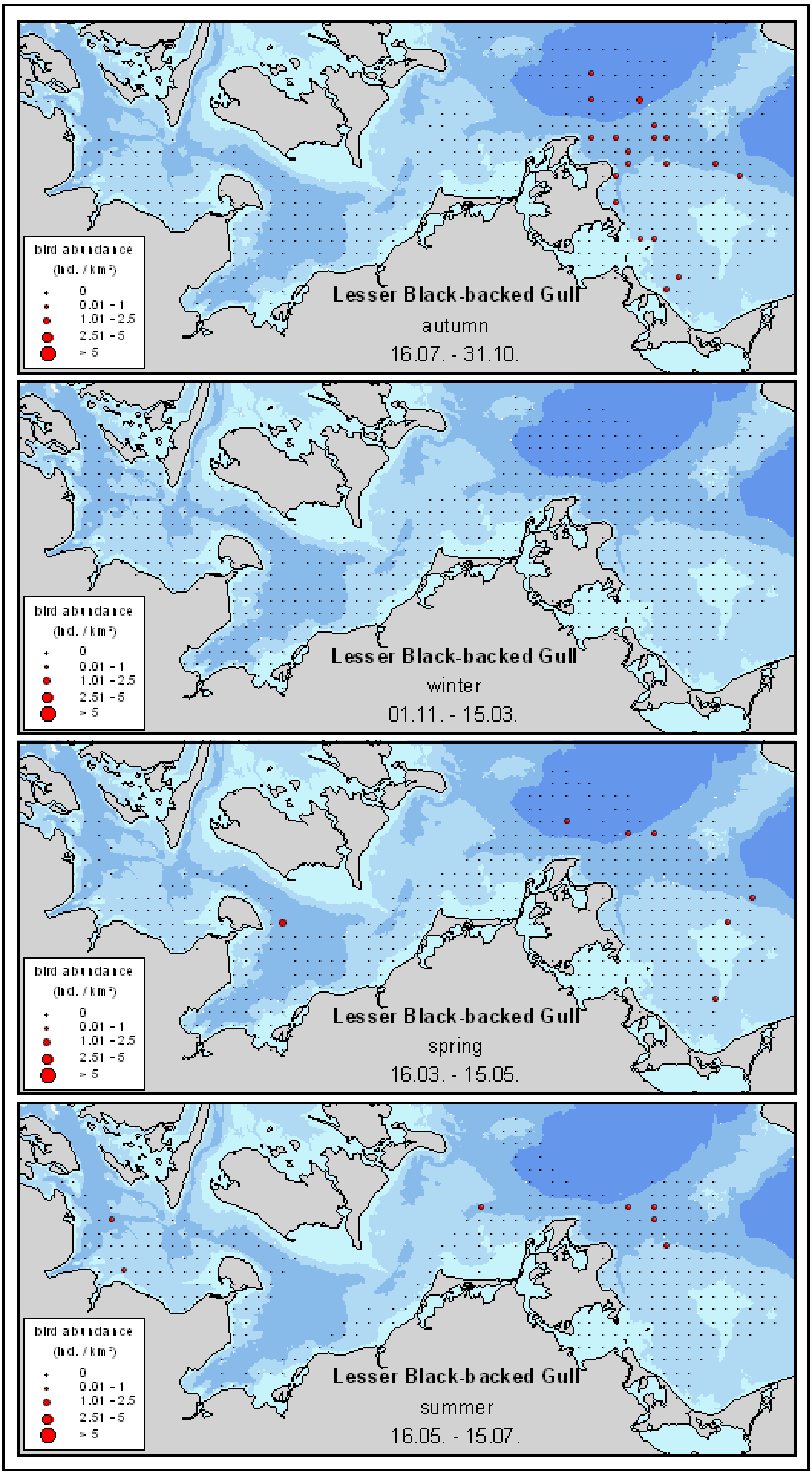

Fig. 1.20. Seasonal distribution of Lesser Black-backed Gulls, 2000-2008.

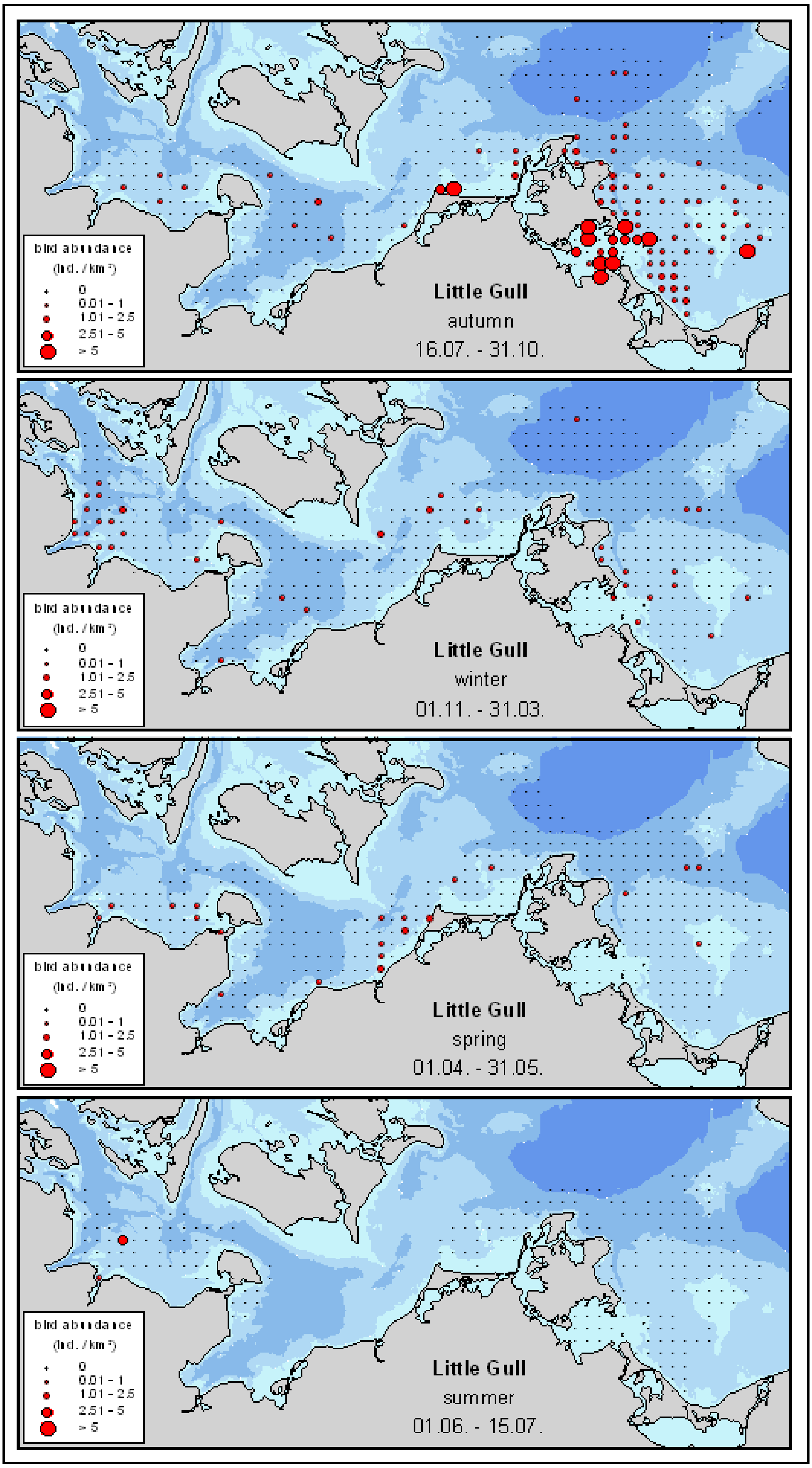

Fig. 1.21. Seasonal distribution of Little Gulls, 2000-2008.

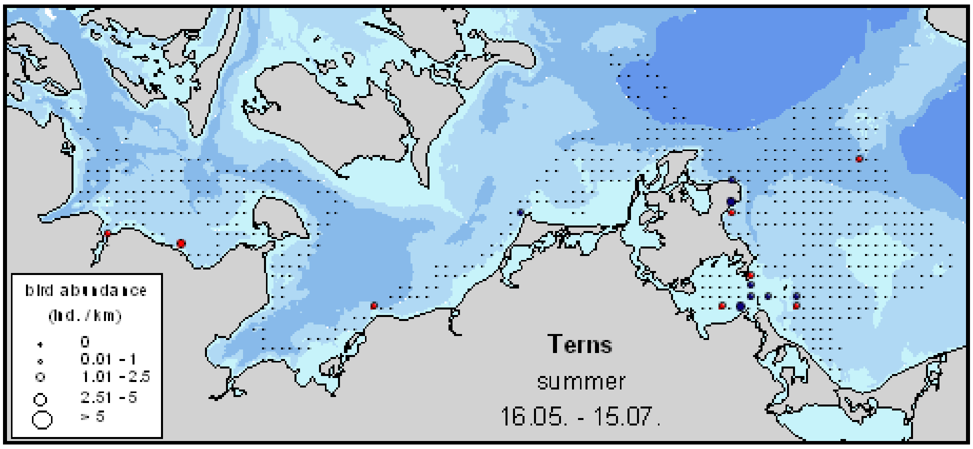

Fig. 1.22. Summer distribution of Sandwich Terns (blue) and Common Terns (red), 2000-2008. Bird abundance was calculated as number of individuals per distance travelled.

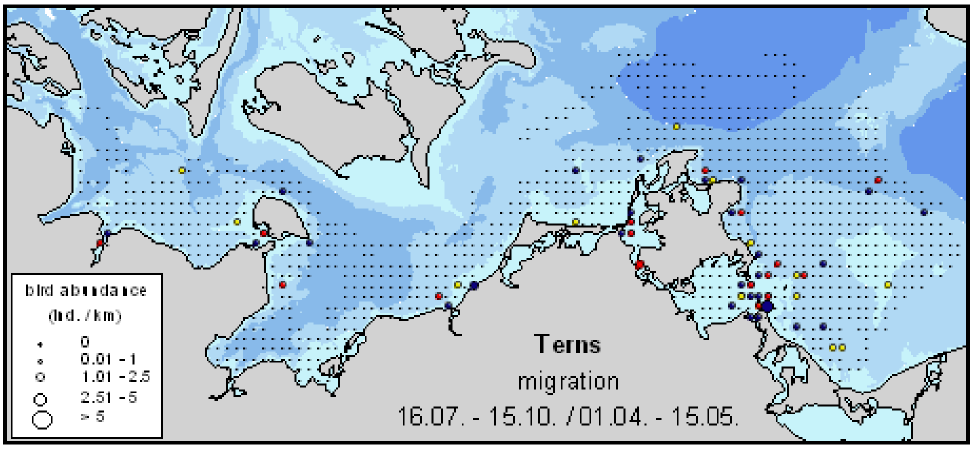

Fig. 1.23. Distribution of Sandwich Terns (blue), Common Terns (red) and Arctic Terns (yellow) during autumn and spring migration, 2000-2008. Bird abundance was calculated as number of individuals per distance travelled.

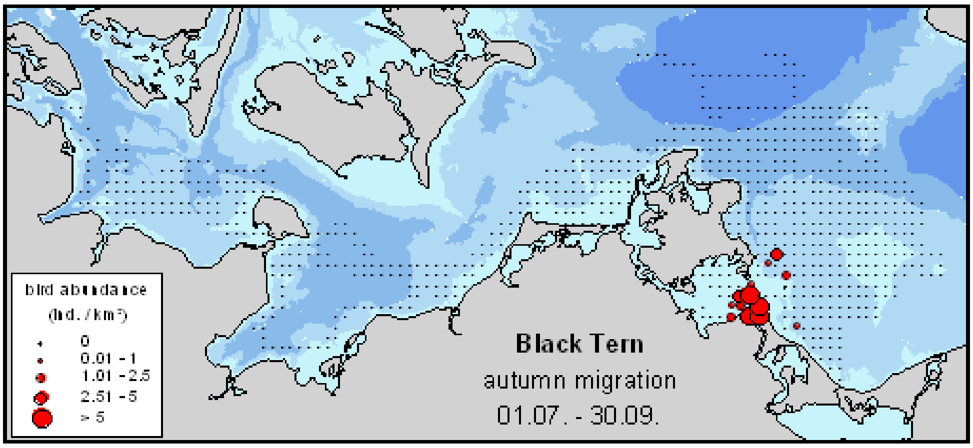

Fig. 1.24. Distribution of Black Terns during autumn migration, 2000-2008.

For most species, the southern Baltic Sea is of greatest importance during the winter half-year (Table 1.1). After leaving their breeding grounds, which mainly lie in the forest and tundra zones of Fennoscandia and northern Russia or along the Baltic Sea coast, they pass through the area during migration or use it as wintering site. Some species also occur in the southern Baltic Sea during summer, either because they have breeding populations nearby or non-breeding individuals use it as resting and / or moulting area. While some species are restricted to coastal waters, others are more widely distributed. Seasonal population sizes are given in Table 1.2.

Table 1.1. Temporal and spatial occurrence of the main seabird and waterbird species in the southern Baltic Sea. For scientific names, see **Annex I**. Species with abbreviations of scientific names given in brackets have been included in the habitat analysis below.
+: main occurrence, **(+)**: minor occurrence, *b*: summer occurrence due to local breeding populations, *m*: summer occurrence due to moult, *nb*: summer occurrence due to non-breeding individuals, *a*: occurrence mainly during autumn migration.

Species	Winter half year	Summer half year	Inshore	Offshore	Feeding
Red-throated Diver (*GAST*)	**+**		**+**	**+**	benthopelagic
Black-throated Diver (*GAAR*)	**+**	**(+)** nb, m?	**+**	**+**	benthopelagic
Great crested Grebe (*POCR*)	**+**	**(+)** b, m?	**+**		benthopelagic
Red-necked Grebe (*POGR*)	**+**	**(+)** b, m?	**+**	**+**	benthopelagic
Slavonian Grebe (*POAU*)	**+**		**(+)**	**+**	benthopelagic
Great Cormorant (*PHCA*)	**(+)**	**+** b	**+**		benthopelagic
Common Eider (*SOMO*)	**+**	**(+)** b	**+**	**+**	benthic
Long-tailed Duck (*CLHY*)	**+**		**+**	**+**	benthic
Common Scoter (*MENI*)	**+**	**(+)** nb, m	**+**	**+**	benthic
Velvet Scoter (*MEFU*)	**+**	**(+)** nb, m	**+**	**+**	benthic
Red-breasted Merganser (*MESE*)	**+**		**+**		benthopelagic (?)
Common Guillemot (*URAA*)	**+**	**(+)** b	**(+)**	**+**	pelagic
Razorbill (*ALTO*)	**+**		**(+)**	**+**	pelagic (?)
Black Guillemot (*CEGR*)	**+**		**(+)**	**+**	benthopelagic
Little Gull		a	**+**		surface
Common Black-headed Gull		**+** b	**+**		surface
Common Gull (*LACA*)	**+**	**(+)** b	**+**	**+**	surface
Greater Black-backed Gull (*LAMA*)	**+**	**(+)** nb	**+**	**+**	surface
Herring Gull (*LAAR*)	**+**	**(+)** b	**+**	**+**	surface
Lesser Black-backed Gull		**+** b	**+**	**+**	surface
Sandwich Tern		**+** b	**+**		surface + 2 m
Common Tern		**+** b	**+**		surface + 0.5 m
Arctic Tern		**+** b	**+**		surface + 0.5 m
Black Tern		a	**+**		surface

Table 1.2. Population sizes of the main seabird and waterbird species in the southern Baltic Sea, taken from Mendel et al. (2008). Calculations are based on data from ship-based bird surveys 2000-2007 and for divers additionally on aerial surveys 2002-2006. Time periods are based on species-specific definitions of seasons according to Garthe et al. (2007). They are specified in the distribution maps. For scientific names, see **Annex I**.
III: population size 11-50 individuals; n.s.: population size not specified.

Species	Autumn	Winter	Spring	Summer
Red-throated Diver	210	3 200	9 000	III
Black-throated Diver	900	2 400	1 900	60
Great crested Grebe	n.s.	8 500	n.s.	n.s.
Red-necked Grebe	n.s.	750	n.s.	n.s.
Slavonian Grebe	n.s.	1 000	n.s.	n.s.
Great Cormorant	n.s.	10 500	n.s.	n.s.
Common Eider	n.s.	190 000	n.s.	n.s.
Long-tailed Duck	n.s.	315 000	n.s.	n.s.
Common Scoter	n.s.	230 000	n.s.	n.s.
Velvet Scoter	n.s.	38 000	n.s.	n.s.
Red-breasted Merganser	n.s.	10 500	n.s.	n.s.
Common Guillemot	21 000	33 000	18 500	7 000
Razorbill	III	3 600	1 000	110
Black Guillemot	260	700	400	III
Little Gull	9 500	220	500	350
Common Black-headed Gull	n.s.	15 500	n.s.	n.s.
Common Gull	n.s.	11 500	n.s.	n.s.
Greater Black-backed Gull	n.s.	7 000	n.s.	n.s.
Herring Gull	n.s.	70 000	n.s.	n.s.
Lesser Black-backed Gull	130	III	60	160
Sandwich Tern	n.s.	0	n.s.	n.s.
Common Tern	n.s.	0	n.s.	n.s.
Arctic Tern	n.s.	0	n.s.	n.s.
Black Tern	n.s.	n.s.	n.s.	n.s.

Basic principles of the habitat choice of selected species wintering in the southern Baltic Sea

The community structure in winter was significantly influenced by all four environmental factors examined (Table 1.3). The eigenvalues of the four axes CCA 1, CCA 2, CCA 3 and CCA 4 were 0.54, 0.06, 0.04 and 0.01, respectively, indicating the descending order of their relevance: the first axis was most important, followed by the second and the third, while the influence of the fourth axis was only marginal. The ordination diagrams of the CCA (Fig. 1.25) revealed that longitude and distance to coast correlated best with the first axis CCA 1. Thus, these two factors had the highest effect on the whole winter community structure. This is also pointed out by their R²-values in Table 1.3, which were highest among the four parameters.

Table 1.3. Results of the CCA, revealing the influence of selected habitat factors on the community structure of birds wintering in the southern Baltic Sea for the two most important axes CCA 1 and CCA 2.

Habitat factors	CCA 1	CCA 2	R^2	p
Distance to coast	0.9995	-0.0324	0.47	<0.001 ***
Water depth	0.0905	0.9959	0.05	<0.001 ***
Sediment type	-0.7114	-0.7028	0.03	<0.001 ***
Longitude	0.9999	0.0030	0.59	<0.001 ***

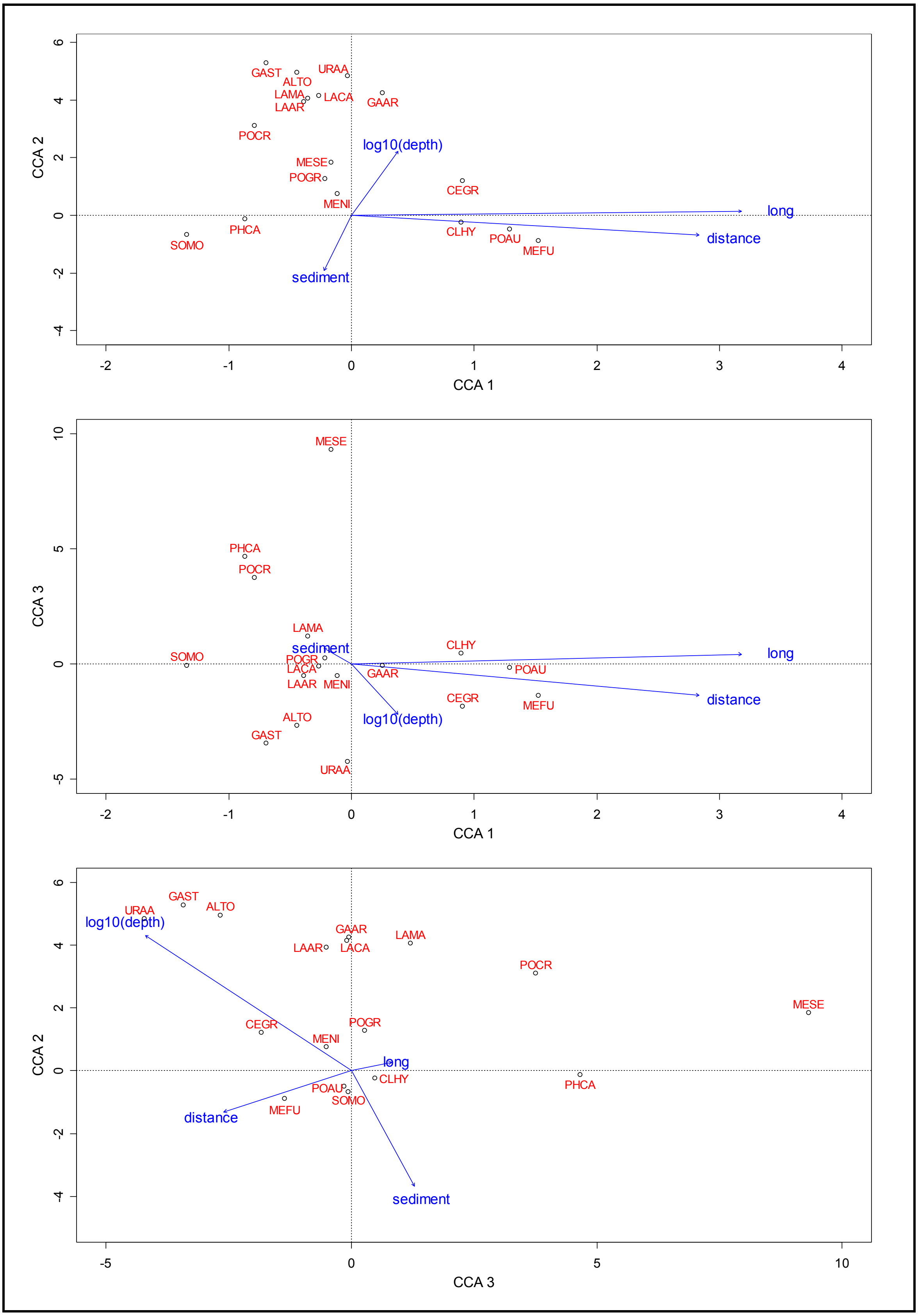

Fig. 1.25. Canonical correspondence analysis (CCA) of 17 species wintering in the southern Baltic Sea in relation to the factors longitude (long), distance to coast (distance), water depth (log10(depth)) and bottom sediment type (sediment). Only three dimensions are shown due to the insignificance of the fourth axis. For species' abbreviations, see Table 1.1.

The four factors differed considerably in their significance for the several bird species. The following results can be derived from the ordination diagram (Fig. 1.25):

Longitude

- Common Eiders were linked with lowest longitude values; Velvet Scoters were linked with highest values, followed by Slavonian Grebes
- within the group of divers, Red-throated Divers were linked with lower longitude values compared to Black-throated Divers
- within the group of grebes, Great Crested Grebes were linked with lowest longitude values, Slavonian Grebes with highest; Red-necked Grebes were intermediate
- within the group of sea ducks, Common Eiders were linked with lowest, Velvet Scoters with highest values; Common Scoters and Long-tailed Ducks were intermediate and differed only slightly from each other
- within the group of auks, Razorbills were linked with lowest longitude values, Black Guillemots with highest; there were only slight differences between Common Guillemots and Razorbills
- within the group of gulls, Common Gulls were linked with lowest longitude values, Greater Black-backed Gulls with highest; Herring Gulls were intermediate

The results fit well with the distribution patterns shown in Figs. 1.2-1.24. Common Eiders, linked with lowest longitude values, are restricted in their distribution to the western parts of the study area up to the Darss pensinsular (Fig. 1.2). Further east, the species occurs rarely and only in low numbers. A similar distribution gradient of Common Eiders was described for Sweden by Nilsson (2005). Velvet Scoters, on the contrary, are mainly distributed in the eastern parts of the study area (Fig. 1.3). Within the groups of divers, grebes and auks, the higher longitude-values of Black-throated Divers, Slavonian Grebes and Black Guillemots indicate a more easterly distribution compared to their related species, respectively, in concordance with the distribution patterns. Longitude can be used as a proxy for salinity, as the Baltic Sea is characterised by strong salinity gradients from west to east (Matthäus, 1996; Telkänranta, 2006). According to Westerbom et al. (2002), a decline in salinity results in a reduction of the size of Common Mussels. Based on this information, Nehls and Struwe-Juhl (1998) suggested that the restriction of Common Eiders to the western Baltic Sea is related to food availability due to the lack of suitable sizes of Common Mussels, the main prey species of Common Eiders, in the eastern parts of the Baltic Sea. For other bird species wintering in the study area, the correlation between distribution patterns and salinity gradients still needs to be further investigated.

Distance to coast

- Red-breasted Mergansers, Great Crested Grebes and Great Cormorants were linked with lowest distance to coast values; Velvet Scoters were linked with highest values, followed by Black Guillemots and Slavonian Grebes
- within the group of divers, Black-throated Divers were linked with lower distance to coast values than Red-throated Divers
- within the group of grebes, Great Crested Grebes were linked with lowest and Slavonian Grebes with highest distance values; Red-necked Grebes were intermediate
- within the group of sea ducks, Common Eiders were linked with lowest distance values, followed by Common Scoters and Long-tailed Ducks; Velvet Scoters were linked with highest distance to coast values
- within the group of auks, Razorbills were linked with lowest and Black Guillemots were linked with highest distance values; Common Guillemots were intermediate and differed only slightly from Black Guillemots
- within the group of gulls, Greater Black-backed Gulls were linked with lowest distance values, Herring Gulls with highest; Common Gulls were intermediate

Comparing the results of the CCA with the distribution maps, it becomes evident that Red-breasted Mergansers, Great Crested Grebes and Great Cormorants are inshore species. They are mainly restricted to coastal waters and only seldom occur in the offshore areas. On the contrary, the distribution hotspot of Velvet Scoters, Black Guillemots and Slavonian Grebes, linked with highest distance to coast values, is situated in the offshore areas of the Pomeranian Bight. Sea ducks are restricted to shallow waters (see below). In the western parts of the study area, these occur mainly along the coast and only seldom extend into offshore areas, Accordingly, Common Eiders, which are restricted to the western Baltic Sea, occur in lower distances to the coast than the other sea duck species, which also winter in large numbers in the Pomeranian Bight with the two shallow banks Odra Bank and Adlergrund far away from the coast.

Sediment type

- Red-throated Divers were linked with finest, Red-breasted Mergansers with coarsest sediment types
- within the group of divers, Black-throated Divers were linked with finer sediment types than Red-throated Divers

- within the group of grebes, Great-crested Grebes were linked with coarsest sediment types; there was almost no difference between Slavonian and Red-necked Grebes
- within the group of sea ducks, Common Scoters were linked with finest sediment types, followed by Velvet Scoters and Long-tailed Ducks; Common Eider were linked with coarsest sediment types
- within the group of auks, Black Guillemots were linked with coarsest sediment types; there was almost no difference between Common Guillemots and Razorbills
- within the group of gulls, Herring Gulls were linked with finest, Greater Black-backed Gulls with coarsest sediment types; Common Gulls were intermediate

Sediment type can be regarded as a proxy for the availability of the preferred prey on or near the sea bottom and should thus be most relevant for benthic or benthopelagic feeders. Different substrate types vary in their benthic communities and thus in their importance for birds. Of the bird community in the study area, sea ducks obtain benthic and many other species benthopelagic prey (Table 1.1), and sediment type is supposed to be of greatest influence on the distribution of these species. Some information in this context is available for sea ducks. The majority of their diet comprises of benthic bivalves, although other invertebrate species as well as fish or fish spawn can also be found locally in the prey composition (compiled e.g. in Fox, 2003; Mendel et al., 2008). Because the biomass of available molluscs is comparable low in muddy sediments, sea ducks concentrate over sand, muddy sand or lag sediments (Kirchhoff, 1981). The main prey of Common Eiders in the Baltic Sea are Common Mussels, a species that is often attached to hard substrates like submerged rock reefs. Accordingly, this species was linked with highest sediment values in the CCA, i.e. more coarse or harder sediment types than the other sea ducks. This is in concordance with an analysis from Mendel et al. (2007), who found a preference of Common Eiders for areas with pebbly and stony substrates in the southern Baltic Sea. Within the study area, large proportions of the diet of Long-tailed Ducks consist of sand-dwelling bivalve species like Sand Gaper, Baltic Tellin or Common Cockles (see Mendel et al., 2008). Consequently, this sea duck is often found in waters over coarse or fine sand (Mendel et al., 2007), albeit they also occur locally over hard substrates, where they exploit Common Mussel banks (Kube and Skov, 1996). This fits well with the second high values of Long-tailed Ducks in the CCA sediment analysis. Common and Velvet Scoters, linked with lowest sediment values, also mainly forage on soft-bottom benthos organisms. According to Fox (2003), they select shallow in- or epi-faunal species which especially live in sandy substrates. In the western Baltic Sea, Common Scoters were predominantly found over sand or sandy mud by Kirchhoff (1979). Locally, Common Scoters seem to consume also large amounts of Common Mussels (Madsen, 1954), but Fox (2003) supposed that they were not taken from rocky substrates, as Common Mussels were also locally found in sandy or muddy areas where they attached themselves e.g. to the shells of conspecifics. Thus, the lowest sediment values in the CCA correspond well with the preferred distribution and foraging preferences of scoters over finer sediments. Information on sediment preferences of Slavonian Grebes is given in **Chapter II**.

Water depth

- Red-breasted Mergansers were linked with lowest water depths, followed by Great Cormorants, Great Crested Grebes, Long-tailed Ducks and Common Eiders; Red-throated Divers were linked with highest water depths, followed by Razorbills and Common Guillemots
- within the group of divers, Black-throated Divers were linked with lower water depths than Red-throated Divers
- within the group of grebes, Great Crested Grebes were linked with lowest, Red-necked Grebes with highest water depths; Slavonian Grebes were intermediate
- within the group of sea ducks, Common Scoters were linked with highest water depths, followed by Velvet Scoters, Common Eiders and Long-tailed Ducks; differences between the species were only small
- within the group of auks, Black Guillemots were linked with lowest water depths; there were only slight differences between Razorbills and Common Guillemots
- within the group of gulls, Greater Black-backed Gulls were linked with lowest, Herring Gulls with highest water depths; Common Gulls were intermediate

Water depth as a habitat factor is mainly related to diet preferences and feeding strategies of the different species. Diving for food involves various physiological challenges for endothermic animals, and diving depth has a particular strong effect on the energetic costs of foraging (e.g. Guillemette et al., 2004; Enstipp et al., 2006). Thus, foraging at the sea bottom implies a trade-off between the energetic value of food obtained from a dive versus the costs of diving and handling prey (Fox, 2003). Furthermore, during the winter season, lower air and water temperatures cause high daily energy expenditures due to e.g. the maintenance of body temperature, higher diving activities to obtain more food or the heating of ingested cold prey (e.g. de Vries and van Eerden, 1995; Wiersma et al., 1995). On the distribution of surface feeders (like gulls) or pelagic feeders (like e.g. Razorbills or Common Guillemots), water depth should have no or only little influence. These species can thus also occur in areas with deeper water (see e.g. Figs. 1.13, 1.14) and were linked with high depth values in the CCA. Black Guillemots are benthopelagic feeders and thus they were linked to lower water depths than the other, more pelagic auk species. Great Cormorants, Red-breasted Mergansers and Great Crested Grebes are supposed to feed mainly on benthopelagic prey species, but their very low depth values in the CCA could also be a result of their strong restriction to coastal areas, which are very shallow throughout the study area. The very high value of Red-throated Divers can not yet be explained. According to Guse et al. (2009), birds wintering in the Pomeranian Bight mainly feed on benthopelagic fish species. However, parts of their diet also consist of Atlantic Herring which they might capture in the water column, or diet composition might differ between different regions of the study area.

Sea ducks are classical benthic feeders. The diet of the four species wintering in the southern Baltic Sea mainly consists of molluscs and small proportions of other invertebrates like crustaceans and polychaete worms. Additionally, small (benthic) fishes or fish eggs are taken (see Mendel et al., 2008). To forage on benthic invertebrates, sea ducks have to dive to the sea bottom, where they take prey items on or within the upper few centimetres of the sediment or over mussel banks. Thus, beside the occurrence of sufficiently abundant and predictable profitable feeding resources, water depth constitutes an important parameter of their habitat selection (see e.g. Durinck et al., 1994; Kube and Skov, 1996; Fox, 2003). The analysis of the occurrence of sea ducks with respect to water depth in the study area revealed that numbers recorded within the observation transect were highest in waters between 6 to 10 metres deep. In all four species, numbers gradually decreased with increasing water depth and more than 90% of all birds were recorded in waters up to 20 m depth, respectively (Table 1.4).

Table 1.4. Occurrence of sea ducks in areas with different water depths in the southern Baltic Sea in winter 2000-2008. Data are corrected for survey effort. Areas with water depths lower than 6 m have not been sufficiently sampled and were thus excluded from the analysis.

	Water depth					
	6-10 m	11-15 m	16-20 m	21-30 m	31-40 m	> 40 m
Common Eider N = 44726	48.1%	24.4%	20.2%	7.3%	0%	0%
Long-tailed Duck N = 73397	50.2%	40.5%	7.4%	1.8%	0.1%	0%
Common Scoter N = 39762	39.2%	38.9%	17.0%	4.6%	0.2%	0.1%
Velvet Scoter N = 14387	51.5%	34.9%	7.0%	6.6%	0%	0%

These results are in good concordance with other studies (e.g. Durinck et al., 1994; Stempniewicz, 1995; Fox, 2003). Although there is considerable variation in the description of depth zones exploited by sea ducks, which probably reflects differences in local water column depth and benthic community types (Fox, 2003), most authors are consistent with the fact that sea ducks preferably forage in shallow waters up to 20 m deep and only seldom occur in areas more than 30 m deep. They are expected to select the shallowest foraging areas possible that contain the highest available suitable prey mass (Fox, 2003). It could thus be concluded that sea ducks are not randomly distributed at sea, but, while selecting specific benthic communities with suitable biomass of harvestable prey (see e.g. Bräger et al., 1995; Kube and Skov, 1996), the energetic constraints of diving in cold water versus derived energy gain forces them to choose shallow water areas as their preferred habitat (Fox, 2003).

Influence of fishing activities on the distribution of gulls

Gulls constitute a group of birds that differ considerably in their ecological habits compared to the other species wintering in the southern Baltic Sea. As they can only exploit the first few centimetres of the water column, factors like water depth or bottom sediment type probably do not influence their habitat selection. Furthermore, the distribution of Herring, Greater Black-backed and Common Gulls within the study area showed no apparent preferences regarding distance to coast or longitude (Figs. 1.16-1.18). The three species are opportunistic feeders, and apart from foraging in marine habitats they have learned to exploit terrestrial as well as anthropogenic food sources like litter or fishery waste (e.g. Garthe et al., 2000).

Most types of fisheries produce considerable amounts of discards and offal that are jettisoned at sea. They comprise of undersized target fish and shellfish, species which quotas are exceeded or which are of low financial value relative to other hauls, as well as of offal produced during fish cleaning and various invertebrate species (Garthe et al., 1999). Many studies have described the utilisation of discards and offal by seabirds worldwide (for reviews see e.g. Garthe et al., 1996; Tasker et al., 2000; Furness, 2003). In some areas and species, the availability of fishery waste was reported to influence not only the distribution of birds at sea, but also breeding parameters, numbers of resting birds, diel activity patterns and diet (e.g. Garthe and Hüppop, 1996; Oro, 1996; Oro et al., 1996; Garthe et al., 1999; Hüppop and Wurm, 2000). For the total Baltic Sea, the amount of fish and fish offal annually discarded into the sea has been estimated to be about 26 000 to 30 000 t (ICES, 2000). Garthe and Scherp (2003) calculated about 6 500 t of fish discards and 16 000 t of offal annually consumed by seabirds in Baltic waters. In their study about the utilisation of discards and offal from commercial fisheries by seabirds, Herring Gulls were clearly the most numerous scavenging species in all areas and seasons investigated, followed by Greater Black-backed, Lesser Black-backed and Common Gulls. These results could be confirmed by the present analysis: in all periods considered, the proportion of Herring Gulls was highest among all species attending fishing vessels, ranging from 50% of all birds recorded within the observation transect in spring to 7% in summer (Table 1.5). Greater Black-backed Gulls were the second most frequent species in summer, autumn and winter, Lesser Black-backed Gulls in spring. However, the latter species occurred in the southern Baltic Sea only in very low numbers, in contrast to the offshore areas of the German North Sea, where Lesser Black-backed Gulls are the most numerous gull species from spring to autumn (Garthe et al., 2007) and one of the most frequently occurring species behind fishing vessels (Garthe and Hüppop, 1998; Schwemmer and Garthe, 2005).

Table 1.5. Number of gull species recorded within the observation transect (total) and percentage of birds associated with fishing vessels (ass. fishery) in different seasons in the southern Baltic Sea.

Species	Dec. - Feb.		Mar. - May		June - Aug.		Sept. - Nov.	
	total	ass. fishery (%)	total	ass. fishery (%)	total	ass. fishery (%)	total	ass. fishery (%)
Little Gull	23	0	63	0	1010	0	260	0
Black-headed Gull	49	0	229	22.7	67	0	189	0.5
Common Gull	513	2.0	399	8.3	72	0	148	19.6
Lesser Black-backed Gull	2	0	14	42.9	13	0	14	0
Herring Gull	3 946	30.5	4 117	50.0	374	7.0	2 211	36.7
Greater Black-backed Gull	791	11.3	350	22.3	94	5.3	291	26.1

Due to the large proportion of Herring Gulls feeding on fishery waste, the occurrence of fishing vessels is likely to influence their distribution patterns. During an aerial survey in the southern Baltic Sea in summer 2004, large concentrations were observed behind or in the vicinity of fishing boats (Fig. 1.26). Greater Black-backed Gulls occurred in much lower numbers, but were also often recorded in association with fishing activities (Fig. 1.27).

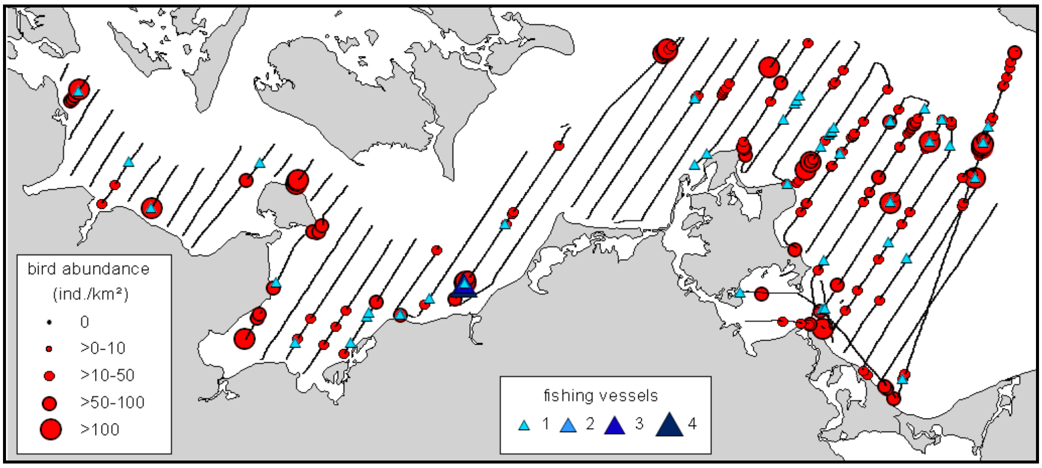

Fig. 1.26. Distribution of Herring Gulls and occurrence of fishing vessels in the southern Baltic Sea in summer 2004, based on aerial surveys.

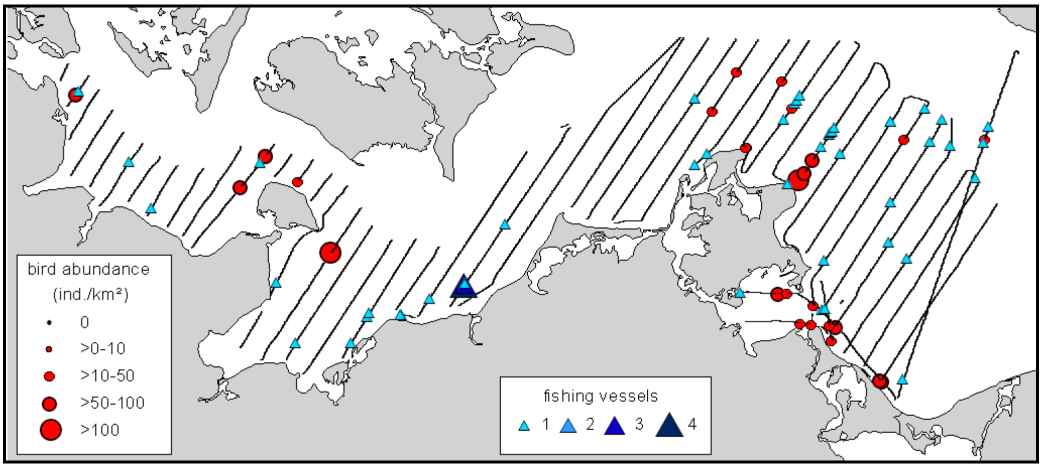

Fig. 1.27. Distribution of Greater Black-backed Gulls and occurrence of fishing vessels in the southern Baltic Sea in summer 2004, based on aerial surveys.

Beside gulls, only few Great Cormorants, two Sandwich Terns and one Common Guillemot were observed attending fishing boats during ship-based surveys in the period 2000 to 2008. With regard to scavenging seabirds, the Baltic Sea can therefore be considered as a one- or few-species system with gulls dominating as ship followers and consumers of fishery waste, as already stated by Garthe and Scherp (2003). Generally, gulls are the outstanding scavengers of fishery waste in the shelf seas and coastal areas, like in the North Sea (e.g. Garthe and Hüppop, 1994), the western Mediterranean Sea (e.g. Oro and Ruiz, 1997) or in the southern Baltic Sea (Garthe and Scherp, 2003; this study).

Conclusions

In this chapter, the seasonal distribution of birds in the southern Baltic Sea and some factors causing the observed distribution patterns were described. The avifauna of the southern Baltic Sea is dominated by the occurrence of (water-) bird species, which mainly breed in freshwater or sometimes brackish waters in the tundra and taiga zones of Fennoscandia and Russia and spend the winter in marine areas. Some species, like Great Crested and Red-necked Grebes, Great Cormorants, Red-breasted Mergansers and Common Eiders, have also breeding colonies along the coast of the study area. Sea ducks are the most abundant and characteristic birds of the Baltic Sea avifauna and have been studied most intensively of all species so far. Auks are the only truly pelagic seabird group occurring in the southern Baltic Sea. Individuals wintering in the study area mainly originate from the Baltic Sea breeding populations, but especially in the western parts, Common Guillemots and Razorbills from the Atlantic populations may also be found (Durinck et al., 1994; Wernham et al., 2002).

Food availability is one of the key factors determining the distribution of seabirds at sea (e.g. Schneider and Piatt, 1986; Hunt, 1990; Shealer, 2002). The different species occurring in the southern Baltic Sea are not evenly distributed, but, according to their feeding techniques and diet preferences, they show clear preferences for certain areas and habitats. Distribution patterns thus reflect areas that hold sufficient amounts of accessible food supplies for the respective species (see Durinck et al., 1994). For birds feeding on benthic or benthopelagic prey species, like sea ducks and grebes, water depth and bottom sediment type are important factors for the habitat selection. These species are restricted to shallow areas (mainly < 20 m deep) and, depending on diet preferences, occur over different bottom substrates. Because shallow waters often extend along the shore, the birds concentrate in the coastal areas. However, as the southern Baltic Sea area comprises of several shallow banks far away from the coast, benthic feeding species can also be found in certain offshore areas. Piscivorous birds foraging on schools of pelagic fish, like some auk species, are not restricted to shallow waters and can thus also occur in deeper offshore areas. Surface feeding species, represented in the study area by gulls, depend on the availability of prey in the upper few centimetres of the water column. While some species also use terrestrial feeding habitats, e.g. Common and Common Black-headed Gulls (Hartwig and Müller-Jensen, 1980; Kubetzki, 2001), or benefit from the accumulation of prey along hydrographical structures like fronts or foam lines, e.g. Little Gulls (FTZ, unpubl. data), the large *Larus*-species have strongly adapted to the use of discards and offal from fishing vessels. They are widely distributed throughout the study area and the distribution patterns are influenced by the occurrence of human fishing activities.

2 A freshwater species wintering in a brackish environment: habitat selection and diet of Slavonian Grebes in the southern Baltic Sea

Abstract

After the breeding season, Slavonian Grebes leave their freshwater breeding habitats and migrate to wintering grounds in marine or brackish waters. The most important wintering area in northwestern Europe is located in the southern Baltic Sea, with largest concentrations in the offshore area of the Pomeranian Bight. Analysis of ship-based surveys revealed that the habitat selection of Slavonian Grebes in this brackish area is significantly influenced by water depth and bottom sediment type. The grebes prefer shallow waters of 4-14 m depth and occur only over sandy sediments. While the diving depths of endothermic animals is limited due to energetic constraints and thermoregulation, sediment type is regarded to be a proxy for food choice. The diet of Slavonian Grebes in the Pomeranian Bight consists mainly of demersal gobies (Gobiidae) that frequently occur over sandy bottom substrates.

Introduction

Apart from their morphological and physiological adaptations to the marine environment, there are various physical, biological and anthropogenic factors that influence the distribution of birds at sea (e.g. Furness and Monaghan, 1987; Shealer, 2002). During the breeding season, the occurrence and location of suitable nesting sites, in combination with sufficient food supply, predominantly determine the distribution of seabirds within their geographical breeding range. In winter, however, they may be able to disperse to a much wider range of habitats. As seabirds interact closely with the marine environment, physical conditions and processes at sea substantially influence their distribution (e.g. Briggs et al., 1987; Hunt and Schneider, 1987; Haney and Solow, 1992; Ainley et al., 2005). However, these factors affect seabirds only indirectly, while food availability and foraging options are the dominant factors underlying the relationship between seabirds and physical parameters at sea (Hunt and Schneider, 1987; Shealer, 2002).

The Slavonian Grebe is a small limnic waterbird species that mainly breeds in the boreal zone of the Holarctic. The breeding grounds are inland freshwater habitats: mostly isolated eutrophic or mixotrophic pools and ponds, marshes as well as sheltered bays and inlets of larger lakes. Occasionally, breeding is also recorded on brackish sounds, highmoor and crater lakes or in open oligotrophic waters with sterile exposed shores (Fjeldså, 1973; Birds of the Western Palaearctic interactive, 2004; Fjeldså, 2004). Around the Baltic Sea, the species is mainly restricted to small and shallow mixotrophic forest lakes, with open water interrupted by patchy, not too high and dense vegetation (Fjeldså, 1973; Fjeldså, 2004). Winter grounds, on the contrary, are predominantly marine, often in coastal or inshore waters and estuaries, but also in offshore areas. Only small numbers winter on large freshwater lakes (Birds of the Western Palearctic interactive, 2004; Fjeldså, 2004). Thus, this freshwater breeding waterbird species turns into a seabird during winter.

Slavonian Grebes are small and quite inconspicuous in non-breeding plumage, and due to the fact that the winter localities may also be situated far away from the coast, they are difficult to discover and investigate (see also Fjeldså, 2004). Ship-based surveys revealed a large winter population of Slavonian Grebes in the offshore area of the Pomeranian Bight in the southern Baltic Sea (Durinck et al., 1994; Skov et al., 2000; Sonntag et al., 2006), which, according to Durinck et al. (1994), is the most important wintering area for this species in northwestern Europe.

At the breeding sites, Slavonian Grebes mainly feed in shallow water and perform only shallow dives up to 2 m depth (Fjeldså, 2004). In the offshore area of the Pomeranian Bight, however, water depth reaches values up to 20 m. Another important wintering area with fairly deep water is in the archipelago from 62° N up to the Arctic Circle in northwestern Norway (Fjeldså, 2004). Diving depth has a strong effect on the energetic costs of foraging in endothermic animals (e.g. Enstipp et al., 2006). Water depth should thus constitute an important parameter for the habitat choice of Slavonian Grebes in the wintering areas, as has already been described for other species in the southern Baltic Sea, e.g. benthivorous sea ducks (Kube and Skov, 1996). However, food availability is considered to be the key factor determining the distribution of seabirds at sea. We chose bottom sediment type as a proxy for the availability of the preferred prey of the grebes on/near the sea bottom. Based on eight years of extensive work at sea, we present in this paper detailed information on the occurrence of Slavonian Grebes in the Baltic Sea and test the hypothesis that water depth and bottom sediment type are relevant factors for the habitat selection of this species in its most important wintering area in northwestern Europe. To evaluate the results regarding bottom sediment, we additionally studied the diet of individuals drowned in set nets in the Pomeranian Bight.

Methods

Study area

The Baltic Sea in northeastern Europe is one of the largest brackish water seas in the world and with a mean depth of 55 m a very shallow water body. Salinity is one of the most important influencing factors and the Baltic Sea is characterised by strong salinity gradients from west to east (Telkänranta, 2006). This study focuses on the southern part of the Baltic Sea (Fig. 2.1). At a smaller scale, the Pomeranian Bight, bordered by the coasts of Germany and Poland in the west and south and extending to the north approximately up to the 20 m water depth contour (Lass et al., 2001), is of particular interest (large box in Fig. 2.1). The bight is characterised by the largest riverine freshwater influx into the western Baltic Sea which strongly influences its hydrographic regime and leads to an average salinity of 7.5 psu (Lass et al., 2001). The shallow Odra Bank comprises the central part of the offshore area. Water depth contour lines and distribution of bottom sediment types for the study areas are shown in Fig. 2.1 and Fig. 2.2, respectively.

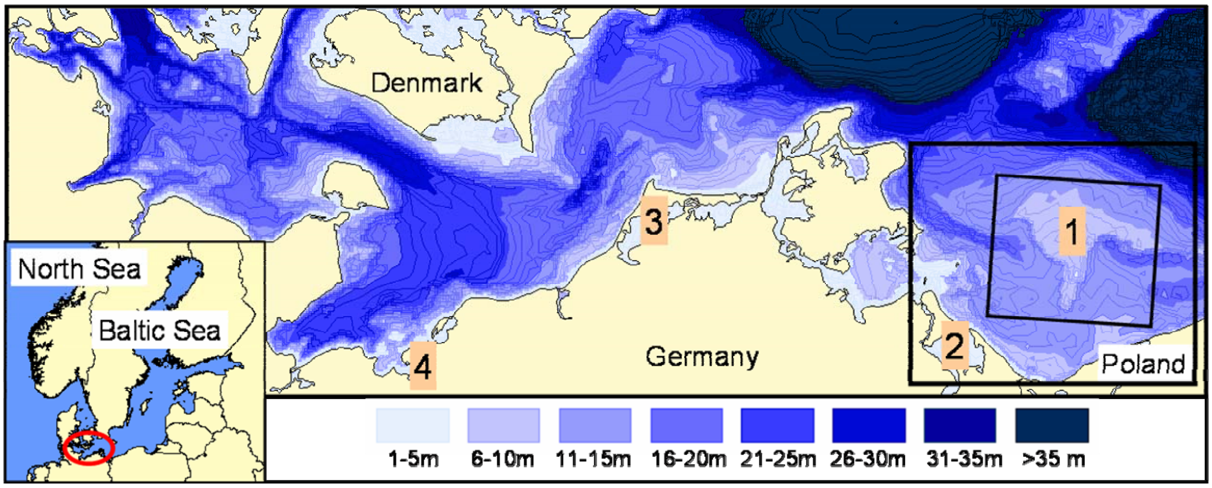

Fig. 2.1. Location and water depths of the study area in the southern Baltic Sea, with the Pomeranian Bight (large box) and the Oderbox (small box). The thin contour lines correspond to areas with equal water depths (isobathes). The numbers describe localities referred to in the text: 1) Odra Bank, 2) Usedom peninsula, 3) Darss-Zingst peninsula, 4) Wismar Bay.

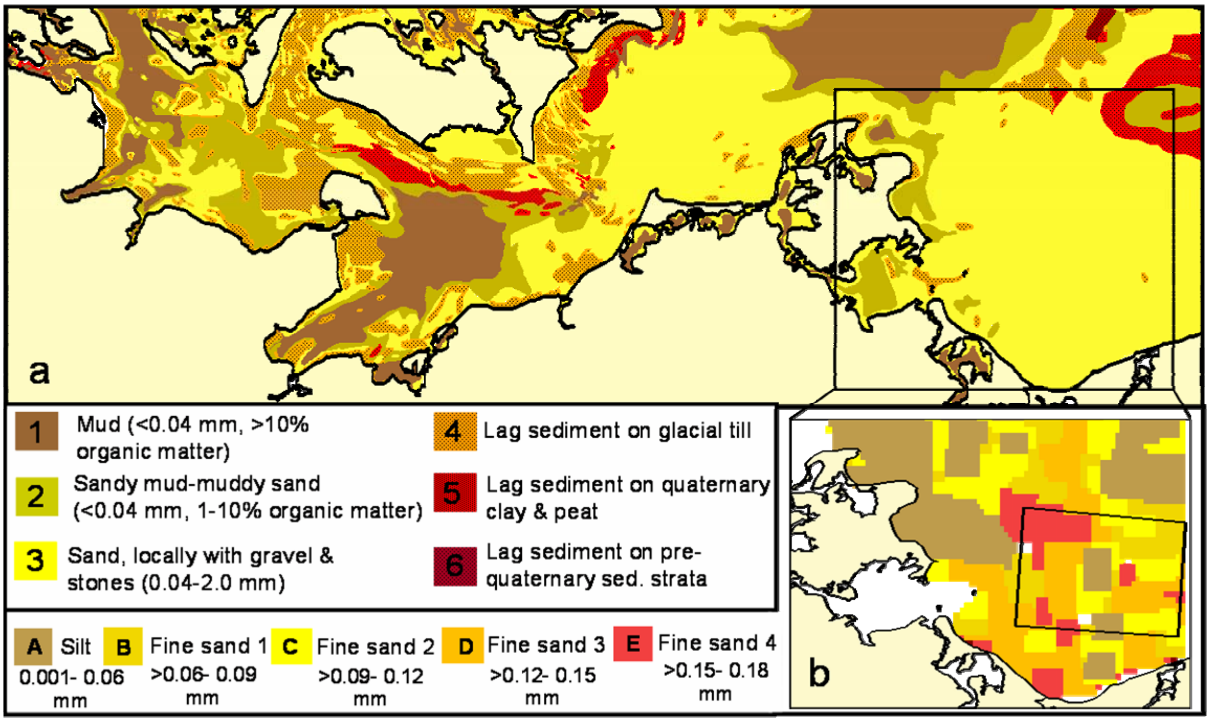

Fig. 2.2. Bottom sediment types in the a) southwestern Baltic Sea and in the b) Pomeranian Bight. Data for the Pomeranian Bight are based on a high resolution classification of the main sediment type sand into 5 sub-classes according to grain size. The black box in Fig. 2.2b indicates the Oderbox used for the small-scale habitat analysis.

Recording of birds at sea

The distribution of Slavonian Grebes was studied by ship-based transect counts following an internationally standardised method for northwest European waters (e.g. Tasker et al., 1984; Camphuysen and Garthe, 2004). From the top deck or bridge-wing of the research vessel two or three observers recorded all flying and swimming individuals within a 300 m wide band transect running parallel to the ship's track on one or both sides. The observers searched for Slavonian Grebes with unaided eyes, but in addition the census area was regularly scanned with binoculars to look for birds diving or flushing in front of the approaching vessel. For flying individuals the *snapshot method* according to Tasker et al. (1984) was applied to avoid overestimates. The length of the transect segments ahead was the distance the ship covered in successive 1-minute counting intervals and therefore depended on ship speed. The surveyed area was calculated from the transect length and the transect width (300 m). Geographic positions were recorded in 1-minute intervals.

Distribution maps

All data used in this study were taken from the German *Seabirds at Sea* database version 5.12 (June 2008; Garthe et al., 2007) that contains more than 30 000 ship kilometres in the southern Baltic Sea for the years 2000 to 2008. Counting intervals with a sea state higher than four (according to *Beaufort* scale; Dietrich et al., 1975) were excluded from analysis as such conditions prevent a thorough recording of small bird species like Slavonian Grebes. Distribution maps are based on abundances, i.e. number of individuals per area surveyed for each counting interval. This way, data were corrected for counting effort. Due to the fact that some swimming birds, particularly those in the more distant parts of the transect bands, might have been overlooked, we applied a correction factor of 1.4 according to Garthe (2003) by multiplying the abundance of swimming birds. Numbers of flying birds were not corrected. Maps were created by radial basis function interpolation in Surfer 8.0, using *multiquadratic* as function method and 20 km as search radius. Visualisation was based on 3x3 km grid cells.

Phenology

To study the seasonal dynamics of Slavonian Grebes we selected an area of the southern Baltic Sea, forthcoming referred to as “Oderbox”. This box covers an area a) within the core distribution of Slavonian Grebes, b) which was intensively studied (high counting effort) and c) with reasonably similar habitat parameters, i.e. water depth and bottom sediment type. The box is situated in the offshore area of the Pomeranian Bight covering the shallow bank Odra Bank (small box in Fig. 2.1). For every day in the study period 2000 to 2008 we calculated the abundance of Slavonian Grebes as number of birds per area surveyed. Only days with a survey effort of at least 5 km² within the box area were included in the analysis. Sample size varied between one day (June) and nine days (April) per month, with a total of 43 days. Monthly means ± confidence intervals are based on bootstrapping 10 000 times the original values.

Diet

We analysed the diet of four Slavonian Grebes accidentally caught and drowned in set nets in the Pomeranian Bight off the coast of the Usedom peninsula (see Fig. 2.1). The sample comprised one female of unknown age (drowned in January 2002), one immature female (February 2005), one adult female (April 2005) and one immature male (April 2005). Following a scoring according to van Franeker (2004), body condition was good in three birds and moderate in one bird. Stomach and guts were removed from the dissected birds and all prey items were collected. Fish remnants were identified to the lowest possible taxon based on otoliths or hard parts of the skeleton like premaxillae and vertebrae according to Härkönen (1986), Watt et al. (1997), Leopold et al. (2001) and an own reference collection. Invertebrates were identified by jaws (polychaete worms), carapace elements (crustaceans) or chitinous parts of the exoskeleton (insects). Prey numbers were calculated as the smallest definite number by considering all remnants of a given species. Items that occur in pairs (like otoliths or jaws) were paired based on species, orientation, size, wear and shape. Otoliths were measured to derive original fish length and biomass using regressions obtained from Leopold et al. (2001) after correction for wear. To assess the biomass of unidentified clupeids, the average value of herring and sprat was calculated as these are the most frequent clupeid fish species in the Pomeranian Bight. Unidentified fishes were excluded from biomass calculations as were crustaceans, as we had no indications of the size of crustaceans found in the samples. Regressions for polychaete worms were adopted from Debus and Winkler (1996).

As is always the case in grebes, the dietary remains in the stomachs of our samples were embedded in a feather ball that also formed a plug in the pyloric exit and prevented the passage of hard prey items into the intestines (see e.g. Piersma and van Eerden, 1989; Fjeldså, 2004). Therefore, the guts only contained a few unspecific fish bones and a single heavily worn fragment of an otolith and were thus excluded from further analyses.

Due to the low sample size the results were not analysed statistically.

Habitat selection

Water depth and bottom sediment type were selected as two abiotic factors with a potential influence on the distribution of Slavonian Grebes in the southern Baltic Sea. Data on water depth within the study area were obtained from the Danish Hydraulic Institute (DHI). These data are classified into 1-metre categories and visualized in Fig. 2.1. Sediment data were obtained from the Geological Survey of Denmark and Greenland (GEUS; Hermansen and Jensen, 2000). These data are classified into six different sediment types based on grain size and content of organic material (Fig. 2.2a). Additionally, we used high resolution data for the Oderbox area that comprise a more detailed classification of the main sediment type sand into 5 sub-classes (grain size 0.001 to 0.180 mm, Fig. 2.2b). They were provided by the Institute for Applied Ecology (IfAÖ) Ltd, Neu Broderstorf, within the IMKONOS project.

The influence of water depth and bottom sediment type on Slavonian Grebe distribution was tested by modelling the abundance of birds (individuals per area surveyed) in relation to both factors with a generalised additive model (GAM; Wood, 2006) using the *mgcv* package (Wood, 2000) in version 2.8.1 of R (R Development Core Team, 2008). Bird abundance served as response variable while water depth and sediment type were used as covariables. A cubic regression spline was used as smoothing function for the covariate water depth and a thin plate regression spline for the covariate sediment type. Because the latter variable included only a few different categories, the degrees of freedom for curve smoothing were restricted to three. As the data set was based on count data, the *Poisson* function should usually form the basis of the analysis (Zuur et al., 2007). However, to prevent overdispersion, *quasi-Poisson* was selected as underlying function in the model frame. In a first step we conducted the habitat analysis for the total study area. At a smaller scale, we further analysed the core distribution area within the Oderbox. For both areas calculations were performed for the total time period where Slavonian Grebes occurred in the study area (October to April) as well as separately for three time periods based on the results of the phenology analysis: autumn (October, November), winter (December to February) and spring (March, April).

In the process of developing our habitat model with the available data set, two aspects had to be considered. Firstly, in the total set of more than 64 000 data, the occurrence of Slavonian Grebes was a very rare event compared to a large number of zero-counts. Standard statistical functions might thus be inappropriate. In addition to the (original) model described above, we therefore applied a two-stage GAM according to Jensen et al. (2005). In the first stage of this analysis, presence or absence of Slavonian Grebes in relation to both habitat factors were modelled using a binomial distribution function. In the second stage only presence data (bird abundance > 0) were modelled as a function of the environmental covariates using the *quasi-Poisson* distribution. Afterwards, the predicted bird abundance was calculated as the product of both stages (combined model). The residuals of the original and combined model were then compared using a Student's t test. As there were no significant differences between these residuals for the total data set as well as the three seasons ($p > 0.995$, respectively), we selected the more simple, original model for our analysis.

Secondly, bird numbers are probably spatially autocorrelated. To avoid spatial autocorrelation within the model, an autocorrelation structure for latitude and longitude usually has to be included, using a generalised additive mixed model (GAMM) with the autocorrelation structure *corEXP* for spatial data (Pinheiro and Bates, 2000). However, by comparing the residuals of the model with and without this autocorrelation structure, we found no difference between both model types. This held true for the model of the total study area ($R^2 > 0.996$) as well as for the Oderbox

($R^2 > 0.998$) and was separately tested for the total data set and the three different time periods autumn, winter and spring. Thus, to keep the model as simple as possible, no autocorrelation structure was applied.

Results

Distribution and phenology

Slavonian Grebes occurred in the southern Baltic Sea in winter and during migration periods. So far, we recorded only a single bird in the summer months. A clear hotspot occurred in the Pomeranian Bight, with largest numbers in the offshore area around the shallow Odra Bank, in about 30 to 50 km distance to the coast. This core distribution area was pronounced in winter as well as during migration (Fig. 2.3a-c). Locally moderate numbers were observed north of the Darss-Zingst peninsula in winter and spring while in more western parts of the study area only few birds were recorded. During spring migration, the coast of Usedom was an important staging area in addition to the hotspot around the Odra Bank. Most observations of Slavonian Grebes comprised single individuals or two birds, and only few aggregations of three or four birds were recorded.

The analysis within the Oderbox revealed a more detailed seasonal pattern (Fig. 2.4). After leaving their breeding localities, Slavonian Grebes first appeared at the Odra Bank in October. Autumn migration peaked in November while numbers were lower during the winter resting period. Birds left the southern Baltic Sea in March and April. Compared to autumn, numbers during spring migration were considerably lower.

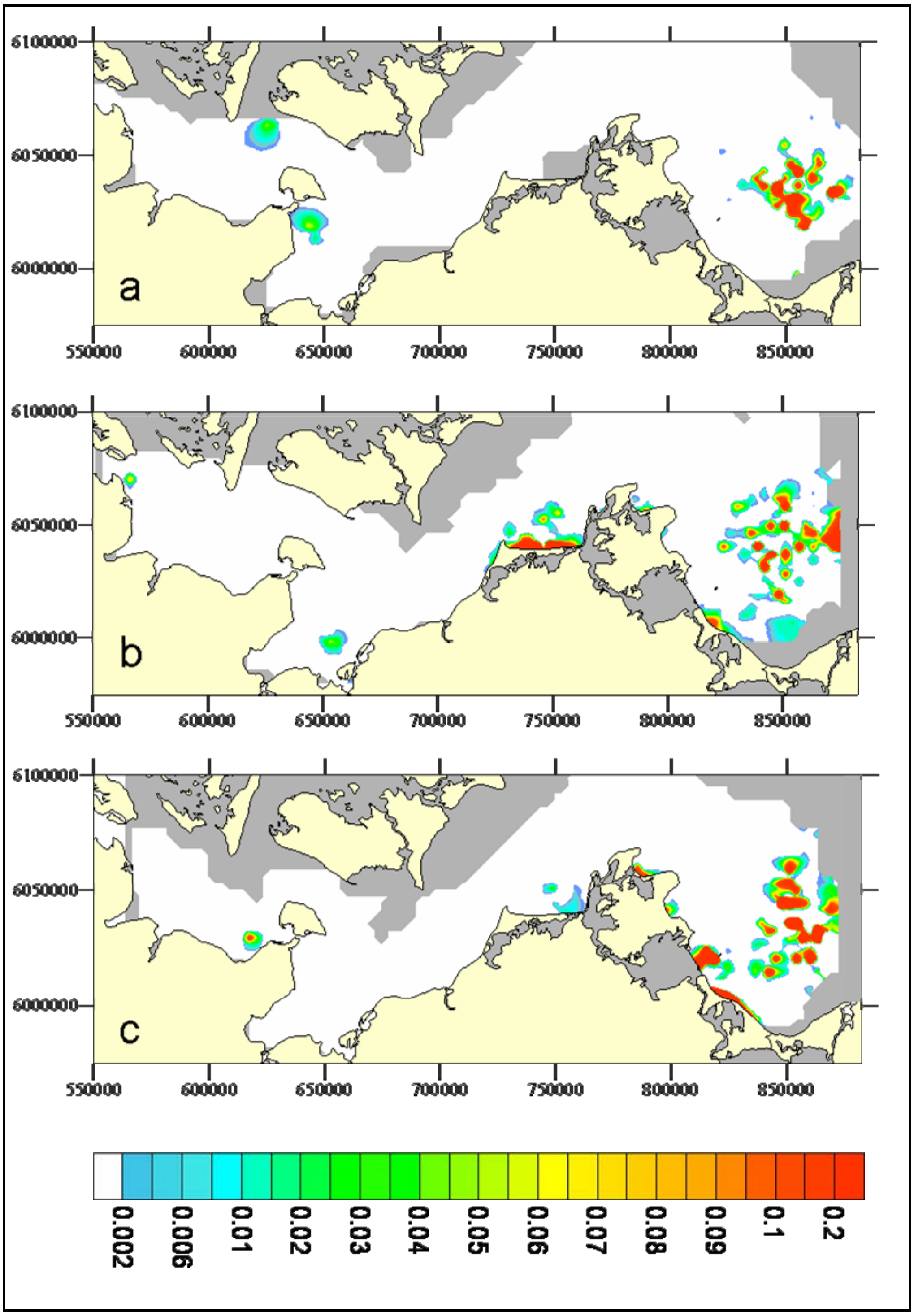

Fig. 2.3. Distribution of Slavonian Grebes in the southern Baltic Sea during a) autumn (Oct.-Nov.), b) winter (Dec.-Feb.) and c) spring (Mar.-Apr.) 2000-2008. The colour scale indicates the abundance as birds/km² on a logarithmic scale. Grey colours mark areas that were not studied.

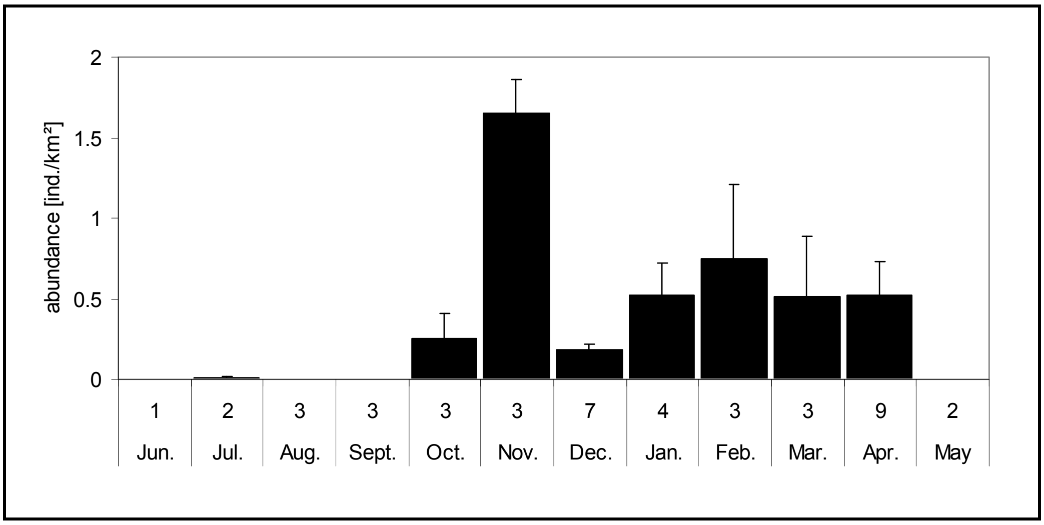

Fig. 2.4. Seasonal abundance (with 95% confidence interval) of Slavonian Grebes within the Oderbox area (small box in Fig. 2.1). Numbers on the x-axis indicate the sample size (days surveyed during each month).

Diet and prey size

All four stomachs contained dietary remains. A total of 576 fish specimens (76% of all prey remnants) from three different families could be identified (Table 2.1). Gobies (Common Goby and Sand Goby) occurred most frequently in the stomachs and accounted for 95% of all fish remains, followed by sandeel comprising 4%. Most sandeels could not be identified to species level as the otoliths found in the stomachs were too heavily worn. All stomachs contained jaws of polychaete worms that accounted for 23% of all dietary remains. Fragments of insects were found in the stomachs of the two birds drowned in April, but they were too heavily worn to be counted.

Gobies dominated the diet not only with regard to numerical abundance but also concerning biomass (Table 2.1). They accounted for almost 87% of the total prey biomass. Polychaete worms were found in the stomachs in relatively high numbers, but their proportion of the total prey biomass was less than 1% due to their small median length of only 1.3 cm (N = 84 individuals measured). Total length of gobies ranged from 3.1 to 5.7 cm (N = 230). Consumed Common Gobies were slightly smaller than Sand Gobies. Sandeels were considerably longer than gobies with a total length of 5.7 to 14.5 cm (N = 13).

Although there was considerable variation in the total number of prey items found in each stomach, the overall results held true for all four individual birds: gobies were the most important prey regarding numerical abundance as well as biomass.

Table 2.1. Diet of four Slavonian Grebes drowned in set nets in the Pomeranian Bight. Frequency of occurrence is the number of stomachs containing the respective prey category. Numerical abundance is the total number of the respective prey category (brackets indicate the percentage of the total number of items). Biomass is the percentage of total biomass calculated for all stomachs.

Prey category			Frequency of occurrence	Numerical abundance [%]	Biomass (%)
Fish					
	Gobies (Gobiidae)				
		Common Goby	4	175 [23.1]	17.4
		Sand Goby	2	14 [1.8]	1.2
		Common / Sand Goby	4	360 [47.6]	68.0
	Sandeel (Ammodytidae)				
		Lesser Sandeel	2	3 [0.4]	0.9
		Great Sandeel	1	1 [0.1]	1.7
		Sandeel indet.	3	20 [2.6]	10.3
	Clupeids (Clupeidae)		1	1 [0.1]	0.1
	Fish indet.		1	2 [0.3]	-
Polychaete worms			4	174 [23.0]	0.4
Crustaceans			4	3 [0.4]	-
		Common Shrimp	3	4 [0.5]	-
Insects			2	?	-

Habitat selection

Water depth and bottom sediment type both proved to have a clear effect on the habitat choice of Slavonian Grebes in the southern Baltic Sea. The results of the model revealed a significant influence of the two physical habitat factors on bird distribution in all time periods analysed except for spring when the influence of bottom sediment type was less pronounced (Table 2.2). The two variables explained between 14.8% (winter) and 32.1% (autumn) of the variation in abundance.

Preferred water depth ranged from 4 to 14 m with optimum values at approximately 6-9 m (Fig. 2.5a). 93% of all birds were observed in waters less than 15 m deep and only one bird was recorded in waters more than 20 m deep. Preferred bottom sediment type was sand (category 3, Fig. 2.5b) where 99% of all birds occurred. The few remaining individuals were observed in areas with sediment type 4 (lag sediment on glacial till). Based on the result that Slavonian Grebes occurred only in areas with water depths up to 20 m, we repeated the model excluding all data with higher water depths to re-evaluate the influence of sediment type. With these restricted data the model resulted in the same findings as the model based on the total data set (Table 2.2).

Although water depth and bottom sediment type had a significant influence on the distribution of Slavonian Grebes in the southern Baltic Sea, the larger proportion of the deviance could not be explained by these two variables. Additionally, the error analysis of the GAM clearly indicated regions within the study area where the original observations of Slavonian Grebes differed from the distribution predicted by the model. Numbers observed in the field were lower than predicted by the model especially in some inshore areas (e.g. Wismar Bay) and in the offshore areas north of the Darss-Zingst peninsula.

Within the Oderbox, water depth and bottom sediment type also had a significant influence on bird distribution in all time periods analysed (Table 2.2). Although water depth in the box mainly ranged from 6 to 14 m, it exceeded the latter in some parts of it. These areas were clearly avoided by Slavonian Grebes. No uniform trend was recognisable for waters 6 to 14 m deep as they lie within the preferred depth zones found for the southern Baltic Sea region. Regarding bottom sediment the results indicated an avoidance of very fine-grained sediment types (especially silt, <0.06 mm) as well as a tendency to avoid areas with sediment type E (fine sand with grain size 0.15-0.18 mm; Fig. 2.5c).

Table 2.2. Results of the generalised additive model for the habitat selection of Slavonian Grebes in the southern Baltic Sea and within the Oderbox.
Significance codes: *** 0.001 ** 0.01 * 0.05.

Southern Baltic Sea	Number of counting intervals (bird density >0)	Water depth		Bottom sediment		Bottom sediment (water depth <=20m)	
		F	p	F	p	F	p
Total (Oct.-Apr.)	64 168 (431)	81.4	<2e-16***	259	<2e-16***	201.1	<2e-16***
Autumn (Oct.-Nov.)	14 993 (98)	2.95	0.0154*	114.64	<2e-16***	82.4	<2e-16***
Winter (Dec.-Feb.)	26 084 (135)	39.29	<2e-16***	111.57	<2e-16***	87.01	<2e-16***
Spring (Mar.-Apr.)	23 091 (198)	38.67	<2e-16***	0.77	0.486	0.91	0.417

Oderbox	Number of counting intervals (bird density >0)	Water depth		Bottom sediment	
		F	p	F	p
Total (Oct.-Apr.)	10 177 (353)	12.38	<2e-16***	17.74	7.09e-10***
Autumn (Oct.-Nov.)	1 984 (94)	13.43	<2e-16***	7.85	0.000131***
Winter (Dec.-Feb.)	3 687 (103)	5.57	9.83e-07***	16.8	4.67e-09***
Spring (Mar.-Apr.)	4 506 (156)	6.85	1.54e-09***	8.22	7.93e-05***

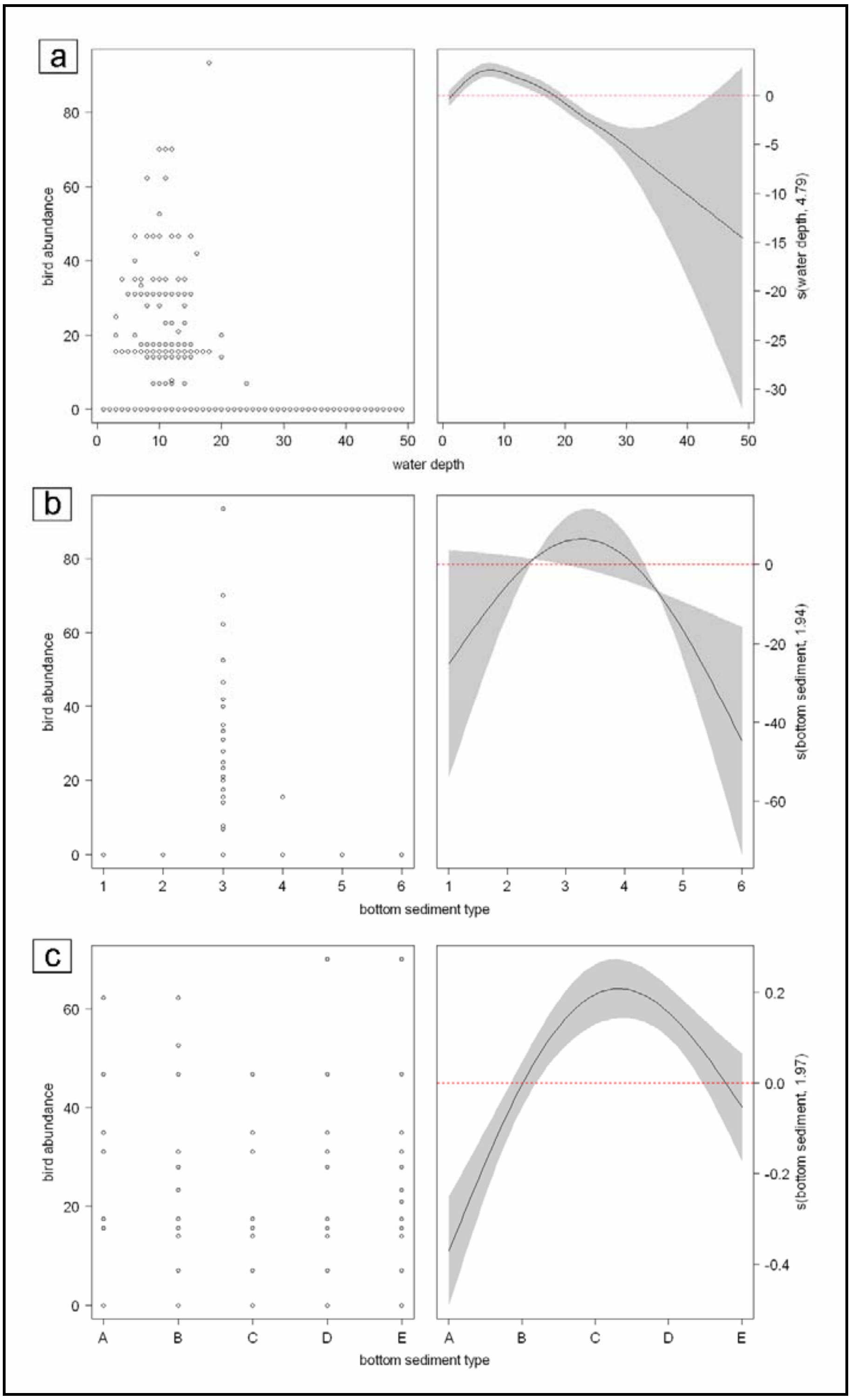

Fig. 2.5. Results of the habitat analyses for the total data set (Oct.-Apr. 2000-2008), showing original data on the left and GAM smoothing curves describing the effect of the predictor variables on bird abundance on the right panels, respectively. Red lines represent mean values which were scaled to zero, shaded areas indicate 95% confidence intervals around the main effects (continuous lines). Bird abundance is represented as a function of a) water depth ($F = 81.4$, $p < 0.001$), b) bottom sediment type for the southern Baltic Sea ($F = 259$, $p < 0.001$) and c) bottom sediment type within the Oderbox ($F = 17.74$, $p = 7.09e-10$).

Discussion

Distribution and seasonal patterns

The occurrence of Slavonian Grebes in the Baltic Sea was first described by Durinck et al. (1994). Recently published population sizes refer to a number of 1 000 individuals in the German part of the Baltic Sea in winter, with largest proportions in the Pomeranian Bight (Mendel et al., 2008). In other parts of the Baltic Sea, only low numbers of wintering birds have been recorded so far, for example in the Bay of Gdansk or along the Kursiu Spit (Durinck et al., 1994; Skov et al., 2000). The occurrence of Slavonian Grebes in the Pomeranian Bight involves migrants and winter residents. Numbers are highest during autumn migration. Some parts of the northeastern breeding population apparently remain in the area for only a short time before moving on to other wintering grounds. These are probably in the more western parts of the Baltic Sea (see Fig. 2.3b) and along the coast of northwestern France, where a winter population has been reported by Gilissen et al. (2002). During the midwinter months December to February, numbers within the Oderbox hotspot area show distinct variations. It is unclear to what extent local movements (e.g. to the Polish side of the Pomeranian Bight) or general seasonal patterns might be responsible. During spring migration, abundances assessed within the Oderbox are considerably lower than in autumn. This might be due to the fact that in spring high numbers occur outside the Oderbox in the coastal areas of the Pomeranian Bight, especially off the coast of Usedom (Fig. 2.3c). Furthermore, Slavonian Grebes might spend less time in the study area on the way back to the breeding grounds where an early arrival could be advantageous for nest site occupation.

Feeding ecology

Although the sample size of our diet study is very small, it provides valuable insights into the prey composition of Slavonian Grebes during winter. Obtaining diet samples of individuals at sea is almost impossible. Non-destructive methods are not applicable and the shooting of this highly protected species is ethically unjustifiable and technically impossible. So far, only two other authors provide information on winter diet in European waters. In a single bird from the Kattegat in late October, Madsen (1957) found small gobies, Sea Sticklebacks, a polychaete jaw and some detrius of insects. In Lake IJsselmeer, The Netherlands, Piersma (1988) identified European Smelt, a pelagic fish species, as the main diet of wintering Slavonian Grebes.

Common Gobies, the dominant prey found in our study, are widespread in the coastal areas of the Baltic Sea. They prefer shallow habitats with macrophytes in the litoral zone up to 12 m water depth whereas Sand Gobies have a wider depth range (e.g. Evans and Tallmark, 1985; Muus and Nielsen, 1999). These habitat preferences are in agreement with the fact that the birds of our diet studies were by-caught in the coastal zone of the Pomeranian Bight. One may speculate that Sand Gobies are the dominant goby species in the diet of Slavonian Grebes on the Odra Bank, because, unlike Common Gobies, they occur in high numbers in this central part of the Pomeranian Bight (Thiel et al., 2007).

Polychaete worms, probably Ragworms due to their high abundance in the study area (M. Zettler, pers. comm.), were very small-sized and accounted for less than one percent of the total prey biomass. It is unclear whether such small individuals were directly captured by Slavonian Grebes – maybe after exposure due to digging activities of sea ducks wintering in the Pomeranian Bight, as described for southwest Norway by Byrkjedal (2000) – or whether the hardly digestible chitinous jaws reached the bird stomachs via gobies preyed upon by the grebes. (Nereid) polychaete worms are described as prey of Common and Sand Gobies by various authors (e.g. Pihl, 1985; Zander, 1990; del Norte-Campos and Temming, 1994; Leitão et al., 2006).

Habitat selection

The results of the model support our hypothesis that both factors analysed substantially influence the habitat choice of Slavonian Grebes in the study area. We consider water depth to be the more relevant parameter than sediment type, as it acts via the maximum possible diving depth of this small bird species. In the breeding areas, Slavonian Grebes forage in shallow water, often only up to 2 m, and perform only shallow dives to catch prey under water (Fjeldså, 2004). This limitation results from the fact that Slavonian Grebes mainly breed in fertile lakes where penetration of light is often very low. Thus, prey is difficult to detect and to pursue in the deeper parts of those waters (Fjeldså, 2004). In marine areas, Slavonian Grebes are able to feed in much deeper water. However, diving depth of endothermic animals is limited due to physiological constraints and the thermal properties of water, and temperature has a strong effect on daily energy expenditures (e.g. Wiersma et al., 1995; Enstipp et al., 2006). In Great Crested Grebes wintering on Lake IJsselmeer, lower air and water temperatures caused an increase in food intake rate due to higher energetic costs for e.g. maintenance of body temperature, higher diving activity to catch more food, and the heating of cold prey in the stomach (Wiersma et al., 1995). Because of a negative exponential relationship between body mass and thermal conductance (which is higher in water than in air), de Vries and van Eerden (1995) assumed that energetic expenditure for thermoregulation may indeed be a constraint for small Slavonian Grebes that spend the whole winter at sea. We therefore postulate that the birds tend to avoid sea areas of the southern Baltic Sea with water depths exceeding 15 m to reduce high energetic costs while foraging in cold water for their favourite prey, demersal gobies.

Slavonian Grebes were almost exclusively recorded in waters over sandy bottom. However, some sediment types (1,5,6) predominantly occurred in deeper waters and were thus, according to our results regarding water depth, located in areas not suitable for Slavonian Grebes. It is therefore difficult to judge whether certain sediment types were truly avoided or were rather out of reach due to the unfavourable water depth. On the other hand, sediment types 2 and 4 did occur within the suitable depth range, but were avoided by Slavonian Grebes, indicating a “real” influence of sediment type. The restriction to sandy sediments indicates that Slavonian Grebes mainly feed on benthic or benthopelagic prey occurring over this sediment type. Common and Sand Gobies, the dominant prey found in our diet samples, are demersal fish species that often occur over sandy bottom sediments, albeit they can also colonise other habitats (Jansson et al., 1985; Zander, 1990; Vorberg and Breckling, 1999). Thiel et al. (2007) found high numbers of Sand Gobies in the sandy Pomeranian Bight. This supports the assumption that, in our study area, Slavonian Grebes find their favoured prey species over sandy bottom substrates and consequently occur mainly in areas with this sediment type. The small-scale differences in distribution found within the hotspot area in the Oderbox might reflect spatial and/or temporal variability in the occurrence of the main prey gobies. At a large scale, the distribution of seabirds at sea often corresponds best with physical phenomena, while biological features like foraging range, social interactions and prey availability often determine distribution patterns at smaller scales (Schneider and Duffy, 1985; Hunt and Schneider, 1987). Ragworms, whether direct prey of Slavonian Grebes or indirectly taken via gobies, are rather euryoecious and can be found in different sediment types (Hartmann-Schröder, 1996). They are widespread within the southern Baltic Sea and were frequently observed in the sandy Pomeranian Bight by Zettler and Röhner (2004) and Zettler et al. (2006). In Lake IJsselmeer, where the diet consists of pelagic European Smelt, water transparency is very low (Piersma et al., 1988), probably impeding foraging near the bottom. Thus, Slavonian Grebes seem to be able to adjust their feeding techniques according to the environmental conditions they encounter in the wintering areas.

Although water depth and bottom sediment type could be described as important habitat factors, the variance explained by both parameters as well as an error analysis implicate that these variables alone cannot sufficiently predict the distribution of Slavonian Grebes in the study area. Consequently, further factors must be effective. Particularly in some inshore areas of the study area, bird numbers observed in the field were much lower than predicted by the model. One reason for this fact is that most coastal areas have low water depths and thus could not be surveyed from ships due to the draught of the survey vessels. Counts carried out from land within the framework of the annual midwinter International Waterbird Census revealed small to medium numbers of Slavonian Grebes in several coastal areas (Scheller et al., 2002; Mendel et al., 2008; DDA, 2009) and can explain some of the discrepancies between modelled data and original field observations. Still, there are regions within the study area with suitable habitat conditions regarding water depth and sediment type where no Slavonian Grebes occur. We therefore assume that at least two other factors might influence the distribution of Slavonian Grebes in the southern Baltic Sea:

1. Competition with other grebe species. Beside Slavonian Grebes, high numbers of Great Crested Grebes and Red-necked Grebes winter in the southern Baltic Sea (e.g. Durinck et al., 1994; Sonntag et al., 2006). During the breeding season there is strong interspecific competition between different grebe species, resulting in a spatial segregation into different breeding habitats (Spletzer, 1974; Fjeldså, 2004). Due to the high abundances of the three grebe species wintering in the study area, and based on our own detailed data on their distribution and diet within the study area, we have indications that interspecific competition might affect the distribution patterns even outside the breeding season (see **Chapter III**).
2. Anthropogenic effects. Within the given possibilities of seabirds to stay at sea set by physical and biological parameters, anthropogenic activities may cause irregularities in distribution and abundances (e.g. Kaiser et al., 2006). The southern Baltic Sea is strongly influenced by various human activities that affect different seabird species to various extents (Garthe et al., 2003; Mendel et al., 2008). Slavonian Grebes are particularly sensitive to ship traffic and show strong fleeing reactions towards approaching ships (Garthe et al., 2004; FTZ, unpubl. data). Frequently used ship routes are therefore likely to influence the distribution of Slavonian Grebes as already described for other species like divers and sea ducks (e.g. Hüppop et al., 1994; Kube and Skov, 1996).

These hypotheses will be the subject of future analyses to further clarify the habitat selection of Slavonian and other grebe species as well as their interactions in the southern Baltic Sea (see **Chapter III**).

Conclusions

While various factors may influence the distribution of seabirds at sea (summarised e.g. in Hunt and Schneider, 1987; Shealer, 2002), prey availability and species-specific feeding options and constraints are considered to be of most relevance in the relationship between seabirds and the marine habitat (Montevecchi, 1993). For Slavonian Grebes wintering in the Baltic Sea, water depth and bottom sediment type strongly influence the spatial distribution patterns. Both factors can be linked to diet preferences. The maximal possible diving depth while foraging for bottom-living gobies is limited due to physiological and thermoregulatory aspects in this small endothermic bird species. Bottom sediment type can be used as a proxy for the availability of demersal prey and provides particularly valuable information when data on the spatial occurrence of prey species and, as in Slavonian Grebes, data on diet in general, are scarce.

3 Can competition explain distribution patterns of grebes wintering in the southern Baltic Sea?

Abstract

Interspecific interactions between Great Crested, Red-necked and Slavonian Grebes wintering in the southern Baltic Sea were investigated based on information on distribution patterns, habitat requirements and diet preferences. The three species mainly occurred in shallow waters up to 15 m depth. Within these preferred areas they exhibited distinctive distribution patterns with only low spatial overlap. Red-necked and Slavonian Grebes were clearly spatially separated from Great Crested Grebes, particularly in the eastern part of the study area where the three species occurred in highest overall numbers. Red-necked and Slavonian Grebes were less clearly separated, but seemed to exclude each other at least in areas with highest local abundances. A generalised additive mixed model indicated that each species significantly influenced the distribution of the others. Increasing abundance of one species caused a strong decrease in the abundance of the other grebes. The overall diet composition of the three species was very similar, with gobies as the most important fish species with regard to numerical abundance. Red-necked and Slavonian Grebes also corresponded with regard to consumed biomass, while Great Crested Grebes slightly differed from the two other species in biomass values.

Due to the high number of birds wintering in the southern Baltic Sea and high energy demands for foraging under water and maintenance of body temperature, interspecific competition was regarded to be a structuring mechanism of the grebe community wintering in the southern Baltic Sea. The results indicated that the three species enabled coexistence within their preferred areas by a spatial segregation rather than by the use of different dietary niches. The findings were discussed in the context of the hypothesis of Spletzer (1974) on niche segregation of grebes outside the breeding season.

Introduction

It is one of the basic principles of animal ecology that species can only coexist in the same habitat if they differ in their ecology, at least with respect to those resources of the environment which determine their numbers. Such ecological isolation is the result of competitive exclusion and is of basic importance for the origin of new species, adaptive and non-adaptive radiation, the diversity of species and the composition of faunas (Lack, 1971). The essence of interspecific competition is that one species suffers a reduction in fecundity, growth or survival as a result of resource exploitation or interference by another species. This competition is likely to affect population dynamics, which, in turn, can influence the distribution of competing species (Begon et al., 2006). According to Lack (1971), there are three basic ways by which competition between species can be reduced: (1) species with identical or similar ecological requirements have excluding geographical distributions (segregation by range), (2) species overlapping in their geographical distributions occur in different habitats (segregation by habitats), or (3) species living within the same habitat exhibit different diet preferences (segregation by feeding).

Strong interspecific competition has been described for the group of grebes (family Podicipedidae) during the breeding season and is supposed to result in the colonisation of different breeding habitats in areas where species geographically overlap (e.g. Spletzer, 1974; Fjeldså, 2004). Fjeldså (2004) stated, that “although up to six species of grebes can be found in one geographical area, it is not often that they manage to coexist on the same body of water”. Typical breeding habitats of grebes are eutrophic lakes, e.g. shallow waters with high biological production and usually with well-developed reed swamps and submergent vegetation. However, they also use mixotrophic lakes, rich in nutrients but influenced by humid acids (e.g. Spletzer, 1974; Fjeldså, 2004; Vlug, 2005). This selection of lake-types reflects the need of grebes for marsh vegetation for construction and safe placement of floating nests as well as for adequate food supplies (Fjeldså, 2004). Such habitats, however, are often limited, which promotes rivalry for the available areas. In his reflection on the role of interspecific competition for breeding habitat colonisation in four species of grebes occurring sympatrically in Schleswig-Holstein, North Germany, Spletzer (1974) set up the following line of arguments (Fig. 3.1): under the constraint of breeding, grebes colonise only those waters which provide good conditions not only for breeding (e.g. suitable nesting sites), but also for chick raising (e.g. suitable food supply), leading to a restriction of adequate habitats. Furthermore, the birds often use only the littoral zone of the breeding waters (especially of larger water bodies), resulting in an enhanced population density in an area with only low water volume available for foraging. Simultaneously, food requirements rapidly increase during chick raising. Enhanced population density, increasing food requirements and reduced food supply force the grebes to exploit the whole prey spectrum available. Coexistence via the formation of dietary niches is not practicable, the species are rather constrained to colonise different habitats (or even geographical areas) to avoid competition. During the breeding season, sympatric grebes are spatially separated (habitat segregation). Outside the breeding season, however, the ecological conditions change. Grebes mainly winter in marine areas or on larger lakes, where they are comparatively less restricted to specific habitats. This mostly involves a more wide-ranging distribution and a decrease in population density. The foraging area increases, resulting in lower interference pressure. Different species can occupy different dietary niches and hence are able to coexist within the same habitat (niche partitioning).

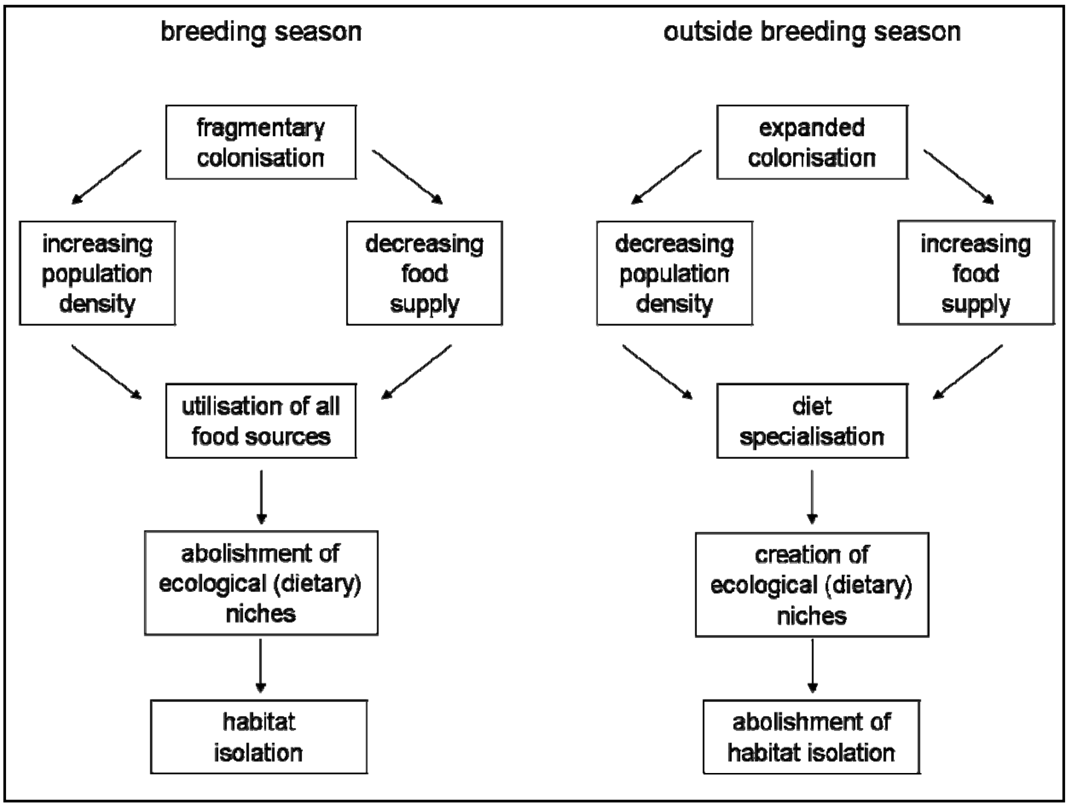

Fig. 3.1. Hypothesis of the main types of ecological segregation in grebes in breeding and wintering areas. Modified from Spletzer (1974).

Spletzer's hypothesis about habitat isolation during the breeding season due to direct competition was criticised by Vlug (1993), who regarded the preferences for different breeding habitats not as a result of competition, but rather as a consequence of relatively large morphological differences that affect feeding and habitat selection and result in sufficiently ecological separation. Fjeldså (2004), on the other hand, describes strong agonistic behaviour between breeding grebes that, in concordance with Spletzer's theory, restricts the inferior species to less suitable habitats.

According to his comprehensive studies on grebes, competition for food and aggressive interference cause “forbidden combinations” and thus lead to complementary distributions of different species within overlapping geographical ranges (Fjeldså, 2004).
While the separation of grebes during the breeding season is conspicuous, the reasons for this segregation are not necessarily relevant for the present analysis, though, as it focuses only on wintering grebes. In the present study, Spletzer’s hypothesis of niche partitioning outside the breeding season (right part of Fig. 3.1) is tested for the southern Baltic Sea, where about 8 500 Great Crested Grebes, 750 Red-necked Grebes and 1 000 Slavonian Grebes occur during winter (Mendel et al., 2008). Hereby, the following aspects are investigated:

- Can competition act as a mechanism for the structuring of grebe communities outside the breeding season?
- If competition exists, how do the three species reduce the conflict? Are they ecologically separated by the use of different dietary niches, as assumed by Spletzer (1974), or does the large number of wintering birds result in a spatial segregation even outside the breeding areas?

The questions are addressed by (1) modelling the habitat requirements of grebes to identify the suitable wintering areas in the southern Baltic Sea, by (2) analysing distribution patterns to describe in which areas the three species actually occur, and by (3) studying the diet of the three species during winter. Based on these analyses, the role of interspecific competition for the distribution of grebes and their separation strategy to enable coexistence outside the breeding season are discussed.

Methodology

Distribution of birds at sea

The distribution of grebes wintering in the southern Baltic Sea was analysed from the German *Seabirds at Sea* database version 5.12 (June 2008; Garthe et al., 2007) that contains more than 30 000 kilometres of ship-based transect counts in the study area for the years 2000 to 2008. Bird surveys were carried out according to an internationally standardised method for northwest European waters (e.g. Tasker et al., 1984; Camphuysen and Garthe, 2004), including the *snapshot method* for flying individuals. For further details, see **Chapter I**. Counting intervals with a sea state higher than four (according to *Beaufort* scale; Dietrich et al., 1975) were excluded from the data as such conditions prevent a thorough recording of grebes. To account for the fact that some swimming birds, particularly those in the distant parts of the observation transects, might have been overlooked during the ship surveys, the numbers of swimming individuals were multiplied by a correction factor of 1.4 (according to Garthe, 2003) for all analyses.

Influence of water depth on distribution patterns

Within a number of various factors possibly influencing the distribution of birds at sea, water depth is considered to be of greatest significance for grebes, which regularly dive to the sea bottom to obtain their food: foraging under water involves a number of physiological challenges for endothermic animals, and depth has a particularly strong effect on diving energetics due to increasing metabolic rates with increasing diving depth. In addition, cold water temperatures and a reduction in body insulation as a consequence of an increase in pressure with dive depth also elevate the energetic costs for animals that forage under water (e.g. Guillemette et al., 2004; Enstipp et al., 2006). Within the geographical distribution of their wintering areas, grebes can thus only occur in waters with a suitable depth to forage on benthopelagic prey within their energetic limits.

Data on water depth within the study area, classified into 1-metre categories, were obtained from the Danish Hydraulic Institute (DHI). Following the procedure described in **Chapter II**, the abundance of birds (individuals per area surveyed) in relation to water depth was analysed with a generalised additive model (GAM; Wood, 2006) using the *mgcv* package (Wood, 2000) in version 2.8.1 of R (R Development Core Team, 2008). Bird abundance served as response variable while water depth was used as covariable with a cubic regression spline as smoothing function. To prevent overdispersion, *quasi-Poisson* was selected as underlying function in the model frame. Two facts had to be considered during the creation of the model: (1) the large number of zero-counts within the data set might make standard statistical functions inapplicable and (2) bird abundance data might be spatially autocorrelated. To account for point (1), a two-stage GAM according to Jensen et al. (2005) was applied by modelling firstly presence or absence of birds in relation to water depth using a binomial distribution function and secondly only bird presence data as a function of depth using the *quasi-Poisson* distribution. Subsequently, the predicted bird abundance was calculated as the product of both stages, and the residuals of this combined model and the original model described above were compared using a Student’s t test. The relationship between the combined and the original model was linear for all three grebe species (Fig. 3.2a) and there was no significant difference between the residuals of both models ($p > 0.99$, respectively). To (2) avoid spatial autocorrelation within the model, an autocorrelation structure for latitude and longitude usually has to be included, using a generalised additive mixed model (GAMM). However, by comparing the residuals of the model with and without the autocorrelation structure *corEXP* for spatial data (Pinheiro and Bates, 2000) no differences were found for all three grebe species ($p > 0.99$, respectively; Fig. 3.2b). Considering these findings, the most simple model without an autocorrelation structure and with *quasi-Poisson* as underlying function was selected.

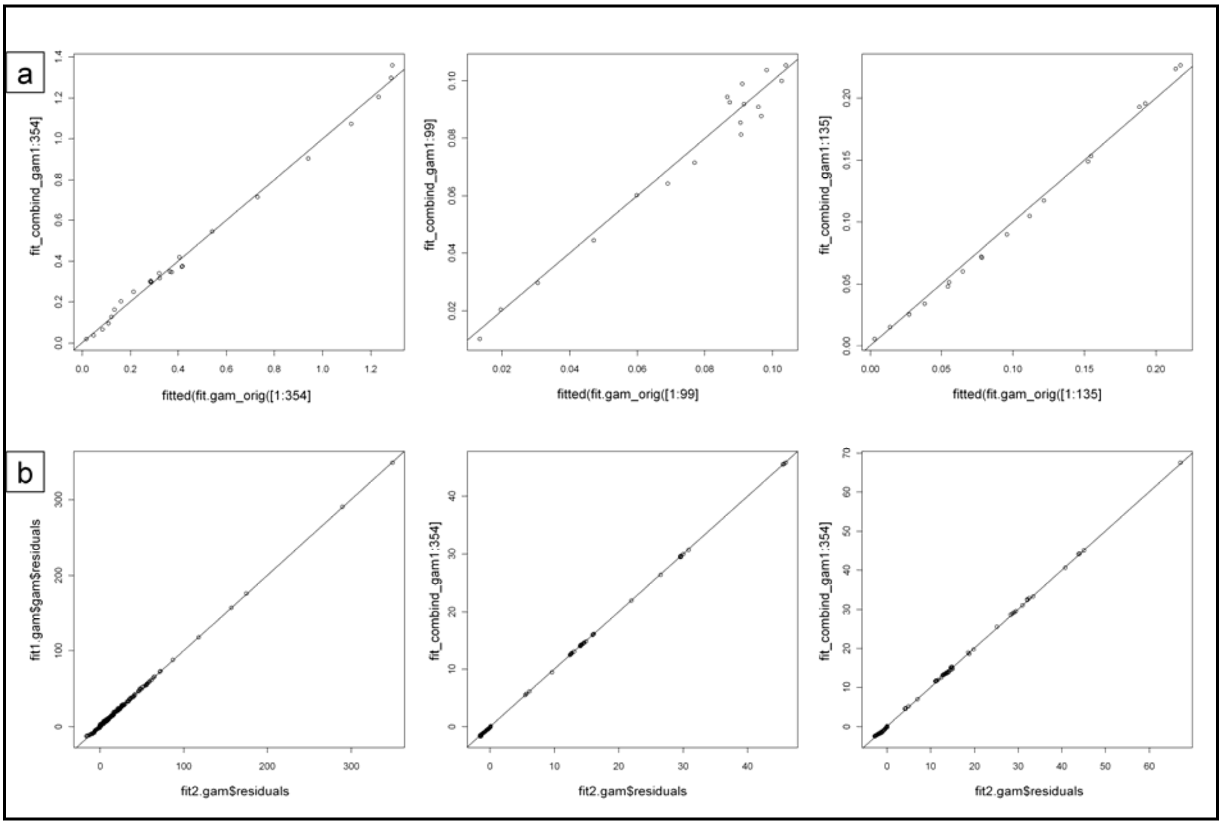

Fig. 3.2. Results of intermediate steps to select the best model to analyse the effect of water depth on grebes wintering in the southern Baltic Sea. 3.2a) Correlation between the residuals of a two-stage GAM and the original habitat model. 3.2b) Correlation between the residuals of the generalised additive model with and without an autocorrelation structure for latitude and longitude. Results for Great Crested, Red-necked and Slavonian Grebes are displayed left, middle and right, respectively. For details, see text.

Spatial interactions of the different grebe species

The spatial overlap of the three grebes was analysed by modelling the occurrence of one species in relation to the two other species, respectively, using *quasi-Poisson* as underlying function within the model frame. To compensate for a skew-symmetric frequency distribution of bird abundances (see Fig. 3.3), the predictor variables within the model were log10-transformed, while the response variables were automatically transformed by the use of the *quasi-Poisson* link function.

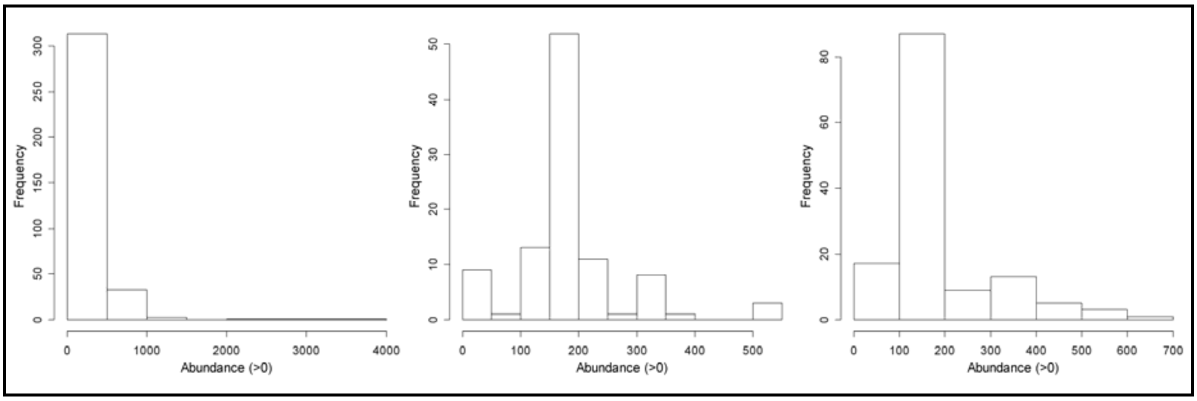

Fig. 3.3. Frequency distribution of abundance values of Great Crested (left), Red-necked (middle) and Slavonian Grebes (right) wintering in the southern Baltic Sea.

Spatial autocorrelation of bird numbers is considered to have a stronger influence on the spatial interactions of different species than on the influence of habitat factors on bird distribution (see above). Thus, in contrast to the habitat model, an autocorrelation structure for latitude and longitude has been included in the model for spatial interactions of grebes. Hence, a generalised additive mixed model (GAMM) was applied, using the autocorrelation structure *corEXP* for spatial data (Pinheiro and Bates, 2000), which proved to best represent the characteristics of the original values.

The model was carried out for each pairwise combination of the three grebe species. Bird abundance within the model was based upon the number of individuals per area surveyed per arbitrarily selected time (counting) units: to consider a possible influence of scale on the spatial interactions of the three grebe species, the model was performed for two different data sets, including a) the abundance of birds per 1-minute time (counting) interval and b) the abundance of birds per 10-minute time interval.

Diet analyses

The diet of grebes was studied by analysing the stomach contents of birds accidentally caught and drowned in set nets in the Pomeranian Bight in the eastern part of the southern Baltic Sea in the years 2001 to 2006. As sample sizes for winter months were rather small, birds drowned in autumn and spring were also included in the analyses. Birds were dissected and stomach and guts removed for further analysis. Following a scoring according to van Franeker (2004), body condition was evaluated due to the condition of the pectoral flight muscles and the presence and quantity of subcutaneous and intestinal fat depots. Birds were aged and sexed based on the development of their sexual organs and the presence or absence of the *Bursa Fabricius*. All samples are indicated in Table 3.1.

Table 3.1. Overview of the samples for diet analyses of grebes in the southern Baltic Sea.

		Autumn (Oct. - Nov.)		Winter (Dec. - Feb.)		Spring (Mar. - Apr.)		Body condition
		male	female	male	female	male	female	
Great Crested Grebe (N = 20)	adult		2	5				17 x good 3 x moderate
	immature		1	4	2			
	?			5	1			
Red-necked Grebe (N = 23)	adult					4	8	21 x good 2 x moderate
	immature		1	1	2	3	4	
	?							
Slavonian Grebe (N = 4)	adult					1		3 x good 1 x moderate
	immature				1	1		
	?				1			

Stomachs and guts were sliced open and all prey items were collected. Dietary remains in the stomachs were embedded in a feather ball, as it is typical in grebe species (e.g. Piersma and van Eerden, 1989; Fjeldså, 2004). The feathers prevent the passage of hard items into the intestines. The guts consequently contained only a few unspecific prey remnants and were thus excluded from further analyses.

Diet samples were examined as described in **Chapter II** and in Guse et al. (2009). Prey items were identified to the lowest possible taxon by otoliths and hard parts of the skeleton (fishes), jaws (polychaete worms) or carapace elements (crustaceans). Prey numbers were calculated as the smallest definite number by considering all remnants of a given species. Items that occur in pairs (like otoliths, otic bullae of clupeids, spines of sticklebacks and jaws of polychaetes) were paired based on species, orientation, size, wear and shape. Otoliths and spines were measured to derive original fish length and biomass using regressions obtained from Hahn (1981), Leopold et al. (2001), Hahlbeck and Müller (2003) and M. Leopold (unpubl. data), after correction for wear according to Guse et al. (2009). In Great Crested Grebes, no differentiation was made between the very similar otoliths of Common Goby and Sand Goby. These otoliths were mathematically treated as Common Goby remnants, because only a small proportion of all otoliths could have been classified as Sand Goby (K. Weber-Streidt, pers. comm.). The loss of precision was considered marginal, as both goby species have similar relations between otoliths size and fish size (Leopold et al., 2001). Unidentified fishes were excluded from biomass calculations. Regressions for polychaete worms were adopted from Debus and Winkler (1996).

Statistical analyses of differences in the diet of the three grebe species could only be performed for Great Crested and Red-necked Grebes. Slavonian Grebes had to be excluded due to the low sample size. Relative proportions of numerical abundance and biomass of different prey categories were compared using a generalised linear model (GLM) with *quasibinomial* as underlying function. To test for differences in fish length, a linear mixed effect model (LMER) in combination with an ANOVA was applied, with each sample (stomach) used as random factor within the model. All analyses were performed in version 2.8.1 of R.

Results

Habitat requirements and distribution patterns

Water depth had a clear effect on the distribution of grebes wintering in the southern Baltic Sea. The generalised additive model indicated a preferred occurrence of Great Crested Grebes in waters up to 26 m and of Red-necked Grebes up to 30 m depth (although not significant). Slavonian Grebes preferred water depths up to 18 m with optimum values at about 10-12 m (Fig. 3.4).

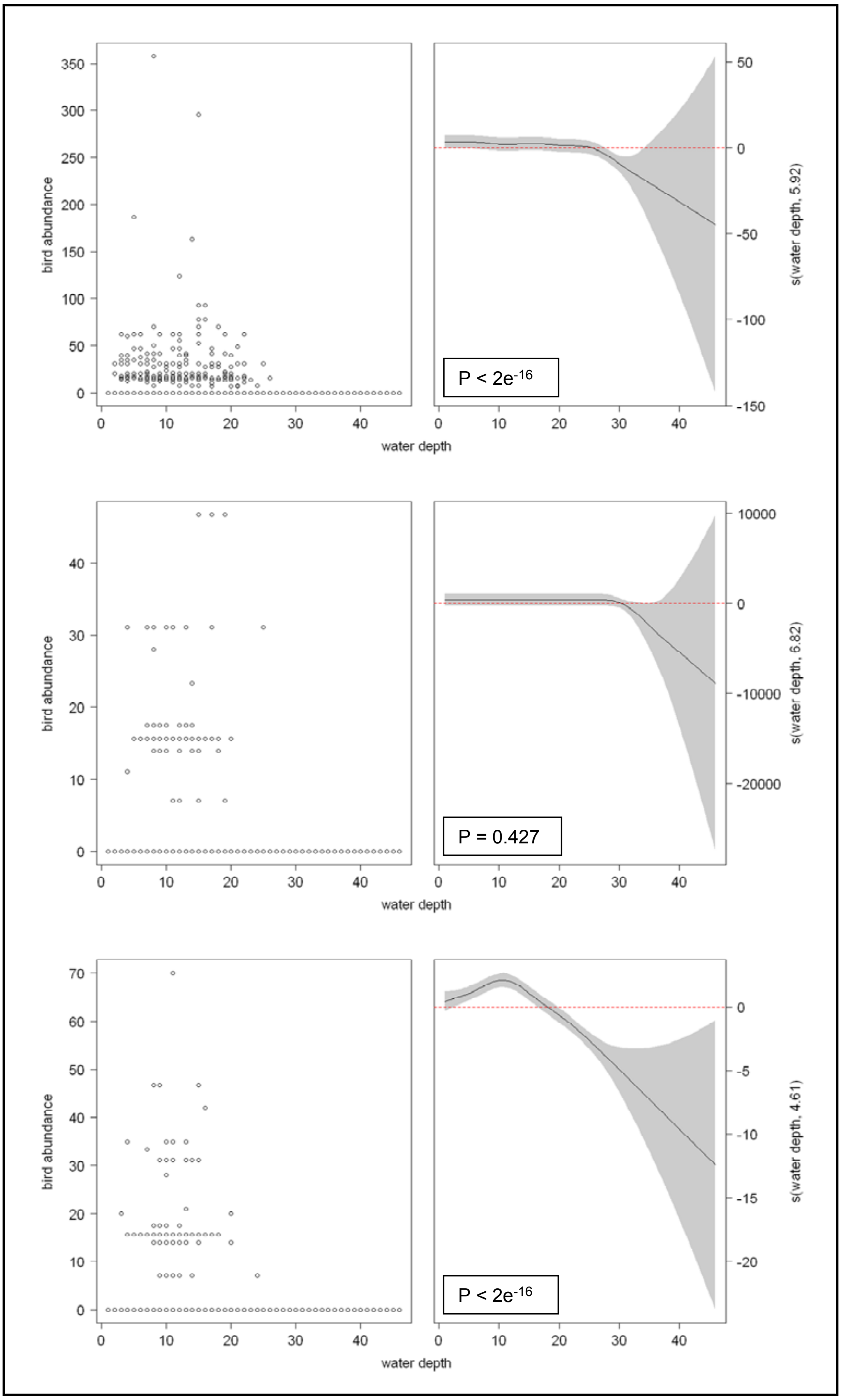

Fig. 3.4. Results of the habitat analyses for Great Crested (top), Red-necked (middle) and Slavonian Grebes (bottom) in winter 2000-2008, showing original data on the left and GAM smoothing curves describing the effect of water depth on bird abundance on the right panels, respectively. Red lines represent mean values, which were scaled to zero, shaded areas indicate 95% confidence intervals around the main effects (continuous lines).

Of all birds recorded within the observation transect, 82% of Great Crested Grebes, 81% of Red-necked Grebes and 93% of Slavonian Grebes were observed in waters up to 15 m depth. Although, according to the GAM, Great Crested and Red-necked Grebes could occur in deeper waters than Slavonian Grebes (see Fig. 3.4), only small proportions were actually found in waters more than 20 m deep (Table 3.2).

Table 3.2. Occurrence (as percentage) of grebes in different water depth zones in the southern Baltic Sea in winter 2000-2008. Data are corrected for survey effort.

	Great Crested Grebe N = 9032	Red-necked Grebe N = 1698	Slavonian Grebe N = 2453
< 10 m	49.1	38.8	50.0
11 – 15 m	33.3	42.0	42.8
16 – 20 m	14.0	17.3	7.1
21 – 25 m	3.4	1.9	0.1
26 – 30 m	0.2	0	0
> 30 m	0	0	0

Within the areas suitable with regard to water depth, the three grebe species exhibited distinctive distribution patterns (Fig. 3.5). Great Crested Grebes were the most widespread species, but they were restricted to coastal areas and lagoons and only seldom occurred in offshore areas. Red-necked Grebes were also widespread throughout the study area but occurred in coastal as well as in offshore areas. Slavonian Grebes were mainly restricted to the eastern study area, with only low numbers in the western part. They concentrated in the offshore area of the Pomeranian Bight, but were also found locally along the coast.

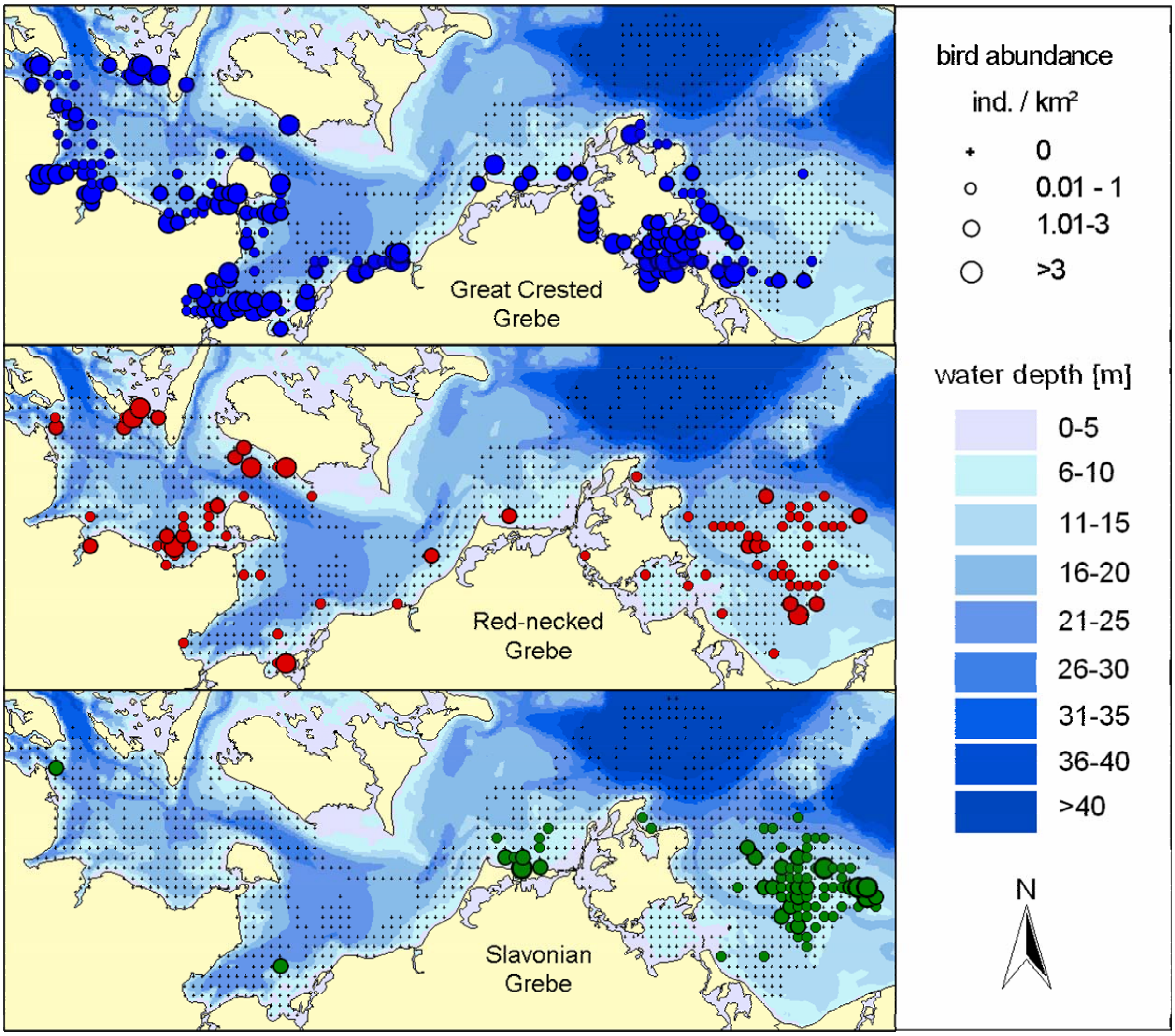

Fig. 3.5. Distribution of grebes in the southern Baltic Sea in winter (Dec.-Feb.) 2000-2008, based on bird abundances per 2' latitude x 3' longitude grid cell (total grid size about 12 km²). Abundances were calculated as number of individuals recorded per area surveyed to account for unequal counting effort.

Spatial interactions

The separate distribution maps indicated only low overlap in the occurrence of different grebe species. This impression was confirmed by a combined map of the three distribution patterns (Fig. 3.6). Red-necked and Slavonian Grebes were clearly spatially separated from Great Crested Grebes, particularly in the eastern part of the study area where the three species occurred in highest overall numbers. Red-necked and Slavonian Grebes were less clearly separated, but seemed to exclude each other at least in areas with highest local abundances.

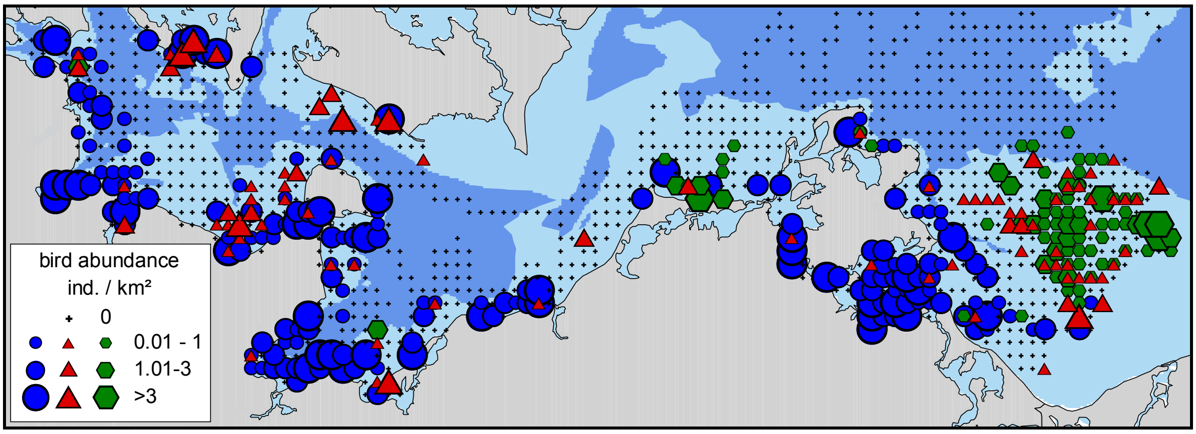

Fig. 3.6. Overlap of the distribution of Great Crested (blue), Red-necked (red) and Slavonian Grebes (green) in the southern Baltic Sea, Dec.- Feb. 2000-2008, based on bird abundances per 2' latitude x 3' longitude grid cell. Light blue water colour indicates the depth zone where all three species, according to the GAM, preferably occurred. The borderline is 18 m as this was the minimal value (for Slavonian Grebes). Dark blue colour indicates deeper waters.

The analysis of a single ship survey carried out over three successional days in the Pomeranian Bight in February 2005 confirmed the spatial differences in the distribution patterns of the three grebe species (Fig. 3.7). This analysis demonstrates that the different species actually occur contemporaneously within the study area and that spatial interactions are not artificially created by pooling data originating from different months and years.

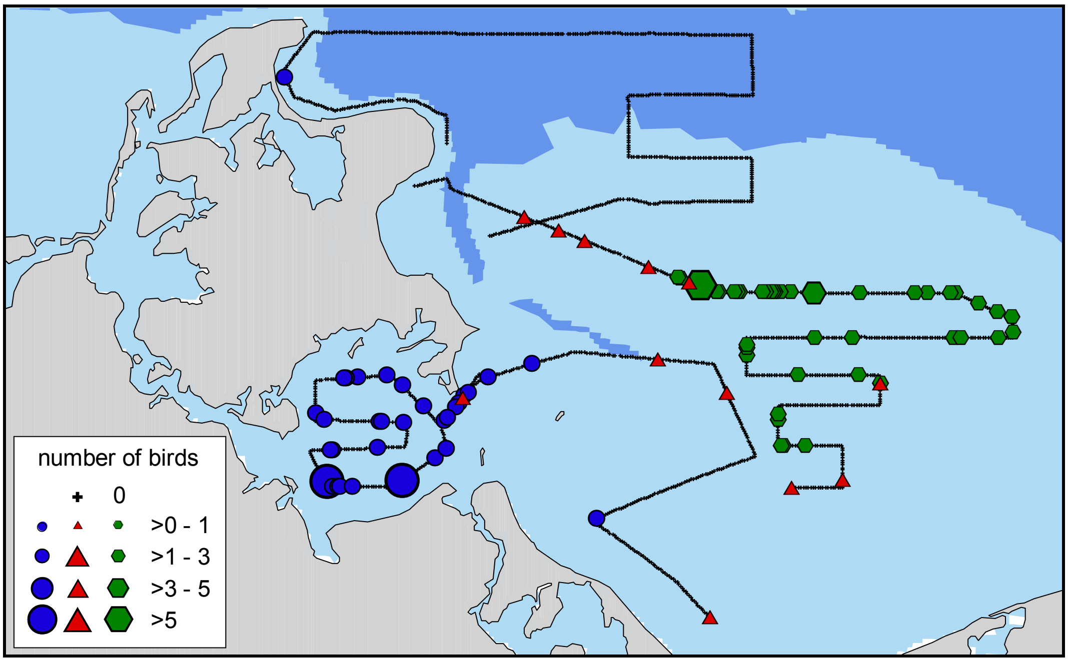

Fig. 3.7. Distribution of Great Crested (blue), Red-necked (red) and Slavonian Grebes (green) during a three-day ship survey in February 2005 in the Pomeranian Bight. Symbols represent the numbers of birds per 1-minute counting interval. For water colours, see Fig. 3.6.

Spatial segregation of the three grebe species was further approved by the generalised additive mixed model which indicated that each species significantly influenced the distribution of the other species, considering bird abundance per 1-minute as well as per 10-minute time interval (Table 3.3). It confirmed the separation of Great Crested Grebes from the two other species and also revealed a separation between Red-necked and Slavonian Grebes. With increasing abundance of one grebe species, the abundance of the others strongly and significantly decreased (Fig. 3.8).

Table 3.3. Results of the generalised additive mixed model for the interactions of grebes wintering in the southern Baltic Sea with bird abundance based on the number of individuals per area surveyed per 1-minute and per 10-minute counting interval.

1-minute time unit	Predictor variables					
	Great Crested Grebe		Red-necked Grebe		Slavonian Grebe	
Response variables	F	p	F	p	F	p
Great Crested Grebe			15.03	7.37e-06	10.10	0.000276
Red-necked Grebe	51.13	<2e-16			30.4	3.63e-10
Slavonian Grebe	19.59	2.66e-07	25.10	1.09e-08		
10-minute time unit	Predictor variables					
	Great Crested Grebe		Red-necked Grebe		Slavonian Grebe	
Response variables	F	p	F	p	F	p
Great Crested Grebe			20.02	2.41e-07	14.52	1.16e-05
Red-necked Grebe	28.43	<2e-16			32.43	1.49e-13
Slavonian Grebe	22.76	3.46e-08	27.36	4.08e-09		

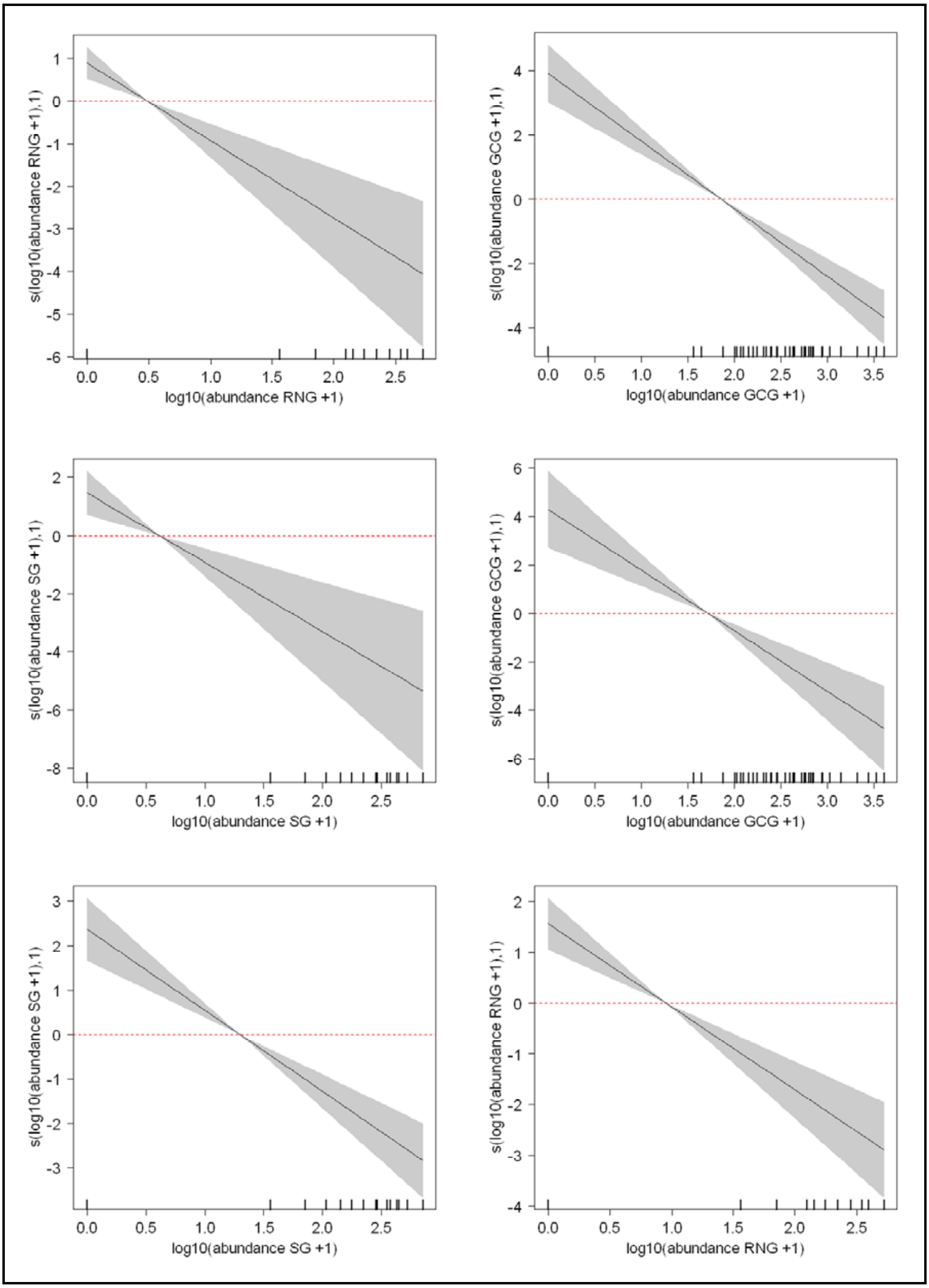

Fig. 3.8. GAMM smoothing curves describing the mutual effects of the three grebe species on the occurrence of each other during winter in the southern Baltic Sea. Top: interactions between Great Crested (GCG) and Red-necked Grebes (RNG), middle: interactions between Great Crested and Slavonian Grebes (SG), bottom: interactions between Red-necked and Slavonian Grebes. Red lines represent mean values, which were scaled to zero, shaded areas indicate 95% confidence intervals around the main effects (continuous lines).

Diet of grebes in the southern Baltic Sea

Prey composition

Fish dominated the diet of the three grebe species and accounted for 69.1% of all prey items in Great Crested Grebes, 85.2% in Red-necked Grebes and 76.1% in Slavonian Grebes. Polychaete worms were the second most frequent prey category, comprising 30.7, 14.5 and 23.0% of all prey items, respectively. Crustaceans played only a minor role in the diets with less than one percent of all prey items (Fig. 3.9). The differences in diet composition between Great Crested and Red-necked Grebes were statistically significant at this taxonomic level ($p = 0.006$).

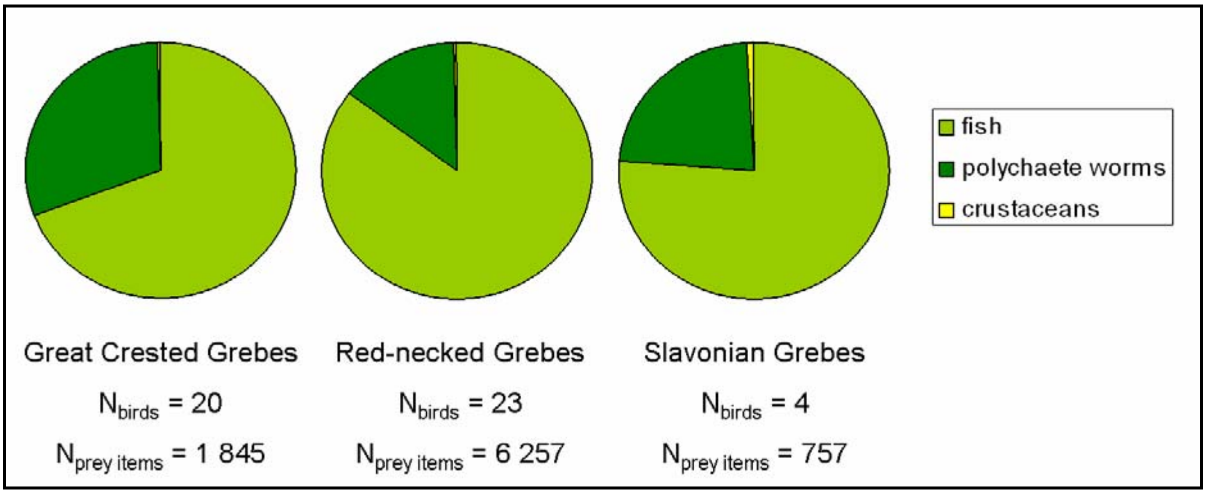

Fig. 3.9. Diet composition of grebes drowned in set nets in the Pomeranian Bight.

In the 47 birds analysed, 15 fish species from ten different families as well as a few unidentified specimens could be found (Table 3.4). Gobies (Gobiidae) occurred most frequently and were the dominant species in all three grebes, accounting for 76.9% of all fishes consumed in Great Crested Grebes, 97.2% in Red-necked Grebes and 95.3% in Slavonian Grebes (Fig. 3.10). In the latter, the remainder fishes comprised only sandeels (Ammodytidae) and one unidentified clupeid fish (Clupeidae), while the diet of the other two grebe species was more diverse. However, except percid fishes (Percidae), which accounted for 20.8% of the numerical abundance in the diet of Great Crested Grebes, all other fish families played only a minor role in the diet composition (Fig. 3.10). The relative proportions of gobies and percids taken by Great Crested and Red-necked Grebes differed significantly ($p < 0.001$, respectively). There was no significant difference in the proportion of consumed sticklebacks (Gasterosteidae; $p = 0.61$).

	Great Crested Grebe			Red-necked Grebe			Slavonian Grebe		
	Frequency of occurrence [%] N=20 stomachs	Numerical abundance [%] N=1275 fishes	Biomass [%]	Frequ. of occur. [%] N=23	Num. abund. [%] N=5333	Biomass [%]	Frequ. of occur. [%] N=4	Num. abund. [%] N=576	Biomass [%]
Clupeidae									
European Sprat	5.0	0.1	0.6						
Clupeidae indet.							25	0.2	0.1
Osmeridae									
European Smelt	5.0	0.7	0.4						
Gadidae									
Atlantic Cod				4.3	0.02	0.01			
Gasterosteidae									
Three-spined Stickleback	35.0	1.4	1.7	60.9	0.86	2.7			
Cottidae									
Shorthorn Sculpin				8.7	0.04	0.7			
Ammodytidae				8.7	0.04	0.2			
Lesser Sandeel							50	0.5	0.9
Great Sandeel							25	0.2	1.8
Sandeel indet.							75	3.5	11.3
Gobiidae	65.0	76.9	18.4						
Common Goby				87.0	7.97	7.5	100	30.4	18.1
Sand Goby				43.5	0.39	0.8	50	2.4	1.2
Common / Sand Goby				91.3	88.77	81.2	100	62.5	66.6
Black Goby				4.3	0.02	0.09			
Crystal Goby				4.3	0.02	0.01			
Percidae									
Pike-perch	55.0	2.1	32.3						
Ruffe	65.0	18.7	46.3	56.5	1.10	5.6			
Pleuronectidae									
Dab				4.3	0.06	0.09			
Dab / Flounder				13.0	0.26	0.8			
Flatfish spec.				13.0	0.09	0.3			
Cyprinidae									
Roach	5.0	0.1	0.3						
Fish indet.				30.4	0.36	-	25	0.3	-

Table 3.4. Fish categories represented in the diet of grebes drowned in set nets in the Pomeranian Bight. Frequency of occurrence is the percentage of stomachs containing the respective fishes. Numerical abundance is the percentage of the respective fish category on total fish numbers found in the stomachs. Biomass is the percentage of the respective fish category of total biomass calculated for all stomachs.

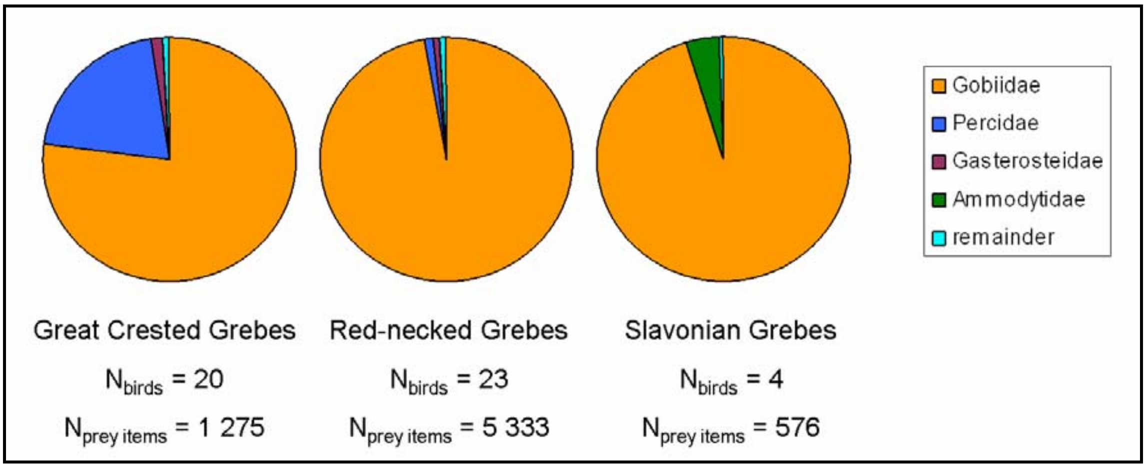

Fig. 3.10. Relative proportions of the abundance of different fish families represented in the diet of grebes drowned in set nets in the Pomeranian Bight.

Due to the great similarity of their otoliths, the differentiation between Common Goby and Sand Goby is rather difficult. Furthermore, goby otoliths found in the diet samples were often heavily worn, making it impossible to identify the species. Therefore, only a minor proportion (e.g. 34% in Slavonian Grebes) of all goby otoliths could be assigned to one of the two species. However, the large proportion of Common Gobies (95% and 93% of all determinable goby otoliths in Red-necked and Slavonian Grebes, respectively) indicates that this species occurred in much larger quantities in the diet of the analysed birds compared to Sand Gobies. In Great Crested grebes, no differentiation was made in the identification of the otoliths of both goby species.

Fish size and biomass

Overall, fish lengths consumed differed remarkably between different fish species (Fig. 3.11). The median length and range of gobies, sticklebacks and flatfish found in the stomachs was rather small, while values were considerable higher in sandeels, Ruffe and Pike-perch. Great Crested Grebes took significantly larger Ruffe ($p = 0.002$) but smaller gobies ($p = 0.008$) than Red-necked Grebes. Differences in Three-spined Sticklebacks were not significant ($p = 0.76$).

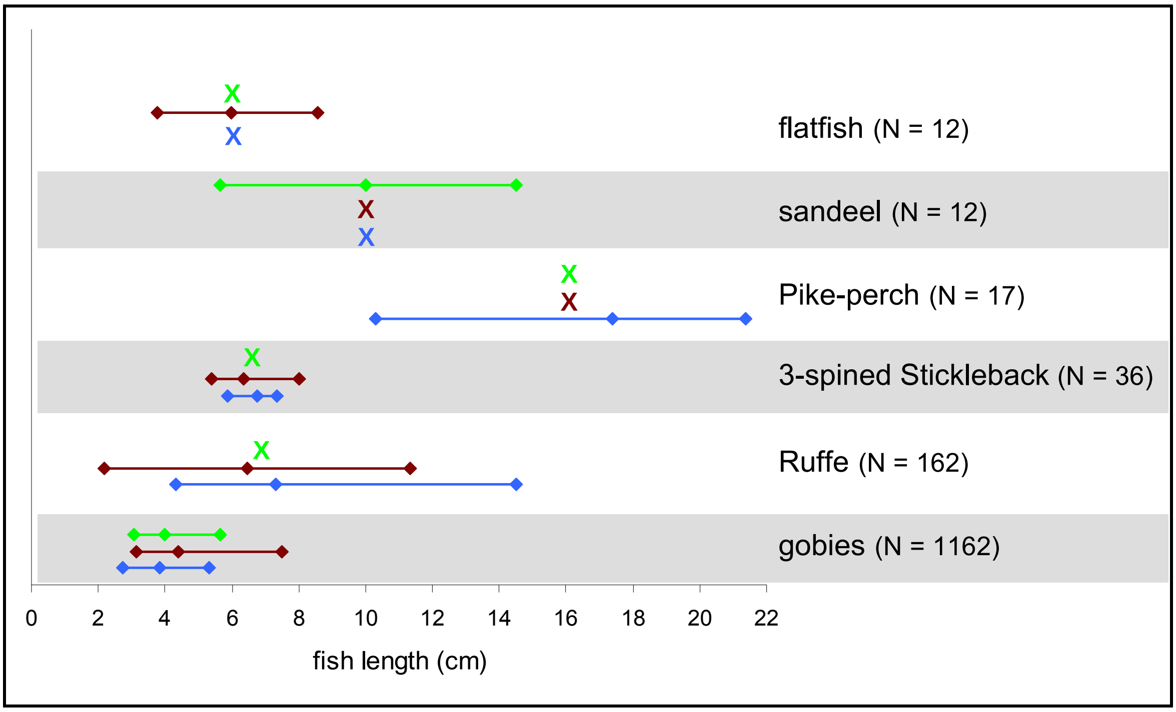

Fig. 3.11. Prey size of the most important fish species in the diet of Great Crested (blue), Red-necked (red) and Slavonian Grebes (green) drowned in set nets in the Pomeranian Bight. Rhombi indicate minimum, median and maximum values. Crosses indicate that fish of the respective group either had not been consumed by the respective grebe species or could not be measured.

The unequal prey sizes accounted for differences in prey biomass (Fig. 3.12). Gobies (Gobiidae), the most important species regarding numerical abundance in all three grebes, also dominated the diet of Red- necked and Slavonian Grebes with respect to total consumed biomass and accounted for 90.3 and 87.0%, respectively. In Great Crested Grebes, percids (Percidae) comprised the majority of consumed fish biomass (79.7%), due to the large size of the specimens taken. The differences between Great Crested and Red-necked Grebes were significant for gobies and percids ($p < 0.001$, respectively), but not for sticklebacks (Gasterosteidae; $p = 0.55$).

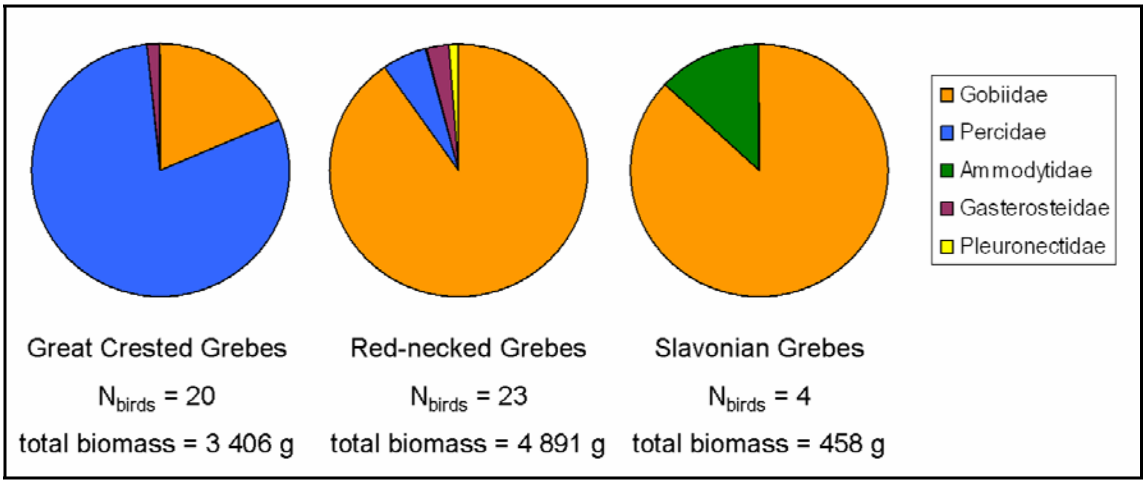

Fig. 3.12. Relative proportions of fish biomass consumed by grebes drowned in set nets in the Pomeranian Bight. Only fish families comprising at least 1% of the total fish biomass were considered.

Invertebrates and putative fish prey

With regard to numerical abundance, polychaete worms (nereids) were the second most frequent prey group found in the stomachs. However, due to their very small median length (1.6 cm in Great Crested and Red-necked Grebes, 1.3 cm in Slavonian Grebes) they accounted for less than one percent of the total prey biomass in all three species. Although polychaete worms could not be identified to species level by jaws alone, they probably originated from Ragworms due to their high abundance in the study area (M. Zettler, pers. comm.). Ragworms are buried in the sediment during most of their life but small specimens occur in the upper parts of the sea bottom (Dierschke et al., 1999; M. Zettler, pers. comm.). However, it is unclear weather such small individuals were taken directly by grebes or originated from the stomachs of the fish prey (**see Chapter II**).

Some stomachs also contained remains of insects, but they were too heavily worn to be counted completely. A few individuals could be identified as hydrophile beetles that frequently occur in waterside vegetation. The grebes might have pecked them from the water surface or directly from plants in the reed lining parts of the study area, as they commonly do in the breeding areas (see Fjeldså, 2004).

Some (fragments of) shells of gastropods and bivalves were also found in the diet samples. However, in most cases they were very small, and are thus considered to either originate from the stomachs of the (fish) prey or to have been accidentally taken by grebes while catching other prey from the sea bottom.

Discussion

“Not until we reach the extreme confines of life, in the arctic regions or on the borders of an utter desert, will competition cease.” Charles Darwin: On the origin of species by means of natural selection, 1859.

Theoretical background on competition

Competition has been considered to be a primary structuring mechanism in bird communities from early on and it is a fundamental principle of competition theory that decreasing resources increase competition between sympatric species (Lack, 1971). There are at least two ways in which competition between species can occur: exploitation competition involves the more efficient use of resources by one species, leaving less for competitors. Interference competition includes processes by which the activities of one species prevent the use of resources by other species (Maniscalco et al., 2001). Interference can be active, a result of direct antagonistic behavioural interactions, or passive, when the superior species obstructs the availability of a resource to another species by non-aggressive behaviour, e.g. food gathering. Exploitation competition should lead to niche partitioning via reduced resource overlap, while interference competition should lead to niche partitioning via reduced spatial overlap. However, beside these factors, many other selection pressures may act upon competing species and their ability to respond to selection to reduce competition might be greatly modified or inhibited. Research on birds indicates that active interference is very common, while exploitation and passive interference is often difficult to detect (Maurer, 1984; Maniscalco et al., 2001).
Lack (1971) stated that resource partitioning, either by habitat segregation or by ecological specialisation, enables closely related species to coexist in the same geographical area. Both strategies can be found in seabird communities. Various studies on the distribution of seabirds at sea suggest that spatial partitioning while foraging may be a common mechanism to avoid ecological overlap (e.g. Weimerskirch et al., 1988; Ballance et al., 1997). Other authors pointed out the existence of adaptations that can act in the segregation of other niche dimensions, like variations in timing of breeding, differences in diet or differential use of foraging areas (e.g. Croxall and Prince, 1980; Lance and Thompson, 2005). However, competition for food in seabirds has predominantly been studied during the breeding season, when food requirements are high and when parent birds are tied to a relatively localised area around the breeding sites where they have to return regularly to feed the chicks. In this context, it has been discussed controversially if prey

depletion around breeding colonies has an influence on colony size and colony distribution (e.g. Ashmole, 1963; Furness and Birkhead, 1984; Hunt et al., 1986; Cairns, 1989; Ainley et al., 1995). In areas with superabundant food resources, different species are apparently able to coexist in the same area without competition (e.g. Furness and Birkhead, 1984; Ainley et al., 1995; Sapoznikow and Quintana, 2003). Other competition studies involved interspecific concentrations of birds foraging on local (natural or artificially created) prey patches. Ballance et al. (1997) described that in areas of high productivity interspecific competition, mainly interference but also exploitation competition plays an important role in the structuring of the feeding flock communities. In birds aggregating behind fishing vessels to feed on fishery waste, flock composition is known to affect the foraging success of different species (Furness et al., 1992; Garthe and Hüppop, 1994; Garthe and Hüppop, 1998).

Segregation strategy of wintering grebes: could Spletzer's hypothesis be corroborated?

In grebes, intensive active interference during the breeding season has been described e.g. by Spletzer (1974) and Fjeldså (2004). Grebes colonise only those waters which provide good conditions not only for breeding (e.g. suitable nesting sites), but also for chick raising (e.g. suitable and sufficient food supply), and in most areas such habitats are restricted, leading to enhanced population densities and increased competition. Outside the breeding season, birds are more flexible in their distribution. According to the hypothesis of Spletzer (1974), decreasing population densities in the spacious wintering areas should result in diet specialisation as a strategy to avoid competition instead of spatial segregation like in the breeding areas. This part of the hypothesis, however, could be rejected by the results of the present analysis, which rather revealed a spatial segregation of the three species wintering in the southern Baltic Sea. The separation is most distinctive between Great Crested Grebes on one side and Red-necked and Slavonian Grebes on the other, but less obvious between the latter species. At first sight, this might be due to the fact that Slavonian, in contrast to Red-necked Grebes, only occur in the eastern part of the study area and potential for overlap is thus a priori reduced. However, a small-scaled analysis of the spatial interactions between Red-necked and Slavonian Grebes in the Pomeranian Bight confirmed that both species negatively influence the occurrence of each other also in this restricted area where they contemporaneously occur. Moreover, the absence of Slavonian Grebes from the western part of the study area might already be the result of interspecific competition, as areas suitable with regard to the relevant habitat factors water depth and bottom sediment type do exist (see **Chapter II**).

On the other hand, the overall diet composition of the three species is very similar, with a dominance of fish and gobies as the most important fish species with regard to numerical abundance. Red-necked and Slavonian Grebes also correspond in the importance of gobies with regard to biomass values and thus show no indication for a separation through different dietary niches. Great Crested Grebes differed from the two other species mainly due to a larger number of Ruffe and the occurrence of some large Pike-perch, the latter completely missing in the diet spectrum of the other two grebe species. Although the numerical importance of percid fishes (Percidae) was low compared to gobies, their much greater length accounted for significant differences in biomass values. However, it is difficult to judge if this result indicates a real difference in diet with the implication of dietary niche separation between Great Crested Grebes and the two other species. As the differences in distribution are much more distinctive than the differences in diet, the latter might be a consequence of the distribution patterns. Pike-perch and Ruffe are freshwater fish species. Due to the low salinity they also occur in the Pomeranian Bight, and within the bight they are more numerous in the lagoons and nearshore areas strongly influenced by riverine freshwater influx than in the offshore areas (Hahlbeck and Müller, 2003; Thiel et al., 2007). Thus, they are probably more available to Great Crested Grebes that also occur in these areas. The diet of Red-necked Grebes, which are also found in some coastal areas, consisted at least of some Ruffe, while percids were completely absent from the diet of the offshore occurring Slavonian Grebes. Although morphological differences in the three grebe species might allow them to feed on different prey sizes, only Great Crested Grebes partly did this in our study. Slavonian Grebes wintering in Lake IJsselmeer, the Netherlands, took on average larger individuals of the main prey European Smelt than Red-necked Grebes, although the bill of the latter is almost twice as large as the bill of Slavonian Grebes (Piersma, 1988). The author concluded that swimming agility of the bird rather than bill dimensions may determine food selections. However, Piersma (1988) also noted that cross-section rather than fish length probably is the most important parameter to compare with bill size of the predator, and Red-necked Grebes in the IJsselmeer took larger European Perch, another percid fish species with a thicker body compared to the slender European Smelt, than Slavonian Grebes. Pike-perch and Ruffe also have a rather high body profile. However, their low number or complete absence in the diet of Red-necked and Slavonian Grebes rather suggest a consequence of the different distribution patterns of the birds.

Hence, grebes wintering in the southern Baltic Sea are spatially segregated rather than ecologically. This is in contrast to Spletzer’s hypothesis of dietary niche partitioning outside the breeding season.

Why should competition occur in wintering areas?

Several reasons could be responsible for the spatial segregation of grebes in the southern Baltic Sea. In the first place, the question arises if competition really is the mechanism behind the observed distribution patterns. Why should there exist any potential for competition in marine wintering areas at all, as the spatial scale of open oceans seems unlimited relative to freshwater systems? However, more than ten thousand individuals of grebes winter in the southern Baltic Sea, and even in wide-ranging areas, food is not superabundant but may be patchily distributed. Furthermore, suitable areas for birds (like grebes) foraging on or near the sea bottom are limited by water depth due to maximum energetically possible diving depths. This strongly restricts the extent of adequate wintering areas and leads to increased bird densities. Beside, energetic requirements for endothermic animals are high during winter, especially for relatively small-sized grebes, while on the other hand, energetic coasts of foraging are high in diving species. Depth has a particularly strong effect on diving energetics and grebes probably forage regularly more than 10 m deep. Additionally, low water and air temperatures result in elevated energetic coasts for e.g. the maintenance of body temperature, higher diving activity to catch more food, and the heating of cold prey in the stomach, and are thus a constraint for small endothermic birds wintering at sea (e.g. de Vries and van Eerden, 1995; Wiersma et al., 1995; Enstipp et al., 2006). Being energetically probably at or near the limit, any additional energy expenditure, e.g. as a consequence of competition via increasing foraging times as a result of lower prey density or antagonistic behaviour against competitors, might result in negative effects on body condition. In consideration of these aspects, it seems likely that competition also occurs outside the breeding areas and that grebes exhibit strategies to mediate coexistence. Although potential prey in the southern Baltic Sea is probably much more abundant than in the usually considerably smaller freshwater breeding sites, the presented data are suggestive that the grebes avoid competition by a spatial rather than by a dietary segregation. Maybe in the larger wintering areas, spatial segregation is the better strategy to meet the high energy demands of the large number of birds in species which have similar foraging strategies and, as pursuit-hunters, a wide foraging radius under water. Under the conditions outlined above, it might be better to separate from competitors spatially instead of giving up a valuable prey resource, the more so as partitioning of food resources will result in stronger intraspecific competition (Noordhuis and Spaans, 1992), which could be especially disadvantageous for the highly aggregated Great Crested and Slavonian Grebes.

Conclusion

Can competition explain the separated distribution patterns?

The presented results, in combination with the rationale that competition can act as a structuring mechanism even outside the breeding area, indicate that the distribution patterns of grebes wintering in the southern Baltic Sea could really be a strategy to avoid interspecific competition. This is further supported by the fact that Slavonian Grebes, in winter mainly restricted to offshore areas, occur in high numbers along the coast of Usedom during spring migration, when Great Crested Grebes have already left this area (see **Chapter I**), in contrast to winter. Whether the stronger separated Great Crested Grebe is the dominant species, displacing the other two grebes into less suitable feeding habitats like presumed for the breeding areas by Spletzer (1974), can only be speculated. Despite the critics on Spletzers theory (Vlug, 1993; see above), the fact remains that the conditions in the majority of breeding waters in Europe, with the exception of very large lakes, do not allow for a habitat sharing via the utilisation of different dietary niches. This also seems to apply to the wintering areas in the southern Baltic Sea. The less clear separation between Red-necked and Slavonian Grebes might be due to their comparably lower abundances. This might result in less interference between the species, permitting their occurrence in identical habitats and the feeding on identical diets, while avoiding direct competition by spatial segregation only in areas with highest abundances.

4 Seabirds and set nets: assessment of conflict potential and vulnerability of birds to bycatch in gillnets in the southern Baltic Sea as tools for conservation management

Abstract

The accidental catch and drowning of birds in gillnets is documented from marine areas worldwide and is considered to have a major impact on bird populations. The quantification of bycatch mortality, however, is rather difficult, and its effect on population level is hardly known. In this study, a spatial overlap approach is presented to indicate the potential conflict for diving birds in relation to gillnet fisheries in the southern Baltic Sea, based on data of diving bird abundances and fishing activities. Secondly, a vulnerability index based on relative bird abundances is developed indicating the maximum susceptibility of birds towards drowning. Bird abundances and fishing activities exhibited spatial and temporal variations. Potential conflict and vulnerability indices were highest during winter and spring in coastal areas and on shallow offshore grounds. The approach presented in this paper provides a valuable tool for conservation management purposes. The analysis of potential conflict indicates priority areas and priority periods, for which the development of conservation measures is of paramount importance. The vulnerability index indicates important areas in terms of diving bird abundance irrespective of fisheries and enables the development of maximum options for conservation management. Accordingly, a suite of measures, like temporal or spatial restrictions, can be derived, despite a serious lack of real data on bycatch and mortality rates. This approach is particularly useful for impacts that are difficult to monitor and where the degree of mortality could not properly be addressed, like artisanal gillnet fisheries. It can provide a baseline for the development of an environmentally sound fishing practice in marine areas worldwide.

Introduction

Static fishing gear is commonly used in the Baltic Sea fisheries and the use of gillnets has substantially increased since the 1990s (ICES, 2007). Gillnets are entangling nets placed vertically in various depths of the water column and can be anchored (set nets) or drifting freely (drift nets). In the Baltic Sea, set nets are widely used and they are mainly operated in the coastal fisheries to target Atlantic Cod, Atlantic Herring, Pike-perch, flatfish and salmonids as well as various freshwater or migratory species (ICES, 2007; Pedersen et al., 2009b). Bottom-set nets usually extend up to 6 m from the sea floor, while nets for pelagic species like Atlantic Herring are set in mid-water. Since the 1970s increasing attention has been paid to the subject of bird mortality in gillnets. Due to the high mortality rates reported and their possible impact on populations, bird bycatch is now an important issue in terms of species protection as well as nature conservation (e.g. ICES, 2008; Soykan et al., 2008; Pedersen et al., 2009a). Bycatch of seabirds in gillnets is documented from all countries bordering the Baltic Sea, and the risk of entanglement is particularly high for diving species. Surface-feeding birds are less affected, as they forage only on or a few centimetres below the water surface. A recently published review on seabird mortality in gillnets summed up the results of national and local studies to a conservative estimate of at least 73 000 birds dying annually in gillnets in the Baltic Sea (Žydelis et al., 2009). However, as bycatch studies are usually carried out on small scales or in short time series, this figure is a likely underestimate and the actual number of birds drowning is probably much higher (Žydelis et al., 2009).

In the southern Baltic Sea, diving piscivorous and molluscivorous bird species are highly abundant. About 773 000 sea ducks, 10 250 grebes, 5 600 divers and 5 800 auks winter in the German part of the Baltic Sea. During summer, the area is used as moulting site, e.g. by sea ducks and grebes (Mendel et al., 2008). At the same time, an intensive fishery with set nets takes place in coastal and offshore waters. The quantification of seabird bycatch, however, is difficult and overall figures are not available. Several small-scale studies reviewed in Žydelis et al. (2009) suggest that at least 20 000 birds are annually bycaught in the German sector of the Baltic. Our study overcomes the lack of bycatch studies by developing a spatial overlap approach to indicate the potential conflict for diving birds in relation to set net fisheries, following the rationale that overlap is proportional to bycatch mortality. In addition, the vulnerability of diving species towards set net mortality is assessed in terms of a relative abundance index. Overlap has already been applied to indicate potential interactions between fisheries and marine mammals (Herr et al., 2009) and is an essential element of ecological risk assessment (Fock et al., 2008). The presented approach enables the derivation of conservation management options for impacts that are difficult to monitor and where the degree of mortality could not properly be addressed.

Methodology

Study area and species considered

The study area is the German part of the Baltic Sea with a focus on both territorial waters (inshore of the 12 nm borderline) and offshore waters of the Exclusive Economic Zone (EEZ; Fig. 4.1). Very shallow nearshore waters could not be included in the study. Large areas of the coastal and offshore waters have been designated as Special Protection Areas (SPAs) within the EU Natura 2000 network of protected areas (Fig. 4.1). They comprise about 45% of the total German Baltic Sea area.

Only species that forage for food by diving, either pursuit or bottom diving, were considered in the present study. We included only those diving species occurring regularly at sea (defined here as the area located at least 1 km off the coast) and with an average total of at least 100 individuals in the German Baltic Sea.

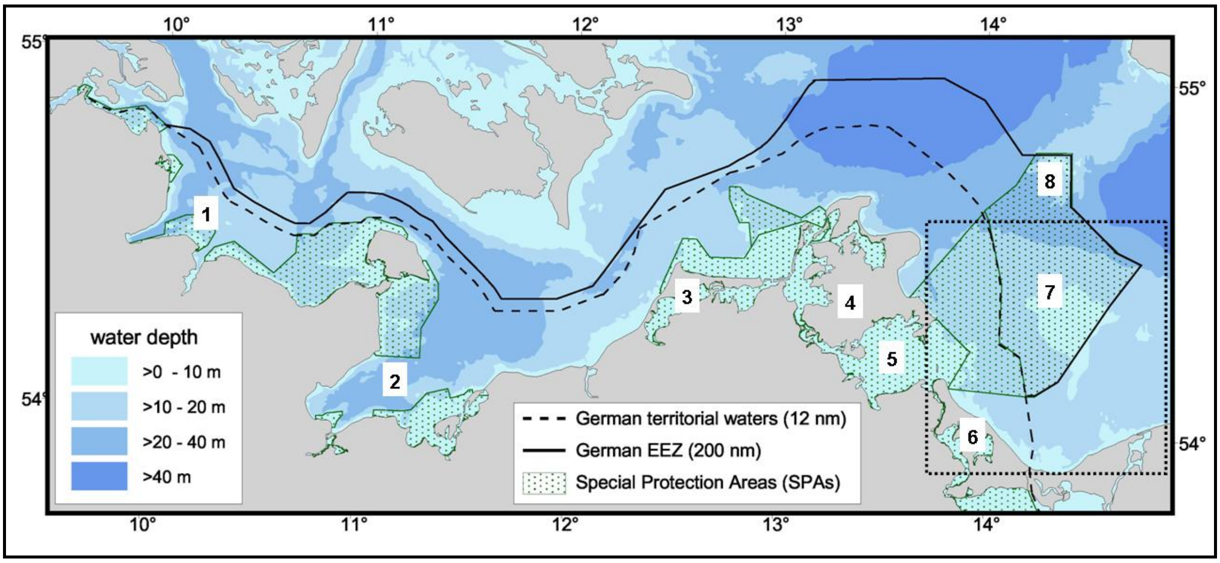

Fig. 4.1. Study area in the southern Baltic Sea with localities referred to in the text: 1) Kiel Bight, 2) Mecklenburg Bight, 3) Darss-Zingst peninsula, 4) Island of Rügen, 5) Greifswald Lagoon, 6) Usedom peninsula, 7) Odra Bank, 8) Adlergrund. The spotted box defines the Pomeranian Bight. Hatched areas indicate Special Protection Areas (SPAs) in the coastal and offshore zones, designated within the EU Natura 2000 network.

Recording of birds at sea

The distribution of seabirds at sea was studied by ship-based transect counts following an internationally standardised method for northwest European waters (e.g. Tasker et al., 1984; Camphuysen and Garthe, 2004). All flying and swimming birds were recorded within successive 1-minute intervals from the top deck or bridge-wing on one or both sides of the research vessel. According to Tasker et al. (1984), transect width is defined by default as a 300 m wide band set parallel to the ship's track. For this study, however, all birds, inside and outside 300 m sidewise, were recorded as far as they could be correctly identified by experienced observers. Transect width thus depended on observation conditions, but counts in unfavourable conditions, i.e. sea state higher than five (according to *Beaufort* scale; Dietrich et al., 1975) and visibility less than 1.1 km were excluded from further analyses. The length of the transect segments ahead was the distance the ship covered each minute and therefore depended on ship speed. The observers searched for birds with naked eyes, but in addition the census area was regularly scanned with binoculars to search for individuals diving or flushing in front of the approaching vessel. Geographic positions were recorded in 1-minute intervals to link all bird observations to their respective position. All bird data used in this study were taken from the German *Seabirds at Sea* database version 5.12 (June 2008; Garthe et al., 2007) that contains more than 30 000 travelled ship kilometres in the southern Baltic Sea 2000 to 2008.

Determining the resolution of the analysis

To account for intra-annual variability in the occurrence of birds and in fishing effort, 2-monthly averages for the entire time period 2000 to 2008 were chosen as reasonable seasonal resolution to provide a spatial coverage for most of the area covered by the German Baltic sector compatible with the VMS records (see Herr et al., 2009). Grid cell size was determined by the resolution of the bird counts at sea, resulting in cells of the size of 2` longitude x 3` latitude (amounting to a total grid size of ca. 12 km²).

Vulnerability of birds towards drowning mortality

The vulnerability of diving birds towards drowning in set nets was analysed by mapping their relative abundances. Abundances were expressed as the number of individuals counted per distance travelled to correct for unequal counting effort. Relative abundance was calculated for each species *i* by dividing the abundance per grid cell *c* ($n_{c,i,s}$) by its average abundance in each seasonal period *s* ($N_{i,s}$), to account for numerical differences in total population of the species. The sum of the relative abundances of all species was then used as vulnerability index $V_{c,s}$ for each grid cell:

$$V_{c,s} = \sum_i \frac{n_{c,i,s}}{N_{i,s}}$$

Vulnerability was classified on a 5-point scale according to the quartiles of its distribution: none: 0, low: >0-0.15, moderate: >0.15-0.86, high: >0.86-2.69, very high: >2.69.

Set net fishing activities

Two different fleets undertake set net fisheries in the German Baltic Sea, each represented in our study by a self-contained data set and measure of activity. A national fleet of small boats operates mainly in the German territorial waters, while an international fleet comprising vessels larger than 15 m mainly operates in the offshore waters of the German EEZ. The latter is equipped with a vessel monitoring system (VMS, see below), so that a year round activity pattern of the vessel can be obtained. For the smaller boats, fishing effort can be assessed e.g. by a measure related to the gear, i.e. counting of set net flags.

Recording of set net flags during seabird surveys

This data set is mostly representative of the fleet of smaller boats and the inshore areas, but also provides observations for the offshore waters. During the ship-based seabird counts described above, the occurrence of set nets was recorded as the number of flags per 1-minute counting interval. For the present study we analysed data from the German *Seabirds at Sea* database, containing information on set net flag distribution in the German Baltic Sea area for the years 2000 to 2008. These flags were recorded systematically along the survey line on both sides of the vessel as far distant as visible with the naked eye. Additionally, we included data for the eastern part of the study area from an ecological impact assessment (EIA) study in the period 2006 to 2008 (data provided by Jochen Bellebaum, IfAÖ). Those set net flags were recorded only on one side of the survey vessel. We therefore multiplied their abundance by two to correct for the unequal counting methods of both data sets. The total abundance (number of flags per distance travelled) was calculated from both data sets combined. Set net flag data collected in unfavourable counting conditions (i.e. sea state higher than five and visibility less than 1.1 km) were excluded from the analysis. Annual counting effort for each 2-month-period is shown in Table 4.1.

Table 4.1. Annual survey effort for the recording of set net flags at sea per 2-month-periods. The total data set contains combined data from the German *Seabirds at Sea* database (2000-2008) and from an ecological impact assessment (EIA) study (2006-2008).

	Jan. - Feb.	Mar. - Apr.	May - Jun.	Jul. - Aug.	Sept. - Oct.	Nov. - Dec.
2000	-	601	39.5	800.3	-	657.5
2001	1 537.5	1 429.6	66.9	97.8	-	132.3
2002	216	1 228.5	824.4	237.9	525.5	1 663.9
2003	395.2	829.1	-	1 960.7	912.8	1 643.1
2004	195.4	1 152.0	837	796.4	873.8	612.1
2005	548.1	796.8	1 052.4	-	986.1	711.2
2006	502.9	1 050.2	936.1	1 067.8	744.8	983.4
2007	1 823.8	1 598.2	-	380.3	116.1	1 301.2
2008	785.7	1 593.1	211.7	-	-	-

Vessel Monitoring System (VMS)

This data set is mostly representative of larger vessels operating in offshore waters. Since 2005, vessels larger than 15 m overall length are obliged to operate VMS (Fock, 2008). While prior to 2006 only position and time data were available for foreign vessels within EEZ bounds, complete data including vessel code, position, time, speed and direction are distributed to EU member states for their national fleets for all waters and for foreign vessels operating within their national EEZ from 2006 onwards (Fock, 2008). For the present study we analysed all available VMS data of set net vessels for the German Baltic Sea for the years 2005 to 2007 (data: Heino Fock, vTI), applying a protocol developed by Fock (2008). VMS data were filtered by ship speed to exclude steaming vessels from the analysis. Most VMS recordings were made at 1-h and 2-h intervals, but also shorter intervals were applied. Data were averaged for the period 2005 to 2007, counting the number of days with VMS records. We chose the parameter of VMS-positive-days per grid cell to avoid biases by single boats being recorded frequently and thus simulating high fishing effort.

Combination of the different data sets on fishing activities

Information on fishing activities based on either gear information, i.e. flag counts, that are roughly related to net lengths but not to soak time, or vessel activity information, i.e. VMS–positive-days, were combined to obtain an overall measure for fishing effort. The precision of flag sightings depends on survey coverage and survey intervals, so that some activities are certainly overlooked. In turn, the precision of VMS based patterns depends on the correct algorithms to distinguish fishing activity from other activities during the observation period so that effort might be over- or underestimated. However, important information on the gear as soak time, net length and net height are not available, so that the combined index merely serves as a proxy to indicate true set net fishing effort.

The rationale behind combining VMS-positive-days (hereafter VMS) and flag counts is that for VMS equipped vessels, both types of data should be available in the same area unit with a linear relationship between both. However, in mixed fisheries in particular in inshore areas, additional flag counts originating from the inshore fleet without VMS recorders likely impose a bias to the VMS-flag counts conversion, leading to a relatively low VMS-to-flag count ratio.

As a first step in the derivation of a conversion factor, the distribution of the VMS-to-flag counts ratio is mapped to test whether the basic rationale is applicable (Fig. 4.2). The ratio is fairly log-normal, and the normalised log of the ratio is separated into four categories, i.e. < -0.5 indicating predominance of flag counts, -0.5 to 0 and 0 to 0.5 supportive of a linear relationship with variability and > 0.5 indicating predominance of VMS. Three inshore areas have prevailing negative logs showing predominance of flag counts in line with the underlying assumption of a strong inshore influence of vessels without VMS (areas 3, 5, and 7 in Fig. 4.2). In turn, four areas (areas 1, 2, 6 and 8 in Fig. 4.2) show a balanced combination of negative and positive logs. The presence of two of the areas (6 and 8) is in concordance with the German gillnet fleet structure in 2008 (Table 4.2), indicating that the domestic VMS-vessels likely operate to some degree in the western section of the investigation area. In turn, the eastern part of the German fleet is characterised by an increasing number of small vessels in both categories 7.5 to 15 m and < 7.5 m. These small vessels likely prefer inshore waters, and inshore fishing effort should be more conspicuous in the respective area (see Fig. 4.4). In turn, the international fleet mostly operates offshore beyond the 12 nautical mile line represented by the remaining two log patches (areas 1 and 2 in Fig. 4.2).

As second step in the derivation of the conversion factor, regression analysis was carried out for seasonally resolved averages for VMS and flags for areas 1, 2, 4, 6 and 8. Areas and time periods are listed in Table 4.3.

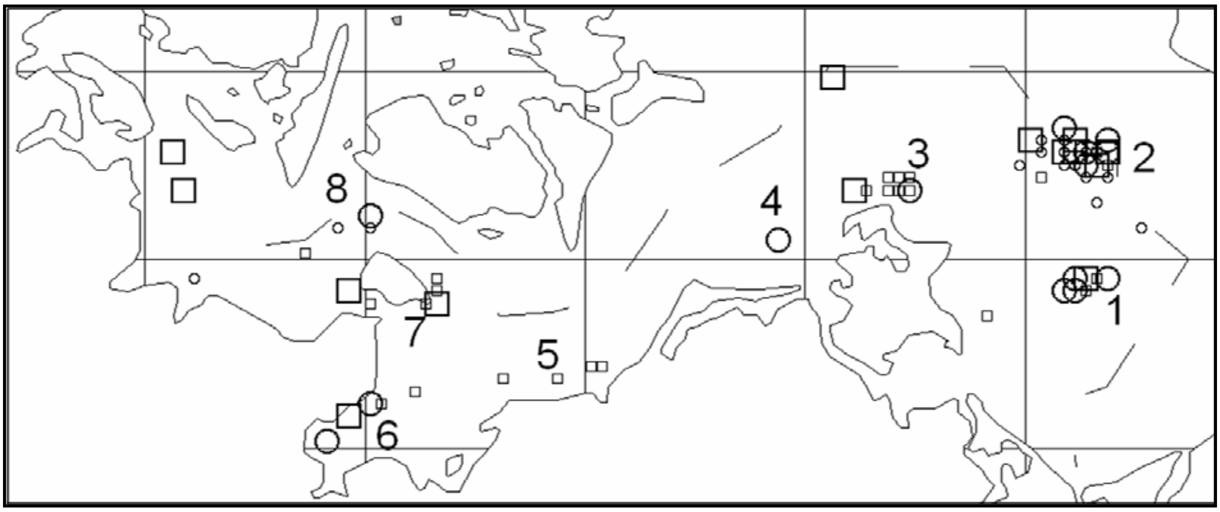

Fig. 4.2. Distribution of normalised log-ratios for the relationship VMS over flag counts without seasonal resolution in the southern Baltic Sea (H. Fock). Small squares indicate negative values < -0.5, indicating relatively much more flag counts than VMS. Small circles indicate values > 0.5, indicating much higher VMS compared to flag counts. Large squares (-0.5-0) and large circles (0-0.5) indicate values around the mean in support of a linear relationship. Three areas (3, 5 and 7) show mainly negative logs with a likely high contribution of non-VMS vessels. Only data from areas 1, 2, 4, 6 and 8 were used in the regression analysis to calculate the conversion factor between VMS and flag counts.

Table 4.2. German gillnet fleet structure in 2008. MVP – Mecklenburg-Vorpommern (eastern section of the investigation area), SH – Schleswig-Holstein (western section of the investigation area).

Area	Number of German vessels		
	< 7.5 m	7.5-15 m	> 15 m (VMS)
Baltic-MVP	591	271	-
Baltic-SH	463	103	6
North Sea	30	20	1

Table 4.3. Areas and periods selected to calculate a conversion factor for set net flag abundance versus VMS. Only grid cells with both VMS and flag counts were used and summed for the respective area and period. Area numbers refer to Fig. 4.2.
*In Jan. - Feb. 2006 the Adlergrund was not covered by flag count surveys, so the 2006 VMS value was excluded from regression analysis.

Period	Used in regression	Area (Area No.)	VMS days	Flag abundance per km travelled
Jan. - Feb.	+	Adlergrund* (2)	210	1.9
Jan. - Feb.	+	Odra Bank (1)	3	0.1
Jan. - Feb.	+	Lübeck Bight (6)	3	0.7
Jan. - Feb.	+	Fehmarn (8)	19	0.4
Mar. - Apr.	+	Adlergrund (2)	53	2.1
Mar. - Apr.	+	Odra Bank (1)	2	0.1
Mar. - Apr.	+	Lübeck Bight (6)	25	1.6
May - Jun.	+	Adlergrund (2)	170	6.1
Jul. - Aug.	+	Adlergrund (2)	2	0.2
Sept. - Oct.	+	Odra Bank (1)	14	2.1
Nov. - Dec.	+	Adlergrund (2)	120	1.9
Nov. - Dec.	+	West of Rügen (4)	5	0.1
Jan. - Feb.	-	Rügen inshore (3)	13	6.7
Nov. - Dec.	-	Rügen inshore (3)	12	7.1

The regression was forced through the origin to avoid calculation of spurious flag counts when no vessel was present at all. Further, the regression depended on the leverage from the high VMS values for area 2 (Adlergrund). Two different SAS regression algorithms were applied to evaluate the robustness of the results depending on the optimisation method (SAS *proc reg* and *proc robustreg*; SAS Institute Inc., 2003). *Robustreg* estimates for the conversion factor ranged between 0.12 and 0.34 reflecting high variability in the regression data though regressions were significant in all cases. The least squares estimate of 0.0203 was used for further analysis.

The following rules for the data sets were applied both for the EEZ and the territorial waters to calculate combined set net fishing effort:

(1) If no flag counts but VMS data were given, fishing effort $E_{c,s}$ in terms of flag counts was calculated from the regression parameters for the offshore relationship: $E_{c,s}$ = VMS*0.0203.

(2) If flag counts and VMS were given, then flag counts were taken under the assumption that both fleet segments were represented properly, i.e. $E_{c,s}$ = flag counts per cell per season.

Intensity of current conflict

Based on data on fishing effort, combined from VMS and flag counts, and data on relative abundances of diving bird species (see above), the overlap of birds and set net fishing activities was calculated as potential conflict and displayed in six bi-monthly conflict maps. For each grid cell *c*, the relative bird abundance of all species ($V_{c,s}$) was multiplied by the combined fishing effort $E_{c,s}$ to obtain the value of potential conflict ($PC_{c,s}$): $PC_{c,s} = V_{c,s} * E_{c,s}$.

PC was classified on a 5-point scale according to the quartiles of its distribution: none: 0, low: >0-0.02, moderate: >0.02-0.11, high: >0.11-0.58, very high: >0.58.

Results

Vulnerability assessment: distribution of bird species sensitive to set nets

17 species of diving seabirds and waterbirds regularly occurred in the coastal and offshore waters of the southern Baltic Sea. The winter period was of major importance, when their numbers summed up to nearly one million individuals (Table 4.4). However, the study area was also intensively used as staging ground during migration and for some species it additionally served as resting and moulting site during summer. 15 species occurred in numbers larger than 1% of their respective biogeographic populations and three species even exceeded 10%.

The relative abundance of diving birds and thus their vulnerability towards drowning mortality in set nets exhibited spatial and temporal variations (Fig. 4.3). After leaving their breeding sites, most species arrived in the study area in October and November. In autumn, vulnerability was especially high in the western coastal areas and offshore in the Pomeranian Bight. Relative abundances peaked in winter and spring and resulted in high or very high vulnerability in many coastal areas and in large parts of the Pomeranian Bight, particularly on the shallow offshore grounds Odra Bank and Adlergrund and within the Greifswald Lagoon. Only in areas with deeper water (e.g. Arkona basin north of Rügen) vulnerability was lower. During summer, bird abundance and thus vulnerability was low in many parts of the study area, except around the Odra Bank, where the year-round presence of diving birds resulted in permanent vulnerability.

Table 4.4. Estimates of mean mid-winter numbers of diving seabirds and waterbirds in the German Baltic Sea, taken from Mendel et al. (2008). Numbers for Common Goldeneye and Goosander were taken from Garthe et al. (2003). Only species regularly occurring at least 1 km off the coast and with an average total of at least 100 individuals were considered. Biogeographic population sizes were taken from Wetlands International (2006), those of auks from Bellebaum et al. (2006).

Species	Number German Baltic Sea	Size of biogeographic population	Proportion of biogeographic population (%)
Common Eider	190 000	760 000	25.0
Greater Scaup	66 000	310 000	21.3
Common Scoter	230 000	1 600 000	14.4
Goosander	22 500	266 000	8.5
Long-tailed Duck	315 000	4 600 000	6.8
Razorbill	3 600	55 000	6.5
Red-breasted Merganser	10 500	170 000	6.2
Slavonian Grebe	1 000	14 200 - 26 000	5.0
Velvet Scoter	38 000	1 000 000	3.8
Common Goldeneye	38 500	1 000 000 - 1 300 000	3.4
Common Guillemot	1 500	50 000	3.0
Great Cormorant	10 500	380 000 - 405 000	2.7
Great Crested Grebe	8 500	290 000 - 420 000	2.4
Red-necked Grebe	750	42 000 - 60 000	1.5
Red-throated Diver	3 200	150 000 - 450 000	1.1
Black Guillemot	700	75 000	0.9
Black-throated Diver	2 400	250 000 - 500 000	0.6

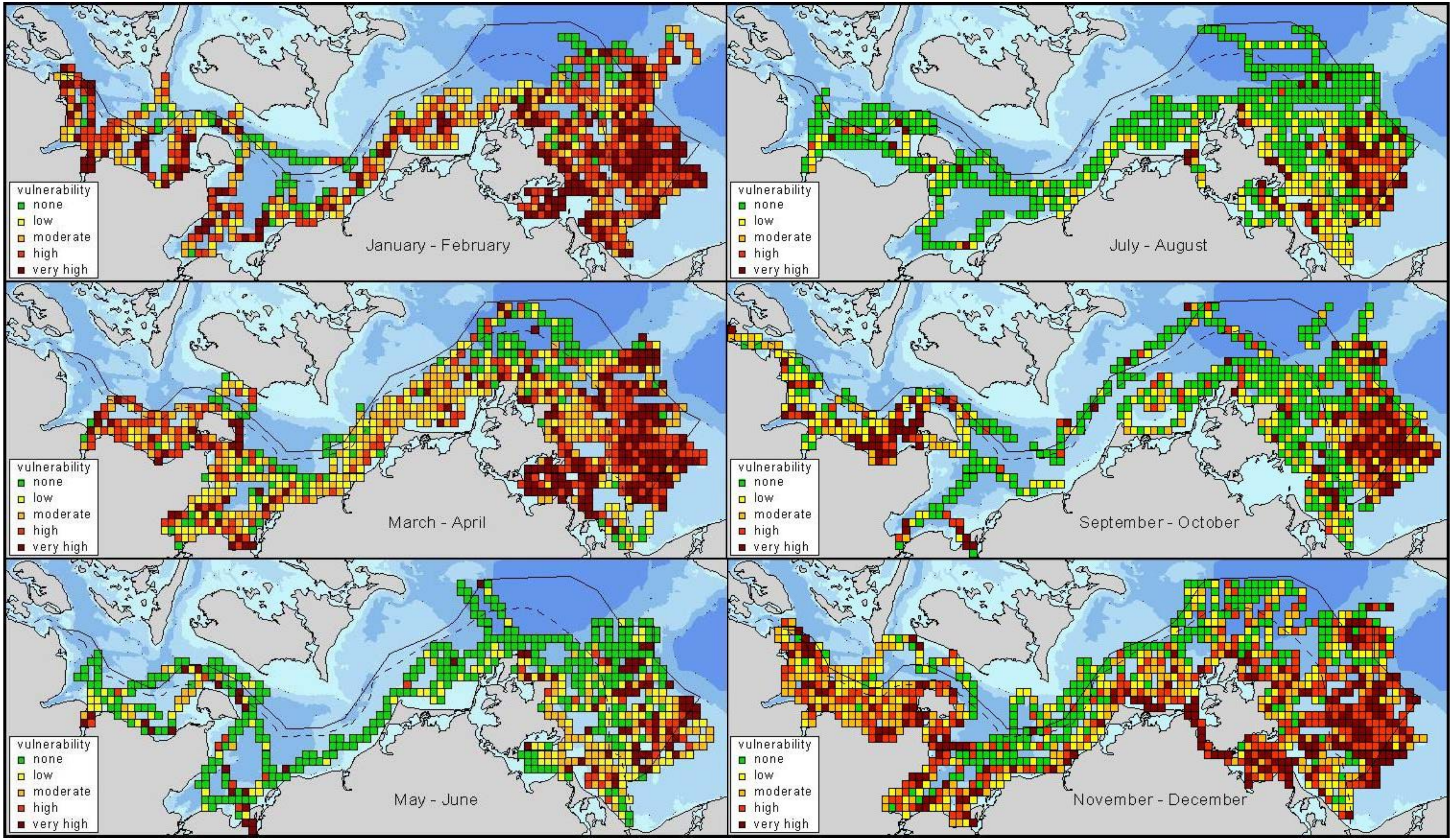

Fig. 4.3. Vulnerability of birds towards mortality in set nets in the southern Baltic Sea 2000-2008. Included are 17 species of diving birds, scaled by relative abundance. Vulnerability was classified on a 5-point scale according to the quartiles of relative bird abundance Jan.-Dec. 2000-2008: none (green): 0, low (yellow): >0-0.15, moderate (orange): >0.15-0.86, high (red): >0.86-2.69, very high (dark red): >2.69.

Set net fishing activities in the southern Baltic Sea

Set net flags were most abundant along the coastal areas of Rügen and Usedom in the eastern part of the study area, where they were recorded throughout the year (Fig. 4.4). Especially large concentrations occurred in the Greifswald Lagoon and along Usedom in spring. High or moderate numbers of flags were also found locally along the coastal areas of Kiel Bight and Mecklenburg Bight in winter and spring. In the offshore areas, set net flags were observed around the Adlergrund from January to June and in the Odra Bank area in late spring and summer.

VMS data, representing the fleet of larger fishing vessels, indicated the occurrence of set net fisheries in large parts of the study area from November to April (Fig. 4.5), with highest intensities in the offshore areas of Kiel Bight and Mecklenburg Bight and around the Adlergrund during midwinter. From May to October, VMS data were mainly recorded from the northeastern offshore areas, especially around the Adlergrund and north of Rügen. While high numbers of set net flags were recorded along the coast of Kiel Bight and Pomeranian Bight, VMS records indicated only very low set net fishing activities in these areas.

Intensity of current conflict

The potential conflict of diving birds and set net fisheries was most pronounced in winter and spring, with moderate to very high values in many coastal waters and in the offshore areas of the Pomeranian Bight, particularly around the Adlergrund (Fig. 4.6). In March and April, conflict values were remarkably high in the Greifswald Lagoon and along the coast of Usedom. Apart from a few locally high values, no conflict existed in the western part of the study area in summer and autumn. However, it was then moderate to very high in some coastal and offshore areas of the Pomeranian Bight, indicating a high year-round local potential conflict in this area.

In April 2005, very high abundances of set net flags were recorded in the Greifswald Lagoon. At the same time, high numbers of Long-tailed Ducks occurred in this area and were often observed in direct vicinity to set net flags (Fig. 4.7a). During a survey in May 2005, large numbers of Common Scoters and set net flags were recorded simultaneously around the Odra Bank area (Fig. 4.7b). Both surveys were representative for the distribution of the species in the studied areas and season. This analysis demonstrated that a direct overlap between the occurrence of birds and set net fisheries actually exists and is not artificially created by pooling the data.

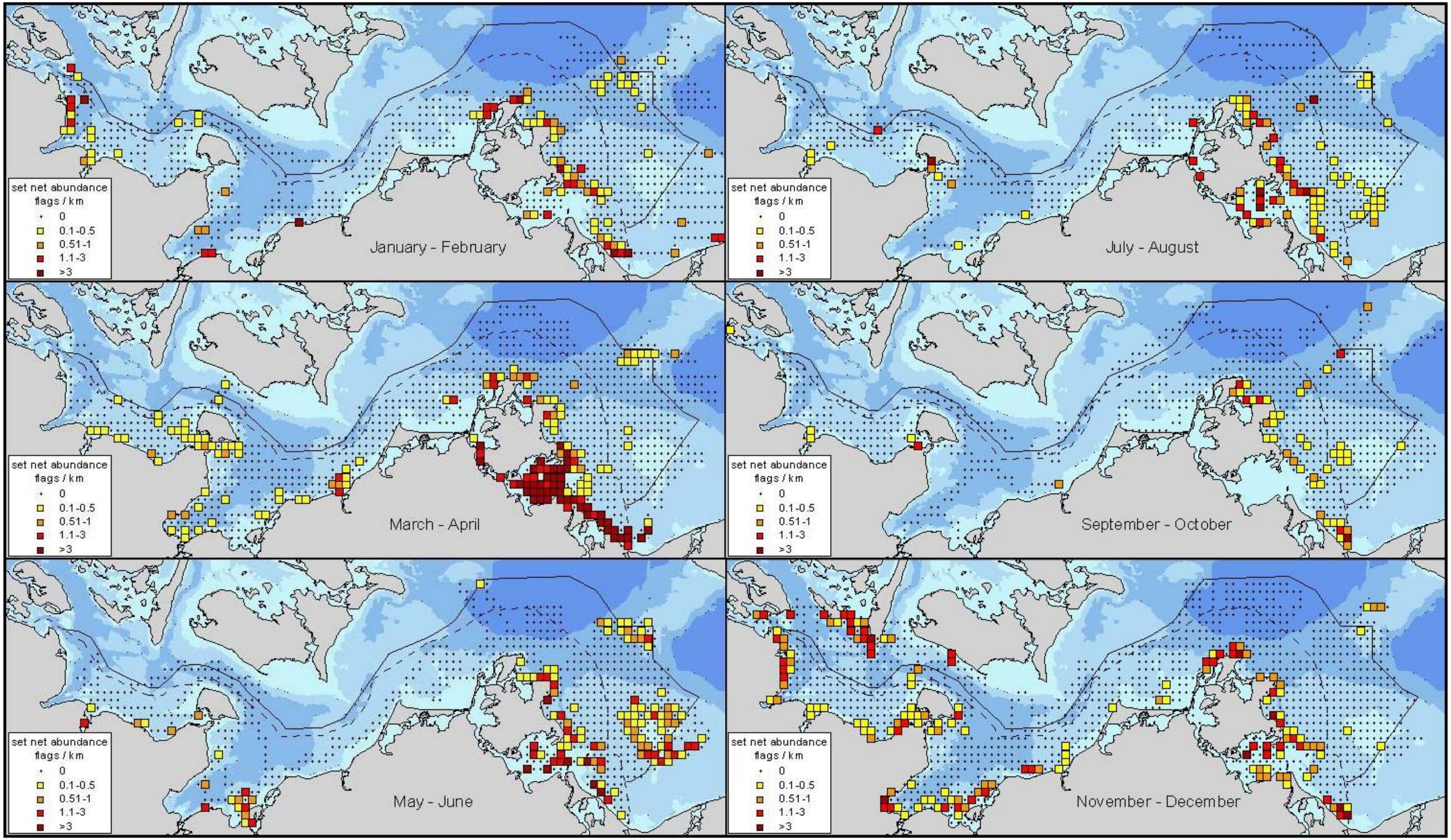

Fig. 4.4. Distribution of set net fishing activities in the southern Baltic Sea, based on ship-based counts of set net flags 2000-2008.

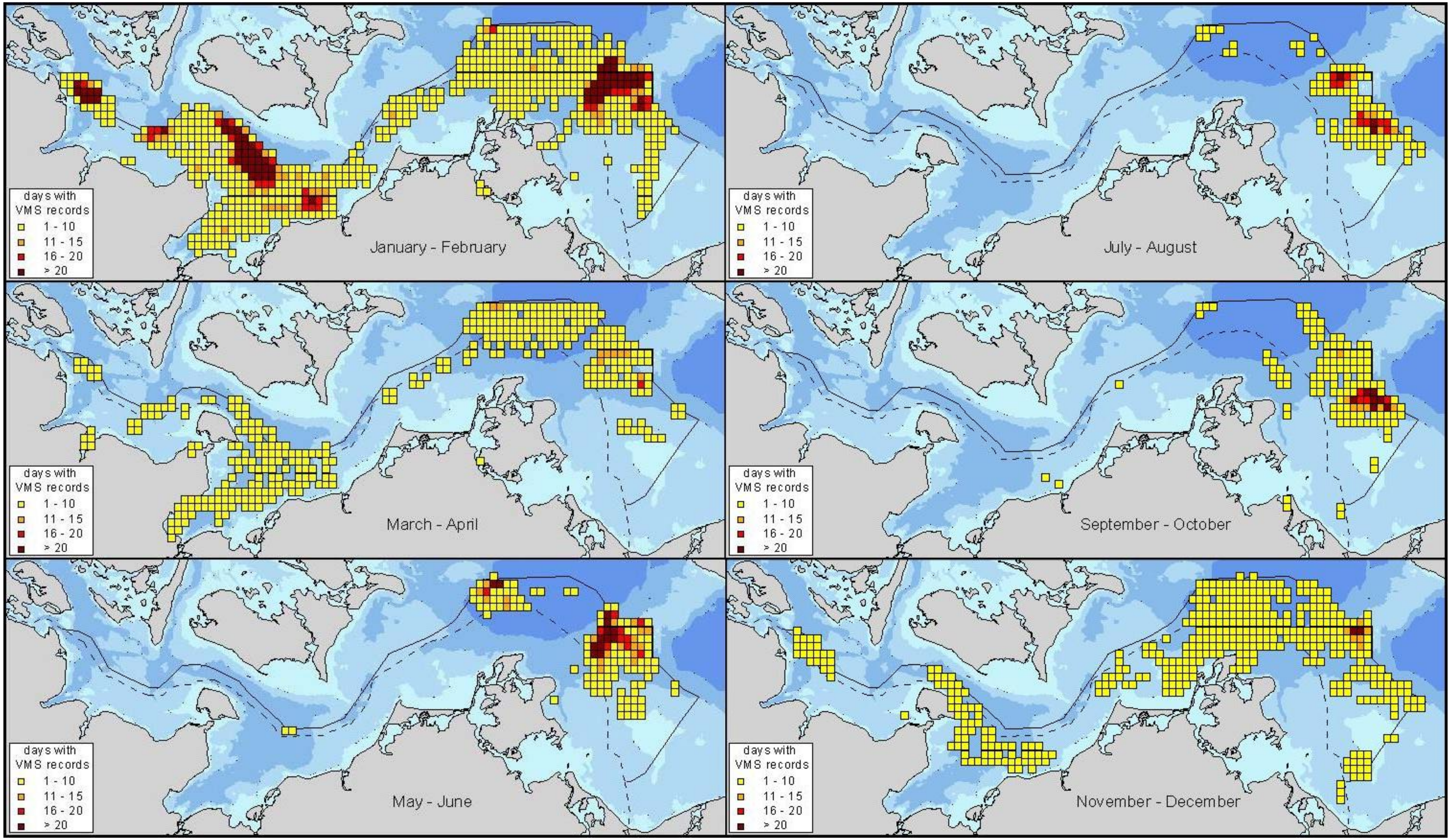

Fig. 4.5. Distribution of set net fishing activities in the southern Baltic Sea, based on records from the Vessel Monitoring System VMS 2005-2007.

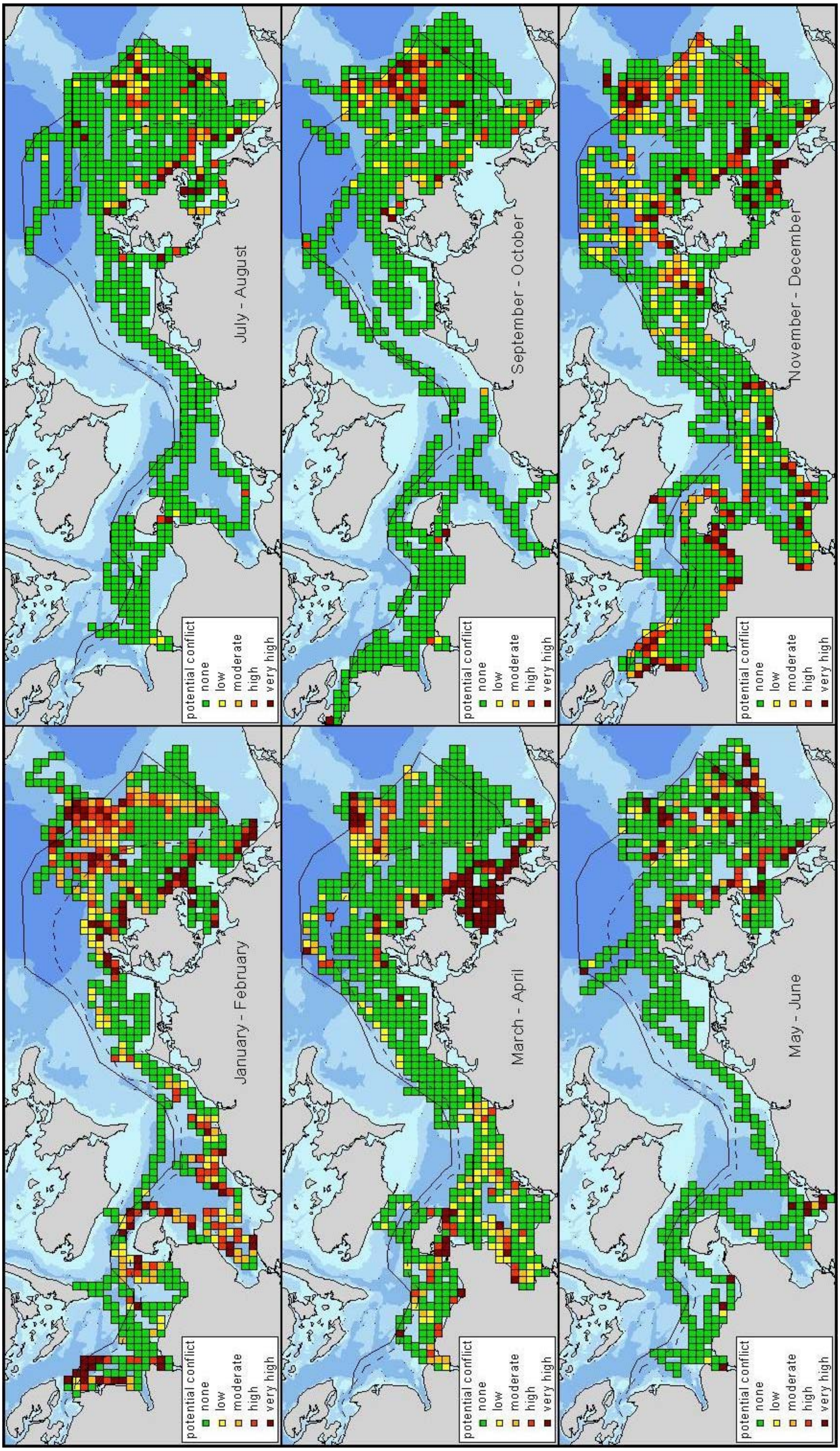

Fig. 4.6. Overlap of set net fishing activities and relative abundances of diving bird species in the southern Baltic Sea 2000-2008, illustrated as potential of conflict (PC). PC was classified on a 5-point scale according to the quartiles of potential conflict Jan.-Dec. 2000-2008: none (green): 0, low (yellow): >0-0.02, moderate (orange): >0.02-0.11, high (red): >0.11-0.58, very high (dark red): >0.58

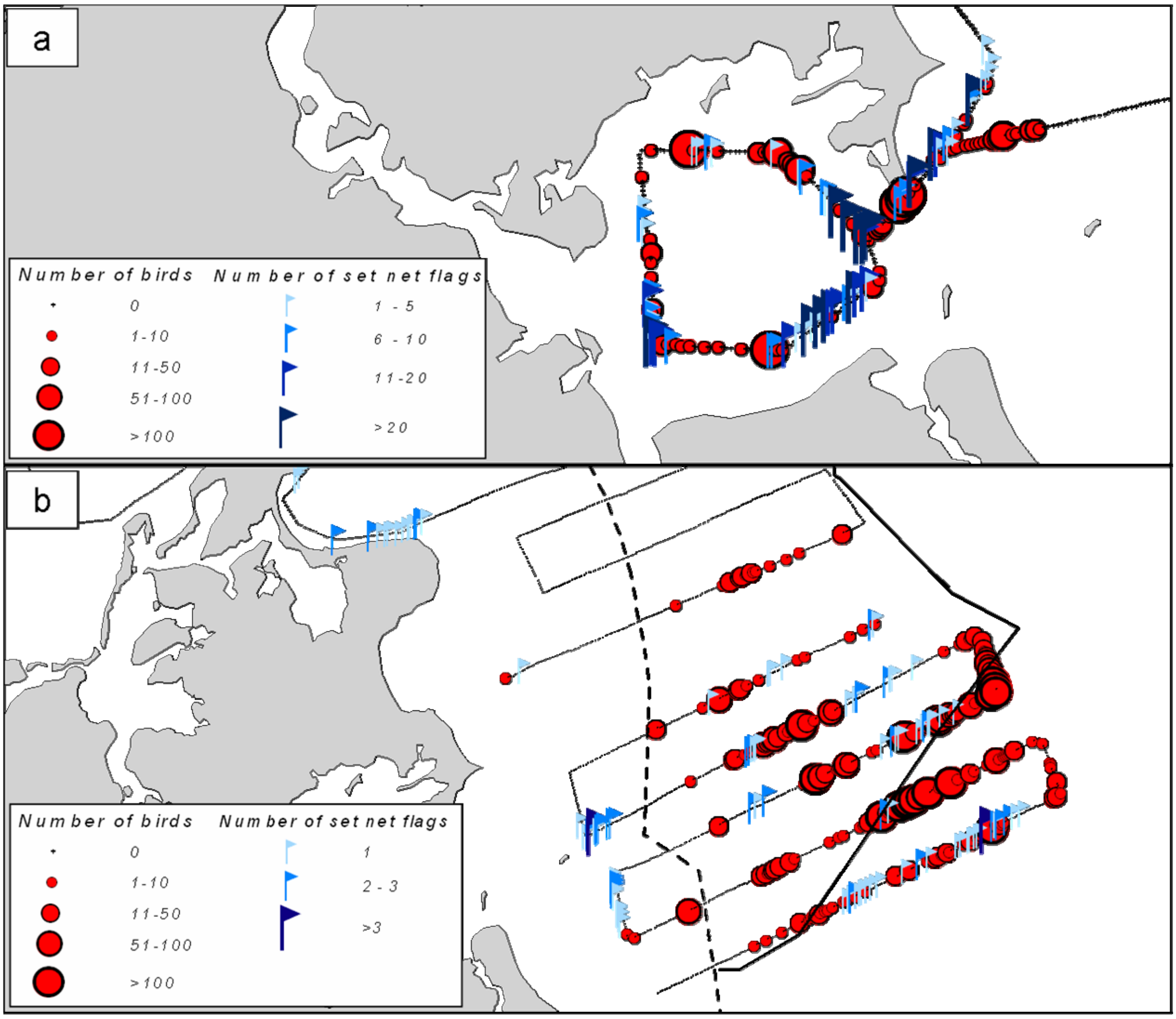

Fig. 4.7. Distribution of set net flags and a) Long-tailed Ducks in the Greifswald Lagoon in April 2005 and b) Common Scoters on the Odra Bank in May 2005, adapted from ship-based counts. Birds and flags are presented as numbers per 1-minute counting interval. Note the different scaling of set net flags in both pictures.

Discussion

Methodical considerations

The differences between the distribution of set net flag observations and fishing activities recorded by VMS show that each method is likely representative of a different fishery that partly overlap. Inshore set net fishing in the southern Baltic Sea is predominantly operated locally with very small boats (see Table 4.2 and e.g. Pedersen et al., 2009b), and are therefore not recorded by VMS which is only operating on larger vessels. Hence, although the precision of sightings depends on survey intervals and coverage, and flag counts thus only represent the situation during the surveys, the counting of set net flags in addition to VMS data is an essential and appropriate method in the attempt to describe set net fishing activities as complete as possible, given the lack of other adequate sources of information. Important parameters for set net fishing effort such as a measure of net length and soak time are not available (e.g. Fock, 2008; Žydelis et al., 2009). While the number of flags in any given area is roughly related to the length of the nets set but not to soak time, VMS records only the duration of fishing activity for each vessel irrespective of the size of the nets operated. Hence neither of the two methods measures actual fishing effort completely, but the significant flag count-VMS regression suggests a strong relationship between both and a combined data set provides a valuable basis for the assessment of fishing activities.

Due to methodical reasons, VMS and set net flag records could include some data from fishing activities with longlines that could not be separated from the data on set net fisheries. However, longline fishing is of minor importance in the German Baltic sector, accounting for an annual catch of some 340 t as compared to > 11 000 t for gillnets (Pedersen et al., 2009b). Thus, we assume that the distribution and abundance of set net fishing presented in this analysis is not biased from longline fishing.

Conflict between seabirds and set net fisheries

For trophic reasons, fish, fisheries and marine birds concentrate in the same food-abundant regions of marine ecosystems, and this spatial and temporal overlap inevitably leads to conflicts (Stempniewicz, 1994). Bycatch in fishing gear is one of the most important pressures for birds in coastal seas and supposed to be responsible for some local population declines (e.g. Strann et al., 1991; Stempniewicz, 1994; van Eerden et al., 1999; Österblom et al., 2002). According to Lien et al. (1989), monofilament gillnets typically account for the largest numbers of incidental catches of marine birds and mammals. These nylon nets are almost invisible to diving birds (Furness, 2003) and they are more dangerous with increasing mesh size (Dagys and Žydelis, 2002). Numerous published studies document that diving birds are accidentally killed in gillnets in nearly all Baltic Sea regions (reviewed in Žydelis et al., 2009). The overall extent and importance of bycatch, however, has not yet been assessed. So far, studies of bird bycatch have been carried out locally and mostly with different methods and approaches, preventing the evaluation of its effects on population levels (see Žydelis et al., 2009). In the southern Baltic Sea the best indication of the dimension of bird bycatch in set nets is available from Kirchhoff (1982) and Schirmeister (2003), but their studies focus on only small parts of the German waters.

With a lack of large-scale bycatch studies in the German Baltic sector, the present approach of spatial overlap of fishing effort (e.g. VMS and set net flag data) and bird abundance data enables us to describe areas of potential conflict, under the assumption that true bycatch is proportional to overlap. Simultaneous observations of birds and set net flags hereby prove the existence of actual overlap. The main conflict areas in the southern Baltic Sea were identified in many coastal areas and offshore in the Pomeranian Bight and around the Adlergrund in winter and spring. In one of the few bycatch studies existing for German Baltic Sea waters, Schirmeister (2003) summed up more than ten thousand birds that drowned in set nets along the coast of Usedom in the period September to May 1989 to 2001 and has collected further victims each following winter (B. Schirmeister, pers. comm.). This confirms that birds are actually killed in set nets in areas where our maps indicate high conflict potential. Another area with high overlap is the Greifswald Lagoon, which is one of the most important spawning sites of the western Baltic spring spawning stock of Atlantic Herring (Gröhsler, 2003). This results in a very high set net abundance in the lagoon in March and April (up to 70 flags per km!) but also attracts large numbers of Long-tailed Ducks which use Herring spawn as an additional food source in spring (Leipe, 1985). On some cruises, the manoeuvrability of the survey vessel was hindered by the high abundance of set nets, and onboard guidance by an experienced fisherman was needed to avoid entanglement of the research vessel aside the main shipping routes. Set net fisheries occurring in very shallow waters off the Darss-Zingst peninsula and in the lagoons around Rügen (J. Bellebaum, unpubl. data) are not represented in our maps, as these areas could not be surveyed by ships.

Fishing activities can change from day to day, based on weather conditions and fish availability, as well as on a yearly basis, depending on factors like total allowable catch and effort allocation, market and fuel prices or catchability (ICES, 2008). As flag counts only represent the situation during the surveys, some conflict areas might have been undetected so far, due to an incomplete mapping of fishing activities. The consideration of conflict maps alone might thus lead to misinterpretations of the actual threat to birds. As indicated by the vulnerability maps, diving species concentrate in coastal areas and on shallow offshore grounds, mainly up to 20 m water depth. Considering thus an average diving depth of the birds of about 20 m and an average net height for bottom set nets of 6 m, all waters up to 26 m water depth are prone to potential conflict, and mortality is likely to occur as soon as any set net fishing takes place. In deeper waters, bycatch risk is comparatively low, but Razorbills and Common Guillemots also occur and forage in such areas. Vulnerability is most pronounced during winter and spring due to highest bird abundances, but the Odra Bank in the offshore area of the Pomeranian Bight is of great importance year round. During summer, Common and Velvet Scoters use this area as moulting site (Sonntag et al., 2004), as well as a so far unknown number of Great Crested and

Red-necked Grebes (FTZ, unpubl. data). During moult, when birds are unable to fly, they can react to disturbances only by diving, thus possibly further increasing their vulnerability towards entanglement in set nets. Consequently, any set net fishing activities on the Odra Bank at any time of the year bear the potential of high seabird mortality, a fact that could not have been derived by considering conflict maps alone.

Implications for conservation management

Mid-winter numbers of 15 species in the German Baltic Sea exceed the 1% level of their respective biogeographic population and three species even exceed 10% (Table 4.4). Red-throated Divers, Black-throated Divers and Slavonian Grebes are listed on Annex I of the EU Birds Directive (Council Directive 79/409/EEC), all others are migratory species according to that Directive. Most species are additionally relevant for AEWA (Agreement on the Conservation of African-Eurasian Migratory Waterbirds, www.unep-aewa.org/), and some are named on the Red Lists because of negative population trends, small biogeographic populations or geographical restrictions. German conservation responsibility is thus high for these species.

The reproductive strategy of most seabirds (e.g. divers and auks) is characterised by a high adult survival rate, late maturity and low reproductive output (Furness and Monaghan, 1987). In species with such life histories, adult survival rate is a key parameter of population dynamics (e.g. Cairns, 1992; Sæther and Bakke, 2000). Negative population trends are difficult to reverse, and any factor increasing adult mortality will result in particularly strong negative effects on population dynamics (Furness, 2003; Lewison and Crowder, 2003). Such species are especially vulnerable to mortality caused by human activities and impacts affecting adult survival rates, like mortality in gill nets, are thus particularly significant for seabird conservation (Tasker and Becker, 1992; Heppell et al., 2000; Furness, 2003). However, detailed demographic parameters are often unavailable and hardly feasible to obtain, especially for migratory birds that have a wide geographic distribution. The ability to predict influences of bycatch mortality on population level is thus very limited (Heppell et al., 2000; Soykan et al., 2008).

Large areas of the German Baltic Sea are protected areas (see Fig. 4.1) and the implementation of management objectives for these SPAs is currently under process. Due to the high sensitivity of diving birds towards drowning mortality and the proven occurrence of bycatch as outlined above, a change in the current performance of set net fisheries is indispensable to ensure the required bird conservation. The approach presented in this paper, involving an improved understanding of the spatio-temporal occurrence of potential bycatch events and an assessment of bird vulnerability towards bycatch, provides two valuable tools for such management purposes. Firstly, the analysis of potential conflict indicates priority areas and priority periods, for which the development of measures is of paramount importance. Secondly, the vulnerability index is indicative of outlining important areas in terms of diving birds abundance irrespective of fisheries and thus enables the development of maximum options for conservation management. For example, to achieve the goal of reducing bycatch to zero, gillnet fisheries have to be excluded from the Odra Bank area throughout the year, while in other areas temporal closures in the winter half year might substantially contribute to mitigate the potential conflict. Thus, by analysing existing information on the distribution of diving birds and set net fisheries in the presented ways, reliable conclusions for the development of conservation management measures can be drawn. At the same time, gear modifications as another option for bycatch reduction have to be developed further, like the application of visual and acoustic alerts (see e.g. Melvin et al., 1999; Trippel et al., 2003). Although, from a species conservation point of view, the effective prevention of seabird bycatch is the ultimate goal of mitigation measures, such tools should not only be evaluated by their ability to reduce seabird bycatch, but also by their economic viability and practical implementation for fisheries (Bull, 2007). Both aspects are essential to be considered, investigated and monitored to develop an environmentally sound fisheries management that on one side achieves effective protection and conservation of birds but on the other side also gives consideration to the needs of fishermen.

Conclusion

The approach described in this study, i.e. the development of management options based on the knowledge of potential conflict and vulnerability, is suggested to be generally applicable to any marine area or species worldwide. By now, we know from countless studies in the world's oceans that gillnets cause mortality of large numbers of birds and other diving animals like turtles or marine mammals (e.g. Tasker et al., 2000; Peckham et al., 2008; Scheidat et al., 2008; Soykan et al., 2008; Moore et al., 2009). With the knowledge of the spatial and temporal distribution of these species on one hand, and the occurrence of existing or intended gillnet fishing activities on the other hand, the identification of potential conflict is straightforward. Appropriate measures can be derived accordingly, without the need to further prove mortality in a specific conflict area. We consider our procedure particularly useful for impacts that are difficult to monitor and where the degree of mortality could not properly be addressed, like artisanal gillnet fisheries.

General conclusion

This thesis aimed to improve our understanding of the relationship between seabirds and the marine environment and thus to further unravel the functionality of marine habitats for seabirds in the southern Baltic Sea. It comprised investigations on seasonal and temporal variations in distribution patterns and basic principles of habitat selection (**Chapter I**), habitat modelling and diet analyses of key species (**Chapters II and III**), the influence of interspecific competition on distribution patterns (**Chapter III**) and addressed the conflict between birds and human activities (**Chapter IV**). Considerable gaps in knowledge could be filled and the understanding of the ecology of birds in the southern Baltic Sea could be substantially improved. Methods comprised the interpretation of long-term and dedicated seabirds at sea surveys, the creation of mathematical models for bird-habitat relationships and interactions between species, analyses of stomach contents and the development of a spatial overlap approach to evaluate anthropogenic impacts on seabirds. The following key questions were addressed:

- Which natural factors influence and drive the observed distribution patterns of birds at sea?
- Which is the connecting link between seabirds and the identified habitat factors?
- Which role do interspecific interactions and competition play?
- How can the impact of anthropogenic activities on seabirds be assessed?

Factors influencing the distribution of birds at sea

The most basic information about the biology of seabirds comprises their distribution patterns. These patterns are unequal in different species and often vary seasonally due to migratory movements or interannually because of oceanographic and climatic factors (Ballance, 2007). The distribution of birds in the southern Baltic Sea is reasonably well studied and the different species exhibit distinctive seasonal variations in their occurrence (Sonntag et al., 2006; **Chapter I** of this thesis). They predominantly arrive in late autumn, after leaving their subarctic or arctic breeding grounds, reach peak numbers during winter and leave again in early spring. Only few species are present year-round or only during summer. Furthermore, most species are not evenly distributed throughout the southern Baltic Sea but show preferences for certain areas. The understanding of the factors and processes causing these observed patterns is no easy task, because an ocean habitat is neither static nor homogeneous. Surface currents, physical features and water masses define distinct habitat types for oceanic organisms, but these factors change considerably in space and time (Ballance, 2007).

Seabirds often associate with physical features, and hydrography proved to be a key determinant of seabird distribution in many areas worldwide (e.g. Hunt and Schneider, 1987; Haney and Solow, 1992). In the German Bight in the southeastern North Sea, large-scale and small-scale hydrographic structures like water masses, sea surface temperature and salinity, fronts or tidal stages significantly influence seabird occurrence patterns and their variations on seasonal and daily scales (Markones, 2007; Garthe et al., 2009). Beside, meteorological factors like wind field and air pressure were found to have an influence on the composition of the seabird community and on species' distribution (Garthe et al., 2009).

Within the scope of this thesis, three fixed habitat parameters (distance to coast, water depth and bottom sediment type) and large-scale salinity gradients were investigated. An influence of these factors on the bird community in the southern Baltic Sea as well as on the habitat selection of single species was found (**Chapter I).** Detailed analyses on grebes proved that water depth and bottom sediment type significantly influenced their distribution patterns (**Chapters II** and **III**). Both factors were also described to determine the habitat selection of seaducks (e.g. Kirchhoff, 1979; Kube and Skov, 1996; Fox, 2003; Mendel et al., 2007). However, a variety of fixed and variable natural conditions can influence the occurrence and behaviour of birds at sea (see Fig. GI-1 in **General Introduction**) and their significance for different species will depend on their respective morphological, physiological and ecological adaptations, capacities and constraints. Thus, additional habitat parameters have to be considered in future investigations to further improve the ecological understanding of birds in the southern Baltic Sea. The habitat model presented in **Chapters II** and **III** of this thesis provides a good basis for such studies and can be extended to other species and habitat factors (see e.g. Garthe et al., 2009).

Diet and feeding strategies: link between seabirds and habitats

It is commonly accepted that the relationships between birds and their marine habitat mainly reflect predator (bird) – prey – relationships. Prey distribution and abundance on one hand and foraging strategies on the other are certainly the most decisive factors determining the distribution and habitat choice of seabirds at sea (Schneider and Piatt, 1986; Hunt et al., 1990; Shealer, 2002; Ballance, 2007). Hydrographic processes are most relevant for seabirds, when they cause predictable prey aggregations, either regular or irregular (Garthe, 2005). Frontal zones are often regions of biomass accumulation (e.g. Hesse et al., 1989; Maravelias et al., 2000), attracting predators like fish larvae, fishes and thereby also planctivorous or piscivorous birds (Valenzuela et al., 1991; Markones, 2007). Hydrographic processes determine foraging habitats for seabirds and are thus linked to food availability, while meteorological factors are assumed to be relevant by setting the conditions for flight during foraging trips (Garthe et al., 2009). Hereby, they are most relevant for birds feeding on or near the surface, like gulls, terns or Northern Fulmars, or for species feeding on pelagic fishes that are attracted to such regions of prey accumulation, like divers or auks (e.g. Skov and Prins, 2001; Garthe et al., 2009; Schwemmer et al., 2009). In the southern Baltic Sea, many species feed on benthic or benthopelagic prey. As they have to dive to the sea bottom to search for and catch their prey, water depth above all is likely to determine their feeding habitats. Diving capacities of endothermic animals, i.e. diving depth and duration, are limited by physiological constraints, while low temperatures during winter and the thermal properties of water cause high daily energy expenditures due to e.g. the maintenance of body temperature, higher diving activities or the heating of ingested cold prey (Wiersma et al., 1995; Guillemette et al., 2004; Enstipp et al., 2006; see **Chapters II** and **III**). Thus, foraging at the sea bottom implies a trade-off between the energetic value of food obtained from a dive versus the costs of diving and handling prey (Fox, 2003). A reduction of energetic costs by foraging in areas with lower water depth might thus be an effective strategy for (small) endothermic birds that spend the whole winter at sea.

Bottom sediment is regarded to be only of indirect influence on bird distribution, but it can be used as a proxy for the availability of sessile, buried or demersal prey species that often show preferences for specific substrate types. Birds feeding on such prey species are often likewise restricted to areas with these sediments, like Slavonian Grebes in the southern Baltic Sea (**Chapter II**). This habitat factor provides particularly valuable information when data on the spatial occurrence of prey species or on diet in general are scarce.

The role of interspecific interactions and competition on the distribution of seabirds

While large-scale physical properties of the ocean might set limits to the potential habitat of an organism, its local distribution within this habitat might be determined by ecological interactions such as competition or predation (Fauchald, 2009). As shown by Schneider and Duffy (1985) and Hunt and Schneider (1987), seabird distribution often corresponds best with physical phenomena at a large scale while biological features like foraging range, social interactions and prey availability often determine distribution patterns on smaller scales. Foraging and feeding set the stage for various interactions between birds, including predation, competition and commensalism (Ballance, 2007), and competition is widely believed to occur among seabirds at sea, mainly in the context of prey depletion around breeding colonies or within feeding flocks (e.g. Ashmole, 1963; Harrison et al., 1991; Ballance et al., 1997; see **Chapter III** for further discussion and sources). Detailed analyses on grebes proved that competition can also occur in wintering areas (**Chapter III**). Seabirds have been described to reduce interspecific competition via resource partitioning, either by habitat segregation or by ecological specialisation (e.g. Weimerskirch et al., 1988; Lance and Thompson, 2005). Grebes wintering in the southern Baltic Sea seem to mediate interspecific coexistence by spatial segregation. In this area, more than 32 000 individuals of fish eating bird species occur during winter (Mendel et al., 2008) and many of them obtain their prey by pursuit-diving. Brooke (2002) stated that this foraging method is highly energy-demanding and can only support high numbers of individuals in very productive areas, at least at a larger spatial scale. The fish fauna of the southern Baltic Sea is quite diverse due to the occurrence of marine and freshwater species (see **General Introduction**), but in the vast domains of marine areas, prey is often patchy in space and time (e.g. Ballance et al., 1997). Although the diet of the various piscivorous bird species is not fully known, the existing information (e.g. Guse et al., 2009; this thesis), together with apparent morphological differences and comparable studies from other areas (compiled in Mendel et al., 2008) suggest that they exhibit different strategies to avoid interspecific competition while wintering in the southern Baltic Sea.

Anthropogenic threats to seabirds and ways to evaluate the extent of conflicts

Enclosed by nine neighbouring countries, the Baltic Sea is an inland sea and thus strongly influenced by human activities. Due to the restricted water exchange with the open ocean, the continuous stratification and the basin structure set by underwater barriers, it is particularly sensitive to natural or anthropogenic impacts (Matthäus, 1996). Different human activities influence seabirds to various extents, depending on species-specific capacities and constraints and thus habitat requirements and feeding strategies. While on land or in coastal areas birds are mainly affected by disturbances or habitat destruction, e.g. by tourism and recreational activities or coastal zone development, the most prominent threats to birds at sea are oil pollution, ship traffic, sand and gravel extraction, the intended construction of marine wind farms and fisheries (e.g. Garthe et al., 2003; see Fig. GI-2 in **General Introduction**). The consequences of these impacts are various, and can consist in the alteration or destruction of habitats, the displacement of birds from favourable areas, prey depletion or direct mortality. While some of these threats are addressed in case studies, the overall extent of the influences and impacts on birds is often difficult, or rather impossible to evaluate. Only small proportions of dead or oiled birds are washed ashore after an oil spill, while ongoing oil pollution is even more difficult to assess. Birds colliding with technical constructions are difficult to collect, fishermen are not willing to deliver total bird bycatch in fishing gear, and, finally, how can habitat destruction and prey depletion in the vast expansions of an ocean be evaluated? Other approaches are needed to identify the whole range of human activities on seabirds, and a comprehensive knowledge of the morphological and physiological adaptations of different species and their demands on and requirements in the natural marine environment is fundamental in this context. An example was presented in **Chapter IV** of this thesis which addressed set net fisheries as probably the most prominent threat to birds in the southern Baltic Sea. Some small-scaled studies in this area have already proved the accidental bycatch and mortality of birds in set nets (e.g. Kirchhoff, 1982; Schirmeister, 2003), but overall figures are not available. Furthermore, detailed information on fishing effort, like net lengths or soak time, are not available for scientific analyses. To overcome this lack of comprehensive knowledge, an approach has been presented including an assessment of bird vulnerability towards bycatch and an improved understanding of the spatio-temporal occurrence of potential bycatch events. Based on information on feeding strategies, i.e. capturing prey under water by bottom or pursuit diving or foraging on or near the surface, species sensitive to drowning mortality were identified. Their susceptibility towards set net fisheries was described based on information on distribution and abundance (vulnerability index), while the intersection of data on bird abundances and fishing activities indicated areas of potential conflict (conflict index). This approach provides a valuable tool for conservation purposes, especially in the recently designated Special Protection Areas for birds in the southern Baltic Sea, where the implementation of management measures is currently under process, but it is generally applicable to any marine area or species in the world. Furthermore, the sensitivity of seabirds to other human impacts can be assessed the same way, and several indices have already been applied in recent years, for example with regard to wind farms, based on e.g. flight characteristics (Garthe and Hüppop, 2004), or to oil pollution, e.g. based on aggregation behaviour and the proportion of swimming activity (Camphuysen, 1989; Williams et al., 1995). Using the presented approach, ideally in combination with case studies that document the consequences of an impact, the identification of potential conflict is straightforward. Appropriate measures can be derived accordingly, without the need to further prove mortality in a specific conflict area. This procedure is particularly useful for impacts that are difficult to monitor and where the degree of mortality could not properly be addressed.

Outlook

The present thesis has substantially contributed to an improved ecological understanding of seabirds in the Baltic Sea, and has also demonstrated the relevance of such knowledge for seabird protection and conservation management. Furthermore, seabirds have many attributes that render them important as indicator or monitoring species and can therefore provide valuable information on ecological processes, health and change in the oceans (e.g. Furness and Camphuysen, 1997; Ballance, 2007). In consideration of the increasing utilisation of marine areas by humans, habitat selection and ecological requirements of all affected species need to be well known to evaluate the consequences of anthropogenic impacts in the forefront of their implementation and to take appropriate measures. Major declines in numbers have been described of certain seabird populations and species in the Baltic Sea (ICES, 2003), and anthropogenic threats are assumed to be one factor responsible for the observed trends (ICES, 2004). Seabirds and waterbirds are usually wide-ranging animals, covering large areas of the Baltic Sea during migration and paying no attention to arbitrary political boundaries. Especially in the Baltic Sea, international cooperation and joint action is needed to identify population trends and to assess the influence of natural and anthropogenic factors on numbers and distribution. Based on the information on decreasing abundances of wintering birds, the research project SOWBAS (status of wintering waterbird populations in the Baltic Sea) was set up in international cooperation in the winter periods 2006 to 2008 to investigate the distribution patterns and hotspot areas of resting birds and to calculate trends in abundances compared to data from previous studies. More such international cooperation is urgently needed for future research projects. Besides, there are still considerable gaps in the ecological knowledge of various bird species and groups, e.g. the habitat selection and diet preferences of auks and mergansers. Furthermore, the potential of different species to switch from the preferred habitats and feeding grounds to other areas, either as a consequence of long-term climatic changes, extended ice cover or anthropogenic activities, needs to be addressed in future studies. For this purpose, regular monitoring programs focusing on changes in numbers and distribution and analysing the causes of the observed variations have to be set up, not only within the Special Protection Areas, but in all areas with important seabird concentrations.

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Annex I

English, scientific and German names of bird species according to Bauer et al. (2005)

Arctic Tern	*Sterna paradisaea*	Küstenseeschwalbe
Black Guillemot	*Cepphus grylle*	Gryllteiste
Black-legged Kittiwake	*Rissa tridactyla*	Dreizehenmöwe
Black Tern	*Chlidonias niger*	Trauerseeschwalbe
Black-throated Diver	*Gavia arctica*	Prachttaucher
Common Black-headed Gull	*Larus ridibundus*	Lachmöwe
Common Eider	*Somateria mollissima*	Eiderente
Common Goldeneye	*Bucephala clangula*	Schellente
Common Guillemot	*Uria aalge*	Trottellumme
Common Gull	*Larus canus*	Sturmmöwe
Common Scoter	*Melanitta nigra*	Trauerente
Common Tern	*Sterna hirundo*	Flussseeschwalbe
Goosander	*Mergus merganser*	Gänsesäger
Great Cormorant	*Phalacrocorax carbo*	Kormoran
Great Crested Grebe	*Podiceps cristatus*	Haubentaucher
Greater Black-backed Gull	*Larus marinus*	Mantelmöwe
Greater Scaup	*Aythya marila*	Bergente
Herring Gull	*Larus argentatus*	Silbermöwe
Lesser Black-backed Gull	*Larus fuscus*	Heringsmöwe
Little Gull	*Hydrocoloeus minutus*	Zwergmöwe
Long-tailed Duck	*Clangula hyemalis*	Eisente
Mute Swan	*Cygnus olor*	Höckerschwan
Northern Fulmar	*Fulmarus glacialis*	Eissturmvogel
Northern Gannet	*Sula bassana*	Basstölpel
Razorbill	*Alca torda*	Tordalk
Red-breasted Merganser	*Mergus serrator*	Mittelsäger
Red-necked Grebe	*Podiceps grisegena*	Rothalstaucher
Red-throated Diver	*Gavia stellata*	Sterntaucher
Sandwich Tern	*Sterna sandvicensis*	Brandseeschwalbe
Slavonian Grebe	*Podiceps auritus*	Ohrentaucher
Velvet Scoter	*Melanitta fusca*	Samtente

Annex II

English, scientific and German names of fish species according to www.fishbase.org

Atlantic Cod	*Gadus morhua*	Dorsch
Atlantic Herring	*Clupea harengus*	Hering
Atlantic Salmon	*Salmo salar*	Lachs
Black Goby	*Gobius niger*	Schwarzgrundel
Broad-nosed Pipefish	*Syngnathus typhle*	Grasnadel
Common Goby	*Pomatoschistus microps*	Strandgrundel
Crystal Goby	*Crystallogobius linearis*	Kristallgrundel
Dab	*Limanda limanda*	Kliesche
European Perch	*Perca fluviatilis*	Flussbarsch
European Plaice	*Pleuronectes platessa*	Scholle
European River Lamprey	*Lampetra fluviatilis*	Flussneunauge
European Smelt	*Osmerus eperlanus*	Stint
European Sprat	*Sprattus sprattus*	Sprotte
Flounder	*Platichthys flesus*	Flunder
Garpike	*Belone belone*	Hornhecht
Great Sandeel	*Hyperoplus lanceolatus*	Gefleckter Großer Sandaal
Lesser Sandeel	*Ammodytes tobianus*	Tobiasfisch
Nilsson’s Pipefish	*Syngnathus rostellatus*	Kleine Seenadel
Pike-perch	*Sander lucioperca*	Zander
Roach	*Rutilus rutilus*	Rotauge
Ruffe	*Gymnocephalus cernuus*	Kaulbarsch
Sand Goby	*Pomatoschistus minutus*	Sandgrundel
Sea Stickleback	*Spinachia spinachia*	Seestichling
Sea Trout	*Salmo trutta trutta*	Meerforelle
Shorthorn Sculpin	*Myoxocephalus scorpius*	Seeskorpion
Straightnose Pipefish	*Nerophis ophidion*	Kleine Schlangennadel
Three-spined Stickleback	*Gasterosteus aculeatus*	Dreistachliger Stichling
Turbot	*Psetta maxima*	Steinbutt
Twaite Shad	*Alosa fallax*	Finte

Annex III

English, scientific and German names of invertebrate species according to Hayward and Ryland (1995) and Køie and Kristiansen (2001)

Baltic Tellin	*Macoma balthica*	Baltische Tellmuschel
Common Cockle	*Cerastoderma edule*	Gemeine Herzmuschel
Common Mussel	*Mytilus edulis*	Gemeine Miesmuschel
Common Shrimp	*Crangon Crangon*	Nordseegarnele
Ragworm	*Hediste diversicolor*	Seeringelwurm
Sand Gaper	*Mya arenaria*	Sandklaffmuschel

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

The chapters of this thesis are either published (**Chapter II**) or submitted (**Chapter IV**) or will very soon be prepared for submission to peer-reviewed journals (**Chapters I** and **III**). The following list provides details on my contributions to each of the multiple-author papers:

Chapter I: Characterisation of the seabird fauna of the southern Baltic Sea: spatio-temporal distribution and basic habitat selection patterns

Authors: Nicole Sonntag, Stefan Garthe, Sven Adler
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Prepared for submission

Stefan Garthe and Nicole Sonntag developed the idea for the study. Field work was conducted by Nicole Sonntag and various observers. Data analyses were conducted by Nicole Sonntag and Sven Adler. Nicole Sonntag and Stefan Garthe discussed the results, Nicole Sonntag wrote the manuscript, reviewed by Stefan Garthe.

Chapter II: A freshwater species wintering in a brackish environment: habitat selection and diet of Slavonian Grebes in the southern Baltic Sea

Authors: Nicole Sonntag, Stefan Garthe, Sven Adler
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Nicole Sonntag and Stefan Garthe developed the idea for the study. Field work was conducted by Nicole Sonntag and various observers, diet analyses were carried out by Nicole Sonntag. Data analyses were conducted by Nicole Sonntag and Sven Adler. Nicole Sonntag and Stefan Garthe discussed the results, Nicole Sonntag wrote the manuscript, reviewed by Stefan Garthe and Sven Adler.

Chapter III: Can competition explain distribution patterns of grebes wintering in the southern Baltic Sea?

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Stefan Garthe and Nicole Sonntag developed the idea for the study. Field work was conducted by Nicole Sonntag and various observers. Nicole Sonntag carried out most of the diet analyses, male Great Crested Grebes were analysed by Karoline Weber-Streidt. Data analyses were conducted by Nicole Sonntag and Sven Adler. Nicole Sonntag and Stefan Garthe discussed the results, Nicole Sonntag wrote the manuscript, reviewed by Stefan Garthe.

Chapter IV: Seabirds and set nets: assessment of conflict potential and vulnerability of birds to bycatch in gillnets in the southern Baltic Sea as tools for conservation management

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Submitted to Ecological Applications

Stefan Garthe and Nicole Sonntag developed the idea for the study. Field work was conducted by Nicole Sonntag and various observers. Heino Fock and Jochen Bellebaum provided additional data. Data analyses were conducted by Nicole Sonntag, Henriette Dries and Heino Fock. Nicole Sonntag and Stefan Garthe discussed the results, Nicole Sonntag wrote the manuscript, reviewed by Stefan Garthe, Heino Fock, Jochen Bellebaum and Henriette Dries.

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Erklärung

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

Dies ist mein erstes Promotionsvorhaben. Die Arbeit wurde keiner anderen Stelle ganz oder zum Teil im Rahmen eines Prüfungsverfahrens vorgelegt.
Die Promotion soll im Fach Zoologie erfolgen. Für die Prüfung wird die Form der Disputation gewählt. Der Zulassung von Zuhörern bei der mündlichen Prüfung wird nicht widersprochen.

Kiel, den

Nicole Sonntag