Aus dem Forschungs- und Technologiezentrum Westküste

der Christian-Albrechts-Universität zu Kiel

Distribution and habitat selection of the Common Scoter

Melanitta nigra in the eastern German North Sea

Dissertation

zur Erlangung des Doktorgrades

der Mathematisch-Naturwissenschaftlichen Fakultät

der Christian-Albrechts-Universität zu Kiel

vorgelegt von

Johanna Kottsieper

Kiel, Dezember 2020

Erster Gutachter: Prof. Dr. Stefan Garthe

Zweiter Gutachter: Prof. Dr. Martin Wahl

Tag der mündlichen Prüfung: 24.01.2020

CONTENTS

ACKNOWLEDGMENTS

First and foremost, I would like to thank Stefan Garthe for giving me the opportunity to carry out a PhD in his working group. The last four years have been filled with uncountable adventures, which I highly value and which created lasting memories. I was able to learn a lot, expand my horizon, travel to wonderful places and meet plenty of interesting and charming people. Additionally, you gave me the chance to develop and incorporate my own ideas into the thesis. I very much appreciate these experiences and I remain grateful for your support.

I would like to thank Tony Fox, who kindly agreed to get in as my second supervisor. I will remain grateful for the warm welcome at your institute and your enthusiasm, which you kept during the entire period. I very much appreciate all your support and your willingness to discuss even the smallest and silliest details.

I would like to express a special thanks to Ib Krag Petersen. You always contributed valuable insights into our discussions and were a great help to focus myself. Moreover, I am very grateful that I was able to join your field work. I very much enjoyed our time on Iceland and learned a great many things during my stay.

A special thanks goes to Nele Markones and Philipp Schwemmer. You helped me in choosing the appropriate methods and approaches to my field work and data analysis and you were supportive in teaching and guiding me during the PhD. Additionally, my thanks goes to the other members of the working group for their support and their help with the lab work, particularly Britta Egge and Daniela Koch.

I especially want to thank Ulrike Schückel for her support with the benthos analysis. I enjoyed working with you very much and remain deeply grateful for your help. Your enthusiasm for bivalves, worms and all the other crawlies has infected me and you might have turned me into a statistics enthusiast as well.

I would like to thank Sven Adler for his guidance and support in the statistical modelling. You were a great help in introducing me to the methods and handling the statistical approach.

Maria Stage and Klaus Ricklefs helped me with the collection of several samples and taught me a lot about coastal geology. I remain grateful for their support.

The Helmholtz-Zentrum Geesthacht and the Alfred-Wegener-Institut Sylt kindly provided us with research vessels for several cruises. Without the support of the vessel crews, the collection of the countless samples would not have been possible. Thus, a special thanks goes to them.

During my fieldwork, I was accompanied and supported by several people. First, I would like to thank Margus Ellermaa, Mikko Koho and Axel Zinke. Margus Ellermaa was an indispensable support in organising our trip to Finland. Thanks to his effort and enthusiasm, he always kept us motivated. Mikko

Koho and Axel Zinke have always done their best and never hesitated when we had to walk yet another long distance through the finish bogs and mires. Secondly, I would like to thank everyone, who helped with the moulting catches in Denmark. Tony Fox and Ib Krag Petersen kindly shouldered most of the organisational tasks and I remain deeply grateful for this. Christian Sonne and Mona Iykke Jacobsen provided us with their veterinary skills and although we have not been successful in the end, they always cheered on us. I very much appreciated that. Moreover, I would like to give a special thanks to Jens Peder Hounisen and Michael Albert Schmidt for driving out with us in the boats. They put in a lot of effort and they were eager to help and contribute ideas from the very beginning. I very much appreciate this.

A special thanks goes to the Integrated School of Ocean Sciences (ISOS), particularly Avan Antia and Wiebke Basse. Many things I achieved (in my professional skills as a scientist, but also regarding my personal skills) were greatly supported by or only made possible due to your PhD program. I am also very thankful for the funding support you offered me to travel to conferences. I hope that you can carry on your program and support more PhD candidates in the future.

I would like to thank the via:mento_ocean mentoring program of Kiel University, particularly Marta Chiarinotti. You offer young scientists a space in which they can freely express their thoughts and concerns regarding their future career, thus encouraging us to realise our own ideas. In my opinion, this is very helpful as there are not many chances to discuss these things with other young researchers. You supported me in defining questions relating to what I want to do in the future and you guided me in asking myself how I can achieve this. I am very grateful for this experience.

I especially would like to thank Wolfgang Fiedler. You kindly agreed to being my mentor during the via:mento_ocean program and I am very grateful for your guidance and support. I always enjoyed our discussions and very much appreciate that you were willing to share your experiences and thoughts with me on equal terms.

Lastly, I would like to thank my friends and family for their continuous support during the last years. They never grew tired of listening to my endless stories and they were willing to share this experience with me. A special shout out goes to Rahel, Danny, Christine, Bianca, and Lukas. I was able to create a lot of precious memories since you accompanied me on this journey and I will cherish them dearly.

AUTHOR CONTRIBUTION

The current thesis is based on five different chapters, which have either been submitted and are currently under review or were prepared for submission in scientific journals. In the following section, I will explain the contribution of my own and of the co-authors to each manuscript.

Chapter I

Changes in moulting and wintering distribution patterns of Common Scoter *Melanitta nigra* in the south-eastern North Sea 2006 - 2017

Johanna Kottsieper, Nele Markones, Anthony D. Fox, Stefan Garthe

Status: prepared for submission

JK was responsible for planning and conducting the study supervised by NM. NM was responsible for the Seabirds at Sea monitoring, which the data was taken from. JK carried out data analysis under supervision of NM and drafted the manuscript. ADF and SG guided the data analysis. ADF provided language checking. All authors read and approved of the manuscript.

Chapter II

Comparison of bivalve communities between moulting and wintering areas used by Common Scoter *Melanitta nigra* in the German North Sea

Johanna Kottsieper, Ulrike Schückel, Philipp Schwemmer, Anthony D. Fox, Stefan Garthe

Status: published in Estuarine, Coastal and Shelf Science Volume 229 (2019)

JK and PS were responsible for planning and conducting the study. JK carried out sample collection and data analysis and drafted the manuscript. US helped with choosing appropriate statistics and supervised the data analysis. NM was responsible for the Seabirds at Sea monitoring. ADF provided language checking. All authors read and approved of the manuscript.

Chapter III

An invasive alien bivalve apparently provides a novel food source for moulting and wintering benthic feeding sea ducks

Johanna Kottsieper, Philipp Schwemmer, Nele Markones, Anthony D. Fox, Stefan Garthe

Status: published in Helgoland Marine Research 73, 11 (2019)

JK and PS were responsible for planning and conducting the study. JK carried out sample collection and data analysis and drafted the manuscript. NM was responsible for the Seabirds at Sea monitoring. ADF provided language checking. All authors read and approved of the manuscript.

Chapter IV

Large-scale depth-related seasonal dispersal patterns of a benthic-feeding sea duck in two contrasting marine systems

Anthony D. Fox, Johanna Kottsieper, Ib K. Petersen, Nele Markones, Philipp Schwemmer, Stefan Garthe

Status: submitted to MEPS, revision requested

ADF and IKP were responsible responsible for planning the study. ADF and IKP carried out the data analysis for the Danish Baltic Sea, JK carried out the analysis for the data from the German North Sea. ADF, IKP and JK drafted the manuscript. NM was responsible for the Seabirds at Sea monitoring in German Waters. All authors read and approved of the manuscript.

Chapter V

Modelling the distribution of the Common Scoter *Melanitta nigra* in relation to environmental parameters in the eastern German North Sea

Johanna Kottsieper, Sven Adler, Philipp Schwemmer, Maria Stage, Klaus Ricklefs, Kerstin Wittbrodt, Klaus Schwarzer, Nele Markones, Anthony D. Fox, Stefan Garthe

Status: prepared for submission

This chapter used a large data set, which was compiled during a project in which many scientists were involved. PS, HV, LE, MS, KR, KW and KS were responsible for planning and conducting the study as well as collecting and analysing samples taken during this period. JK and PS were responsible for planning and conducting a part of the study, which was customised for the focus of the PhD. JK carried out the data analysis. SA helped with choosing appropriate statistics and supervised the statistical analysis together with PS. NM was responsible for the Seabirds at Sea monitoring. ADF provided language checking. All authors read and approved of the manuscript.

SUMMARY

Understanding the processes affecting the distribution of an avian (and every other) species in time and space necessitates the inclusion of a variety of factors. Choice and utilisation of a habitat should be seen in the context of energetic costs and benefits, as organisms are believed to distribute in order to enhance their survival. In this thesis, the distribution and habitat selection of the Common Scoter *Melanitta nigra* (Linneaus, 1758) a benthic-feeding sea duck spending much of its non-breeding season in the eastern German Bight, southeastern North Sea, was investigated with regard to seasonal differences. As Common Scoters are located in German Waters predominantly during their moulting and wintering season and as these periods reflect different energetic needs, this seasonal variability is expected to have an influence on how they distribute themselves relative to their food and disturbance.

To analyse distribution patterns and habitat selection, Common Scoter count data from Seabirds at Sea surveys collected in 2006-2017 were used, either from a long term data base (FTZ) or obtained from additional surveys conducted during the PhD. To relate bird distributions to their prey base, benthos and sediment samples were collected in separate moulting and wintering areas to investigate benthic community structures. In addition to sediment samples, information on supplementary environmental parameters (such as water depth or bed shear stress) was gathered during surveys or taken from the literature. To determine, which parameter(s) might have the greatest influence on Scoter distribution, Generalised Additive Models (GAMs) with Integrated Nested Laplace Approximation (INLA) were performed for the moulting and wintering season.

The results of this thesis confirmed the long term consistency in Common Scoter moulting and wintering distributions along the coasts of Schleswig-Holstein. They also revealed a recent southbound shift in dispersal patterns with more Common Scoters residing in this area during both periods. A change in prey composition caused by one particular bivalve species, the invasive alien razor shell *Ensis leei* (M. Huber, 2015) could be a possible cause for this. Due to a higher flesh-to-shell ratio and an exceptionally high abundance compared to other bivalves, this species seems to be more profitable. A comparison of core moulting and wintering areas revealed distinct differences in benthic community structures, yet the profitability of both was similar. Contrasting the distribution in two different marine environments - the German North and the Danish Baltic Sea - illustrated that despite differences in terms of habitat characteristics, Common Scoters showed the same dispersal patterns. This supports the hypothesis that they distribute in order to maximise energetic intake rates while simultaneously minimising the costs of obtaining resources. Modelling the distribution of Common Scoter in relation to environmental parameters highlighted the importance of adequately matched spatial and temporal

scales. While the results for the wintering models were quite promising (about 25 % of explained deviance in the best fitting model), those for the moulting models were less convincing (6.53 % of explained deviance in the best fitting model). Water depth, distance to coast, bed shear stress and proportion of fine sand were identified as the most influential factors significantly affecting Common Scoter distribution in all models. The selected benthos variables were not as influential as expected, probably due to a mismatch in spatial and temporal scales. While ship traffic had no significant influence in any model, the smoothing curves clearly showed that the presence of ships had strong negative impacts especially in the moulting season.

Overall, the current thesis provides new insight and more detailed knowledge into how Common Scoter distribute themselves in response to habitat characteristics during the course of the year. Recent shifts in distributions, likely based on changes in prey abundance and profitability of a single bivalve species, were identified. While a previous study proved that environmental parameters can be used to model Common Scoter distribution in the eastern German Bight on a small spatial scale, this thesis made the first attempt to expand this approach to a much larger area. Thereby, the most influential variables impacting Common Scoter dispersal during two different seasons could be identified. While this approach will need more refinement, it can be used to predict their distribution based on (a)biotic parameters including valuable information on the effects of seasonal variability. These findings will not only help us to further our understanding of the ecology of Common Scoter, which has long suffered from a lack of research interest. They will also be relevant for future management and protection strategies.

ZUSAMMENFASSUNG

Die Untersuchung von räumlichen und zeitlichen Verbreitungsmustern von Organismen erfordert die Berücksichtigung einer Vielzahl von Faktoren. Die Wahl und Nutzung eines Habitats müssen im Hinblick darauf betrachtet werden, dass Organismen sich vorranging in einer Art und Weise verbreiten, die ihre Überlebenschancen erhöht. In der vorliegenden Doktorarbeit wurden die Verbreitung und Habitatwahl der Trauerente *Melanitta nigra* (Linneaus, 1758), einer sich von benthischen Organismen ernährenden Meeresentenart, die außerhalb der Brutsaison in hohen Dichten in der östlichen Deutschen Bucht, südöstliche Nordsee, zu finden ist, unter dem Aspekt von saisonalen Unterschieden analysiert. Trauerenten finden sich in deutschen Meeren hauptsächlich während der Mauser- und Winterzeit. Da diese beiden Zeiträume von unterschiedlichen energetischen Anforderungen geprägt sind, ist davon auszugehen, dass diese saisonale Variabilität einen Einfluss auf die Verbreitung von Trauerenten im Hinblick auf Nahrungsverfügbarkeit und Störungsquellen hat.

Zur Analyse der Verbreitungsmuster und Habitatwahl wurden Daten aus Seevogel auf See (SAS) Zählungen aus den Jahren 2006-2017 verwendet, die entweder einer bereits existierenden Langzeitdatenreihe entnommen (FTZ) oder während der Zeit der Doktorarbeit gesammelt wurden. Ergänzt wurde dies durch die Sammlung von Benthos- und Sedimentproben in einem zentralen Mauser- bzw. Wintergebiet, um die Zusammensetzung von benthischen Gemeinschaften zu untersuchen. Neben den Sedimentproben wurden Information zu weiteren Umweltparametern (wie zum Beispiel Wassertiefe oder Schubspannung) erhoben oder anhand von Referenzwerten aus der Literatur bestimmt. Um herauszufinden, welche(r) Umweltparameter den größten Einfluss auf die Trauerentenverbreitung haben (hat), wurden Generalisierte Additive Modelle (GAMs) mithilfe der sogenannten Integrated Nested Laplace Approximation (INLA) für die Mauser- und Winterzeit aufgestellt.

Die Ergebnisse dieser Doktorarbeit bestätigen die langfristige Konsistenz der Mauser- und Winterverbreitung von Trauerenten entlang der Schleswig-Holsteinischen Nordseeküste. Darüber hinaus zeigten sie eine vor kurzem aufgetretene, südwärts gerichtete Verschiebung mit einem erhöhten Aufkommen in diesen Arealen während beider Zeiträume auf. Eine Veränderung in der Beutezusammensetzung, vermutlich hervorgerufen durch die zunehmende Abundanz der Amerikanischen Schwertmuschel *Ensis leei* (M. Huber, 2015), wurde als mögliche Ursache identifiziert. Aufgrund eines höheren Fleisch-Schale Verhältnisses und außergewöhnlich hohen Abundanzen im Vergleich zu anderen Muschelarten, scheint diese energetisch profitabler zu sein. Der Vergleich eines zentralen Mauser- und Wintergebietes zeigte deutliche Unterschiede in der Struktur der benthischen Gemeinschaften. Die Profitabilität beider Regionen war jedoch annähernd gleich. Ein

Gegenüberstellen der Verteilungsmuster in zwei unterschiedlichen marinen Systemen - der deutschen Nord- und der dänischen Ostsee - offenbarte, dass Trauerenten trotz der unterschiedlichen Habitatcharakteristika die gleichen Verbreitungsmuster zeigten. Dies unterstützt die Hypothese, dass die Maximierung der Energieaufnahmerate bei gleichzeitiger Minimierung der Kosten für die Beschaffung von Ressourcen die Verbreitung beeinflusst. Eine Modellierung der Verteilungsmuster in Zusammenhang mit Umweltparametern verdeutlichte die Notwendigkeit, räumliche und zeitliche Skalen aufeinander abzustimmen. Während die Ergebnisse der Wintermodelle vielversprechend waren (knapp 25 % erklärter Abweichung des besten Modells), waren die Ergebnisse des Mausermodells weniger aussagekräftig (6.53 % erklärter Abweichung des besten Modells). Wassertiefe, Distanz zur Küste, Schubspannung und Feinsandanteil wurden als die Umweltparameter mit dem größten Einfluss identifiziert, da sie in allen Modellen einen signifikanten Effekt auf die Verbreitungsmuster hatten. Die selektierten Benthosvariablen hatten jedoch einen geringeren Einfluss als erwartet. Ursache hierfür war vermutlich die Diskrepanz in räumlichen und zeitlichen Skalen. Obwohl Schiffsverkehr in allen Modellen keinen signifikanten Effekt hatte, zeigten die Smoother Kurven, dass dieser Faktor starke negative Auswirkungen besonders während der Mauserzeit hatte.

Insgesamt liefert die vorliegende Doktorarbeit neue und vertiefende Kenntnisse über die Verbreitung von Trauerenten in Bezug auf Habitatcharakteristika im Jahresverlauf. Kürzlich stattgefundene Verschiebungen der Verteilung, die wahrscheinlich durch eine Veränderung in der Abundanz einer einzelnen Muschelart hervorgerufen wurden, konnten identifiziert werden. Während eine vorherige Studie zeigen konnte, dass Umweltparameter für die Modellierung der Verbreitungsmuster von Trauerenten in der östlichen deutschen Bucht in einem kleinen Maßstab verlässlich genutzt werden können, wurde in der vorliegenden Doktorarbeit der erste Versuch unternommen, diesen Ansatz in einem weit größeren Maßstab anzuwenden. Dadurch konnten die Faktoren mit dem größten Einfluss identifiziert werden. Obwohl dieser Ansatz noch einige Verbesserungen erfordert, ermöglicht er die Vorhersage der Verbreitung von Trauerenten im Hinblick auf (a)biotische Faktoren inklusive wertvoller Informationen hinsichtlich der saisonalen Variabilität. Dieser Erkenntnisse werden nicht nur unser Verständnis von der Ökologie der Trauerente, die seit langem einem mangelnden Forschungsinteresse ausgesetzt ist, fördern. Sie haben ebenfalls eine Relevanz für zukünftige Management- und Schutzmaßnahmen.

GENERAL INTRODUCTION

Habitat selection

The distribution of a species is shaped by the need to maximise survival (Salewski & Bruderer 2007). As a consequence, habitat selection should reflect the choices of organisms made to fulfil their energetic requirements while simultaneously minimising predation risk in order to survive (Horne & Schneider 1994). The environment a species occurs in is affected by a variety of parameters either predefined by the habitat itself or by external factors such as anthropogenic activities. Besides habitat quality, conspecifics such as species interactions (within the same or between different species) can influence habitat selection as well, as these can affect population dynamics or regulations and community aggregations (Morris 2003). Prey condition however, is likely the most decisive habitat parameter controlling the distribution of a species (Davoren et al. 2003). It is characterised by prey accessibility, availability, density and abundance, prey species community structures and interactions, as well as seasonality (Harper 1982, Croy & Hughes 1991). Dispersal patterns can thus also be studied as responses to prey distributions and densities, depending on how they fulfil energetic demands during different periods (Davoren et al. 2002).

When studying habitat selection, researchers are faced with the challenge to match different spatial and temporal scales (Jones 2001). Birds for example have different energetic demands during breeding, moulting or wintering seasons, thus influencing habitat selection. Seasonal effects (weather conditions, temperatures etc.) apply to the distribution of their prey as well. Johnson (1980) suggested four different levels of habitat selection ranging from a macro- (geographical range of a species, first-order selection) to a micro scale (representing the accessibility of prey items or nest sites, fourth-order selection). Therefore, if we don't want to miss any key influences, specifying the scale of interest when investigating species habitat selection is crucial (Orians & Wittenberger 1991).

The Common Scoter *Melanitta nigra*

Although not a breeding species in Germany, up to a quarter of the Western Palearctic Common Scoter flyway population occurs in the German North (and Baltic) Sea throughout the entire year, particularly during the moulting and wintering periods (Nehls 1998, Hennig & Eskildsen 2001, Sonntag et al. 2004, Markones & Garthe 2011, Spalke et al. 2013). The moulting season extends from the end of June, when failed breeders and males arrive in German waters, until late October with the arrival of females and juveniles. These individuals spend the subsequent winter in the same areas before starting their migration back to the breeding grounds in late February and March (Mendel et al. 2008).

Common Scoters are protected under a variety of agreements. They are listed in the EU Birds Directive Annex II (regulating hunting activities) and III (prohibiting activities directly threatening individuals) (Directive 2009/147/EC). In the convention on the Conservation of Migratory Species of Wild Animals (CMS) they are mentioned among the species in need of either developing or improving international agreements for their conservation (https://www.cms.int/en/species/melanitta-nigra). Furthermore, they are included in conservation agreements of the African-Eurasian Migratory Waterbirds convention (AEWA, https://www.unep-aewa.org/en/species/melanitta-nigra). The OSPAR commission lists Common Scoter among the waterbird species, which can be used as biodiversity indicators to assess the state of marine bird populations and the quality of their environment (https://www.ospar.org/documents?v=38978). While the IUCN Red List considers them generally as least concerned, they are listed as Red on the national list of the UK (BirdLife International 2019). Nevertheless, Kear (2005) stated that current protection measurements are insufficient and that this species suffers from lack of knowledge and research interest.

Since the German North Sea represents such an important area for moulting and wintering Common Scoters and in respect of the before mentioned convention agreements, the German government has a particular international and domestic responsibility to safeguard these populations. This requires a comprehensive understanding of the population structure, breeding origins, feeding ecology and habitat selection. All this refers not only to factors inside the German North (and Baltic) Sea, but also to those outside (e.g. in breeding grounds or on migration routes). Those features will have effects on the status and demography of the local abundance of Common Scoter. Recently raised concerns about declines in sea duck populations residing in German Waters (and the entire Baltic Sea, Skov et al. 2011) highlight the importance of such adequate knowledge of their ecology to be able to develop and implement suitable conservation measures. Consequently, we need to survey the distribution of Common Scoters in relation to their environment.

Common Scoters are benthic bivalve feeding sea ducks. They dive for prey organisms residing in the upper layers of preferably soft sediment (Madsen 1954, Fox 2004). The time and energy needed to dive for prey are decisively influenced by water depth. Since it is assumed that organisms aim at maximising their nutritional intake while simultaneously minimising the costs needed to gain energy resources (MacArthur & Pianka 1966), it is inferred that Common Scoter select for shallower waters. These would reduce the time needed to dive through the water column and obtain prey. This ratio of expenses and gained benefit should also influence their choice of prey organisms. Individuals in upper layers of soft sediment are easier to reach compared to individuals in lower layers or in harder, consolidated substrates. Moreover, the phenotype of potential bivalve prey is likely of importance, too. Individuals should neither be too big (as they probably could not be swallowed or might damage

the oesophagus) nor too small (as in this case scoters would need to dive more often to obtain sufficient energy). Besides individual size, shell thickness and flesh/shell ratios affect profitability. Individuals with thick shells are more difficult to crush in the gizzard and those containing less flesh relative to shell mass are less profitable than those of similar size with favourable flesh/shell ratios. The distribution of bivalve species is likewise under the influence of environmental parameters (Reiss & Kröncke 2005, Grey & Elliot 2009). Water depth, sediment characteristics, flow velocity and bed shear stress or chlorophyll *a* concentration in the water column are just a few examples. Hence, it is assumed that along with water depth, prey distribution, availability and profitability all affect Common Scoter dispersal.

Another factor controlling the distribution of Common Scoters and their prey is seasonal variability. The moulting and wintering period represent different stages in the life cycle of Common Scoters and should therefore also have an influence on how they distribute. During moult, they replace worn flight feathers and are therefore flightless (Fox et al. 2008). They are expected to disperse in shallower waters, with most easily accessible prey, in areas with least disturbance and predation, as this would reduce diving time, maximise feeding time and avoid escape costs while enhancing survival probability. During the winter, they need to accumulate sufficient energy reserves by building fat depots in anticipation for spring migration. Thus, they are expected to disperse in areas with especially profitable prey, potentially in deeper waters, as moulting birds in the same areas might have previously depleted optimal food resources.

Besides these natural parameters, other attributes such as anthropogenic activities can have an impact on the dispersal of a species. Particularly the German North Sea is subject to a large variety of human actions. It has long been an important region for fishery, gas and oil exploitation and is one of the world's most used ship trafficking areas (Halpern et al. 2008). In recent years, expanding (coastal) recreational activities have added to anthropogenic utilisations of these waters. As the German North (and Baltic) Sea sustains such a large share of the Common Scoter Western Palearctic flyway population, it is crucial to understand features characterising these particular regions. This also involves the assessment of potential threats to acquire specific future management and protection strategies.

Gaps in knowledge

The distribution of Common Scoter in the German North and Baltic Sea has been studied by Seabirds at Sea surveys since the 1990s (e.g. Bräger et al. 1995, Sonntag et al. 2004/2006, Garthe et al. 2007, Markones & Garthe 2011). Based on these studies, we already have information on differences in distribution between moulting and wintering periods on a larger and on a smaller spatial scale within

German Waters (e.g. Garthe et al. 2003, Sonntag et al. 2004, Mendel et al. 2008). Berndt and Busche (1993) published more detailed information regarding seasonal variation in the distribution of Common Scoter in the German North and Baltic Sea. They described dispersal patterns during moulting and wintering seasons starting with migration movements across the Gulf of Finland and along the western coasts of Estonia and Lithuania. Based on aerial surveys, they compiled data on their occurrences and compared them to records sometimes dating back several decades. Due to these previous studies, the moulting and wintering distribution of Common Scoters (often including information about preferred water depths) is well characterised. However, we still lack detailed knowledge on movements on a small spatial scale, i.e. location changes between foraging and resting areas or the exchange of individuals between the German North and Baltic Sea (Mendel et al. 2008).

A number of previous studies have investigated the feeding ecology of Common Scoters (e.g. Madsen 1954, Meissner & Bräger 1990, Degraer et al. 1999, Fox 2004, Kaiser et al. 2006) concluding that their distribution is likely influenced by the distribution of their prey. Moreover, several studies have focused on specific bivalve prey items (i.e. Durinck et al. 1993, Wolf & Meininger 2004, Baptist & Leopold 2009). Food selection and foraging ecology in connection to seasonal variability have however largely been neglected until now (Mendel et al. 2008).

Species distribution models have proven to be a useful and increasingly important tool for conservation and climate change management to predict the distribution of a species based on environmental descriptors (Austin 2007). However, relating the distribution of a species to environmental parameters is a complex procedure as a multitude of parameters needs to be sampled on a similar spatial and temporal scale in connection to the seasonally varying dispersal of the studied species (Austin 2002/2005, Lambert et al. 2017). So far, only very few studies have attempted to establish this connection in case of the Common Scoter (Deppe 2003, Schwemmer et al. 2019). Thus, we still lack knowledge on the habitat selection of this species on larger spatial scales and in relation to seasonal variability.

Objectives and Methods

This thesis aims to analyse the distribution and habitat selection of the Common Scoter in the German North Sea, particularly the areas along the coast of Schleswig-Holstein, to answer the following questions:

- Are there spatial and temporal differences in distribution patterns between the moulting and wintering season?
- Can we identify between and within year variations in moulting and wintering dispersal patterns?

- What influence do environmental parameters such as sediment, benthic communities, water depth and water current or anthropogenic activities (e.g. ship traffic) have on the distribution of Common Scoters in the German Bight?

- Do moulting and wintering areas display distinct differences regarding these habitat parameters?

To analyse distribution patterns in the German North Sea, Seabirds at Sea data were used compiled from surveys undertaken since the early 1990s as well as during the PhD. Benthos and sediment samples were collected in the moulting and wintering area at different times of the year to relate prey availability to seasonal variations. Bivalve specimens found in these samples were analysed in terms of biomass (expressed by ash-free-dry mass) and profitability (expressed by flesh-to-shell ratio) to investigate profitability of available prey resources. Additionally, different environmental parameters were either sampled during the PhD (water depth, sediment characteristics) or taken from previous studies and the literature to model the distribution of Common Scoters in relation to habitat characteristics.

Chapter outline

The thesis takes the form of five different chapters, each of which answers the before mentioned specific questions.

In **Chapter 1**, **long term changes in distribution patterns of moulting and wintering Common Scoters in the German North Sea** are described. This chapter gives a general overview of the dispersal during both periods and of scoter hotspots, but also investigates within and between year variations. Furthermore, shifts in distributions during recent years were identified.

In **Chapter 2**, **bivalve communities are compared between moulting and wintering areas** used by Common Scoters. Sediment and benthos samples were taken in two core areas known for their consistent use by either moulting or wintering scoters. The composition of benthic bivalve communities was determined and compared between areas. Additionally, abundances, biomass and flesh-to-shell ratio of found bivalve species were determined to investigate the profitability of prey resources.

Chapter 3 focuses on **the role of the American Razor Clam *Ensis leei* as a potential novel food source** for moulting and wintering scoters. This invasive alien bivalve was introduced to the German North Sea in the late 1970s and has since then spread across the Wadden Sea. This chapter investigates the extent of its dispersal and its high abundance particularly in the core moulting area of Common Scoters.

In **Chapter 4**, **large-scale depth-related seasonal dispersal patterns of Common Scoters in two contrasting marine systems** are described. The distribution of scoters based on Seabirds at Sea data compiled during the moulting and wintering season in the German North Sea and the Danish Aalborg Bugt are analysed in connection to water depth. This chapter shows that despite environmental differences in both habitats scoters show the same dispersal patterns.

In **Chapter 5**, the **distribution patterns of Common Scoters in the German North Sea are modelled by environmental parameters**. The analysis includes parameters such as water depth, bed shear stress, proportion of fine sand, benthic bivalve prey species and ship traffic as an example of anthropogenic disturbances. This chapter characterises factors having an influence on how scoters disperse during moult and winter.

CHAPTER I

Changes in moulting and wintering distribution patterns of Common Scoter *Melanitta nigra* in the south-eastern North Sea 2006 - 2017

Johanna Kottsieper, Nele Markones, Anthony D. Fox, Stefan Garthe

© Johanna Kottsieper

Prepared for submission

Changes in moulting and wintering distribution patterns of Common Scoter *Melanitta nigra* in the south eastern North Sea 2006-2017

Johanna Kottsieper[1*], Nele Markones[1], Anthony D. Fox[2], Stefan Garthe[1]

[1] *Research and Technology Centre (FTZ), Kiel University, Hafentörn 1, 25761 Büsum, Germany*

[2] *Department of Bioscience, Aarhus University, Grenåvej 14, 8410 Rønde, Denmark*

* Corresponding author, Email: kottsieper@ftz-west.uni-kiel.de

Keywords: German North Sea · *Melanitta nigra* · Seasonal distribution

Abstract

The Common Scoter *Melanitta nigra* (Linnaeus, 1758) is an arctic/sub-arctic sea duck species, which occurs in high numbers in the German North (and Baltic) Sea during moulting and wintering seasons. Seabirds at Sea surveys conducted since the early 1990s revealed that Common Scoter consistently used the waters along the Schleswig-Holstein North Sea coast during both periods. We analysed these data to investigate Common Scoter distribution patterns during 2006-2017 and determine seasonal and between year variations. Our results confirmed the consistent dispersal of Common Scoter in the German North Sea. During moult, birds aggregated close to the coast and in shallow waters. As the winter progressed, Common Scoter spread across wider areas and further offshore into deeper waters. Despite this consistency, our study revealed a southward shift in Scoter distributions during both seasons, as more birds utilised areas west of the North Frisian Islands and even higher numbers west of the Eiderstedt peninsula. Furthermore, we identified an overall increase in the number of moulting and wintering birds during the last five years (2013-2017). Our study highlights the increasing importance of the waters along the Schleswig-Holstein North Sea coast as a vital habitat for moulting and wintering Common Scoter in this flyway population.

Introduction

The German North Sea offers important habitats for moulting and wintering sea ducks, including the Common Scoter *Melanitta nigra* (Linneaus, 1758). This species migrates from arctic/sub-arctic breeding areas that extend from Iceland, UK and Scandinavia to the core breeding areas across northern Russia (BirdLife International 2015) to moult in the German North (and Baltic) Sea and subsequently spend the wintering season in the same general areas (Glutz von Blotzheim and Bauer 1990). During those periods, up to a quarter of the Western Palearctic Common Scoter flyway population resides in German Waters (Mendel *et al.* 2008). Early moulting individuals (males, subadults and failed breeders) arrive in the North (and Baltic) Sea from late June onwards (Mendel *et al.* 2008). The moulting period extends until October, as females, which have successfully bred, as well as juveniles migrate to the German Bight before late summer/early autumn. Starting in February, Common Scoter progressively return towards their breeding grounds leaving some individuals, which stay in these areas throughout the entire year (Mendel *et al.* 2008).

While in German waters, Common Scoter are exposed to threats caused by anthropogenic activities. The North Sea has long been an important area for fishery, gas and oil exploitation, as well as being one of the most intensive ship trafficing areas worldwide (Halpern *et al.* 2008). Intensifying recreational use and offshore wind farm development also pose new threats to waterbird species such as Common Scoter. Since this species is protected under the EU Birds Directive, it is necessary to understand its distribution patterns to assess the risks of potential threats and provide information to support the development of management strategies for an effective protection.

To describe seabird distribution patterns during their annual cycle along German North Sea coasts, standardised ship-based surveys have been carried out since the early 1990s supplemented by surveys from aircraft since 2002 (Garthe *et al.* 2002). These surveys show considerable annual variation in numbers of observed birds, but Common Scoter consistently use the same areas during moult and winter (Markones and Garthe 2011). Earlier studies showed that Common Scoter were highly sensitive to disturbance from ship traffic (Kaiser *et al.* 2006), showing longest flushing distances among all investigated seabird species (Schwemmer *et al.* 2011, Fliessbach *et al.* 2019). In UK waters, a single oil spill temporarily reduced the local population of Common Scoter by almost two-thirds (Banks *et al.* 2008). These are just two examples of impacts of human activities on Common Scoter distribution and abundance. By avoiding disturbance, birds invest time and energy in escape behaviour, suffer elevated stress levels, are displaced from favoured feeding areas and lose foraging time, all factors likely to affect body condition. Disturbance can therefore potentially affect local abundance, and habitat use of Common Scoter in the wintering and moulting areas as well as their reproductive success as a possible carry-over effect.

To assess the impact and risk of disturbance for species and designate, for example, marine protected areas, it is important to determine their distribution patterns during the annual cycle. Since birds have different needs at different times of the year, we expect them to distribute themselves according to these needs. When Common Scoter arrive in the German North Sea to replace their flight feathers during moult, we would expect them to localise in areas with lowest disturbance levels and rich, easily accessible prey resources. Increasing numbers of individuals arriving in the same areas during the moulting season might force them to disperse more widely as prey resources might potentially be depleted. Therefore, we might expect them to move to other areas in the German North Sea during the winter.

To obtain a better understanding of how Common Scoter distribute themselves during moult and winter, we used Seabirds at Sea surveys from the early 2000s onwards conducted in the German North Sea. We analysed these data to (i) characterise the general distribution pattern of Common Scoter along the Schleswig-Holstein North Sea coast, (ii) identify differences in distribution patterns between moulting and wintering periods, and (iii) investigate within and between year variances in abundance and distribution patterns. Additionally, we identified core distribution areas to (iv) analyse potential fluctuations in the dispersal of moulting and wintering birds along the Schleswig-Holstein North Sea coast in more detail.

Material and Methods

2.1 Study area

The study area consisted of an area of 2965 km^2 of the German North Sea along the Schleswig-Holstein coast within the 12 nautical mile zone extending from above the Elbe river in the south (54°2'N, 8°38'E) to the border of the German EEZ near Sylt in the north (55°4'N, 8°24'E, see Fig. 1). The area is located in the sublitoral zone of the Wadden Sea and included areas further offshore with water depths of up to 35 metres. The entire survey area is located in a protected area designated by both the Habitats Directive and Birds Directive and is listed as a Ramsar site (Krause *et al.* 2011).
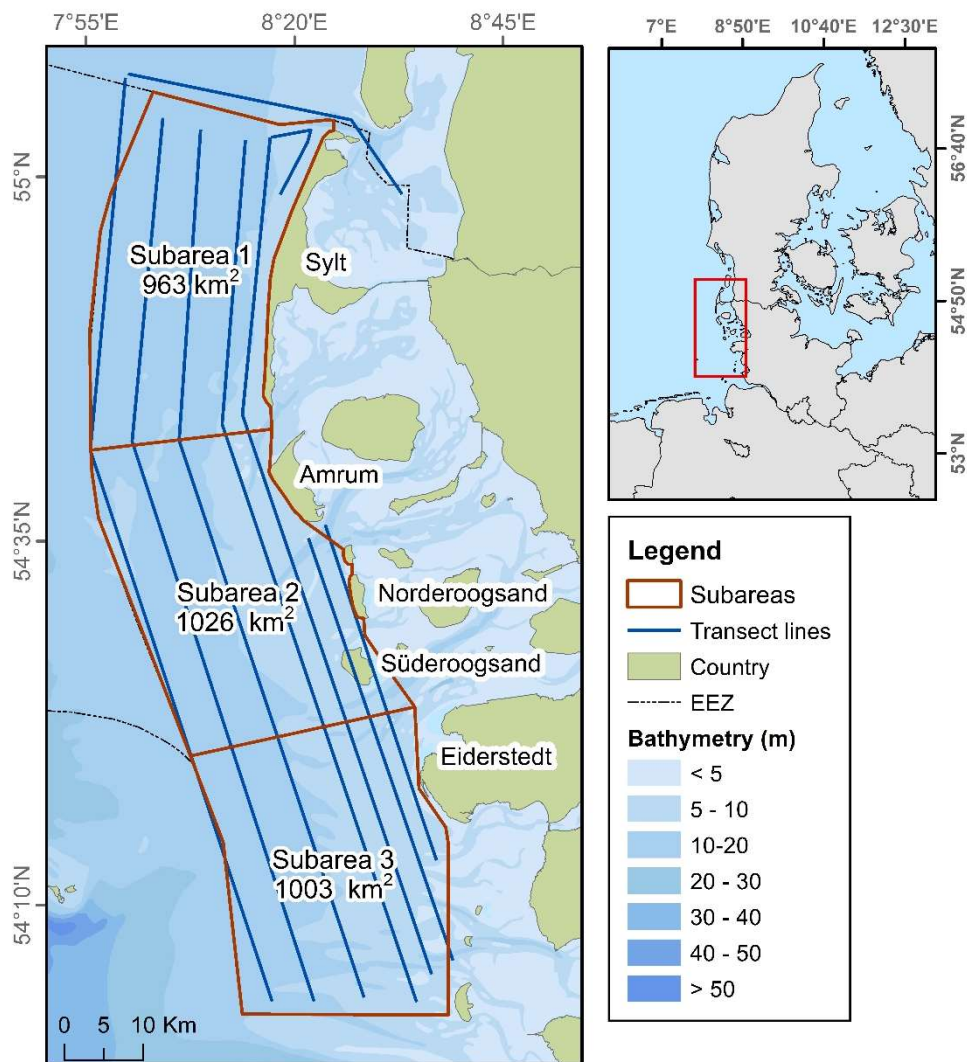

Fig. 1 Study area with aerial transect survey lines and subareas. The number of each subarea as well as their extent are indicated on the map.

2.2 Aerial Seabirds at Sea surveys

Monitoring of waterbirds in the study area has been undertaken at least twice annually (during summer and winter) during 2006-2017 on behalf of the Schleswig-Holstein Agency for Coastal Defence, National Park and Marine Conservation - National Park Authority. During each survey, 7 nearly N-S parallel strip transects were flown (Fig. 1) with a twin-engine Partenavia P68 aircraft flying at 78 meters and at a speed of 90-100 knots. The four innermost transects closest to the coast were spaced at 3 km intervals, the remaining three were spaced at a 6 km interval. In each strip transect, all birds visible between 45 m (since seated observers cannot detect birds in the area directly beneath the aircraft out to 45 m) and 397 m out from the aircraft were counted and assigned to species. Although we recognise declining detectability over this distance, here we consider this as a constant error, acknowledging potential variation in observer skills or sea and light conditions as confounding factors could not be excluded completely. Experienced observers counted all species and stated their numbers (flock sizes or individuals) and behaviour (swimming, diving, flying, flushing, sitting on an object/sandbank and migrating) directly onto a Dictaphone with a time stamp. The predetermined flight track was logged with a GPS at five-second intervals. After interpolating positional information to one-second intervals, each observation could be located accurate to $c.$50 metres. Surveys were not carried out under unfavourable weather conditions (excessive sun glare, wind speed >5.5 m s^{-1}, wave height >1.25 m). For further details of the method see Markones and Garthe (2011).

2.3 Data analysis

All maps were produced using ArcGIS (ESRI, Version 10.2.1, 2013). To investigate distributional differences between the moulting (June-September) and the wintering season (December-February) in the annual cycle of the Common Scoter, and to investigate whether these changed over time, we only considered survey data from those periods. Therefore, 14 moult and 10 winter surveys were included in the analysis (see Table 1). The main objective of this study was the description of overall distribution patterns including the identification of potential hotspots. We used distance corrected count data assuming an equal detection rate across the transects (although we acknowledge that we cannot entirely exclude that birds might have been missed) to visually map observations and capture the overall number of birds assigned to each subarea.

To analyse the long-term distribution patterns in the German North Sea, surveys from moulting and wintering seasons were summarised to three periods each (2006-2010, 2012-2014 and 2015-2017). For logistical reasons, survey coverage differed between years in their timing and area coverage of the moulting and wintering seasons. Consequently, we selected these blocks of years to achieve even survey coverage during the moulting and wintering season. A 1 x 1 km grid square was imposed across

the study area and Common Scoter numbers within each of these grid squares were calculated by spatially combining the point observations from each of the surveys for each period within ArcGIS. The observed number of birds was summarised for each grid cell and expressed as individuals/km^{-2} (ind./km^{-2}.)

To analyse potential variations in distribution between years, the area along the Schleswig-Holstein North Sea coast was separated into three subareas of similar sizes (see Fig. 1). These subareas were based on the core distribution areas of Common Scoter during their moulting and wintering period. Since the survey effort was not equal in all subareas for all flights, we excluded surveys covering less than 80 % of the maximum survey length. Thus, only 8 flights from the moulting and 7 flights from the wintering season could be considered for a more detailed analysis. We especially wished to look for within- and between-year changes in Common Scoter distributions between the three subareas, but insufficient data from earlier years constrained the analysis to 2012-2017, with at least one survey per season in each year. To assign the scoter observations to each subarea, the abundance data from the 1 x 1 km grid squares were spatially joined with the subareas in ArcGIS. The number of birds observed in each subarea was then calculated for every survey by summing all birds counted. Additionally, the proportion of individuals of the overall abundance (in all subareas combined) was calculated for each subarea.

Results

3.1 Distribution patterns

Moulting distribution

During moult, Common Scoter were distributed close to the coast (Fig. 2a-c). The lowest numbers were observed in the first period (2006-2010) when very few moulting scoter were present at all, mostly west of the Eiderstedt peninsula and west of Süderoogsand (Fig. 2a and Table 1). Numbers were higher in the second period (2012-2014, Fig. 2b), when most Common Scoter were located close to the Eiderstedt peninsula and with several flocks spread towards the centre of the study area along the North Frisian Islands. Only a few individuals could be found off Sylt (Fig. 2b). In the latest period (2015-2017), Scoter numbers increased with birds spreading across larger areas and offshore throughout the 12 nm zone, with highest numbers along the North Frisian Islands and west of the Eiderstedt peninsula, but likewise with increasing numbers off Sylt (Fig. 2c).

Wintering distribution

During winter, greater numbers of Common Scoter were present through all three periods compared to during moult (Fig. 3 and Table 1). Birds were more widely distributed throughout the entire Schleswig-Holstein North Sea coast, with many flocks out to the 12 nm border (Fig. 3a-c). During the first period (2006-2010), the majority of flocks was concentrated in the north (close to Sylt) and centre (along the North Frisian Islands, Fig. 3a). During 2012-2014, the majority of Common Scoter occurred in the northern part along the coast off and west of Sylt, as well as in the central subarea close to Amrum and increasing numbers off the Eiderstedt peninsula further south (Fig. 3b). During 2015-2017, greater concentrations occurred in the south close to the Eiderstedt peninsula, relatively fewer birds occurred along the coast of Sylt, but high concentrations could still be found along the North Frisian Islands and further offshore (Fig. 3c).

3.2. Contrasting use of subareas

During the moulting period, the majority of Common Scoter were observed in subareas 2 (centre) and 3 (south), with least observed birds in subarea 1 (north) across all years (Fig. 4a and Table 2). Subarea 1 had a peak in number of birds observed in 2015 (972 ind./km^{-2}) and showed higher numbers in 2016 (1,419 ind./km^{-2}), whereas bird numbers varied between 0 and 167.7 ind./km^{-2} in all other years. In subarea 2, numbers peaked at 6,159.6 ind./km^{-2} in 2015 not exceeding 2,610 ind./km^{-2} in other years. In subarea 3, Scoter numbers peaked at 15,183 ind./km^{-2} in September 2015, but with relatively modest numbers in all other years.

Comparing the proportions of the overall occurrence in each subarea confirms that the majority of birds was observed in subareas 2 (centre) and 3 (south) (Fig. 5a). While only supporting very low numbers during earlier years (2012-2015) and in 2017, more birds were found in subarea 1 in 2016 (ca. 24%). Subarea 2 supported around 87% of the overall occurrence in 2012, but numbers decreased to only 10.56% in 2015. Subarea 3 revealed an increase in number of Common Scoter since 2014. In 2015, around 84% of all observed birds were located here. However, numbers were decreasing to 50% in 2016 and only ca. 42% in 2017.

In all winters, Common Scoter were observed in higher numbers across all subareas (Fig. 4b). Subarea had several peaks with 15,265.8 ind./km^{-2} in 2009, 13,878 ind./km^{-2} in 2014 and 22,360 ind./km^{-2} in 2017, but numbers were comparatively low in all other years. In subarea 2, numbers of birds increased from 414 ind./km^{-2} in 2012 to a peak of 60,415 ind./km^{-2} in 2017. In subarea 3, numbers peaked in 2016 at 172,043 ind./km^{-2}, varying between 2,088 ind./km^{-2} (2012) and 29,106 ind./km^{-2} (2015) in other years. In 2017, numbers decreased to 17,329 ind./km^{-2}.

Comparing the proportions of the overall occurrence in each subarea confirmed these observations (Fig 5b). While subarea 1 supported 52.23% of all birds encountered in 2012, numbers decreased to < 1% in 2016, but increased to 22.34% in 2017 again. In subarea 2, 7.90% of the overall occurrence could be observed in 2012, increasing to 60.35% in 2017. Between 2013 and 2015, numbers varied between 55.36% (2013) and 6.51% (2016). In subarea 3, proportions varied between ca.40% (2012) and 17.31% (2017), peaking with 93.31% in 2016.

Table 1 Summary of the number of Common Scoter observed and the distance travelled (km) on transect per season and year counted during the monitoring flights in the study area.

|	Survey date	Birds observed	Distance [km]
MOULT	23.07.2008	207	504.02
	21.06.2010	972	345.26
	19.06.2012	3186	365.41
	25.07.2012	819	395.2
	19.08.2012	300.6	393.12
	17.06.2013	8201	380.24
	16.07.2013	5673	433.97
	27.06.2014	4023	429.12
	12.06.2015	15519.6	504.55
	28.09.2015	18081	457.2
	07.09.2016	5934	1157.75
	18.06.2017	101630.5	954.19
	06.07.2017	1130.9	991.24
WINTER	22.01.2006	16513.2	366.3
	28.02.2006	13091.4	274.29
	14.02.2009	25520.4	493.12
	07.02.2010	8233.2	436.11
	04.02.2012	5238	502.49
	02.12.2013	18144	405.28
	11.02.2014	17586	483.2
	12.02.2015	40698	521.73
	28.02.2016	184384	1174.77
	17.01.2017	100104	1261.61
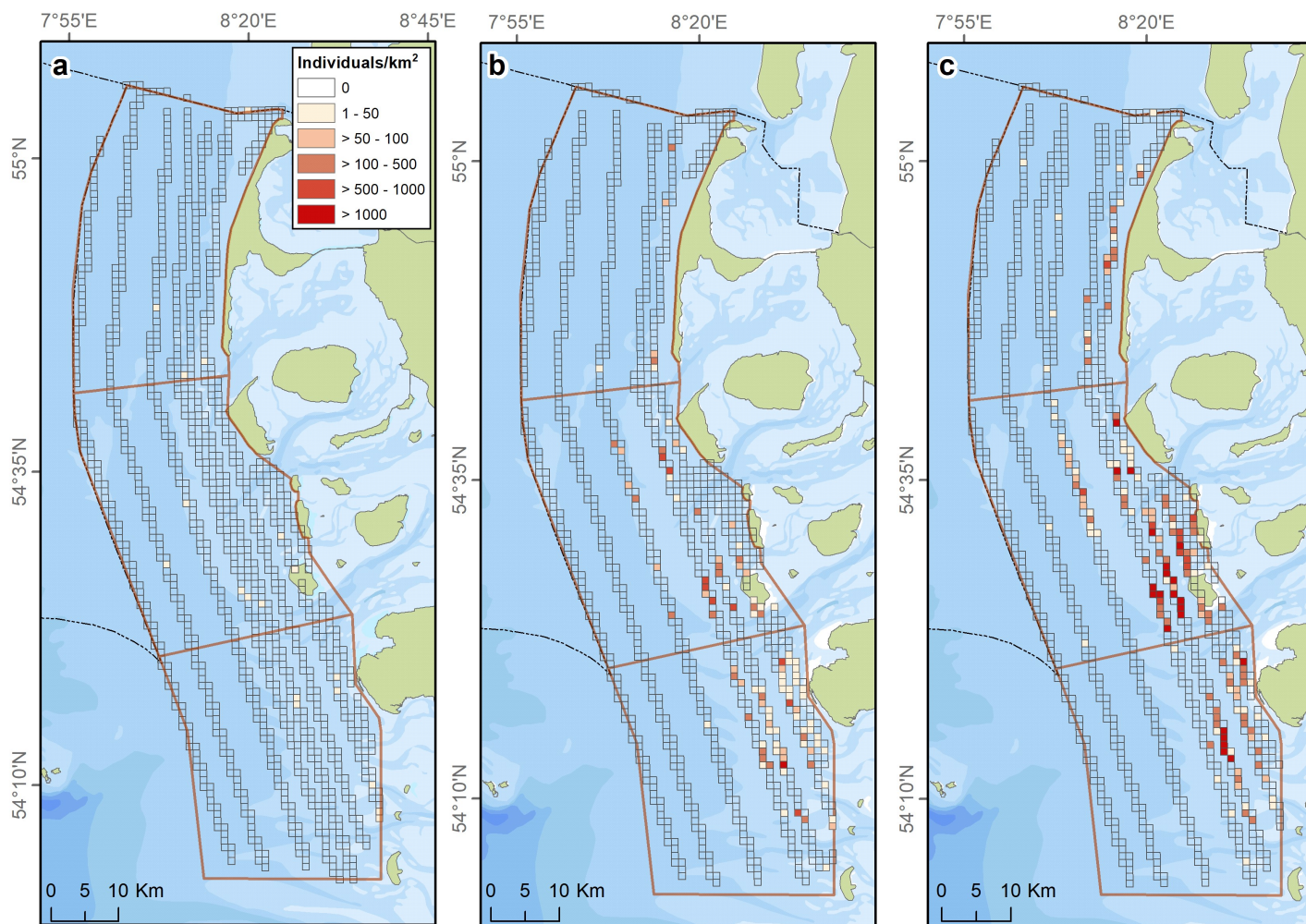
Fig 2 Distribution patterns of moulting Common Scoter during moult in the years **(a)** 2006-2010, **(b)** 2012-2014 and **(c)** 2015-2017. The map for the first period (2006-2010) is based on two surveys only.
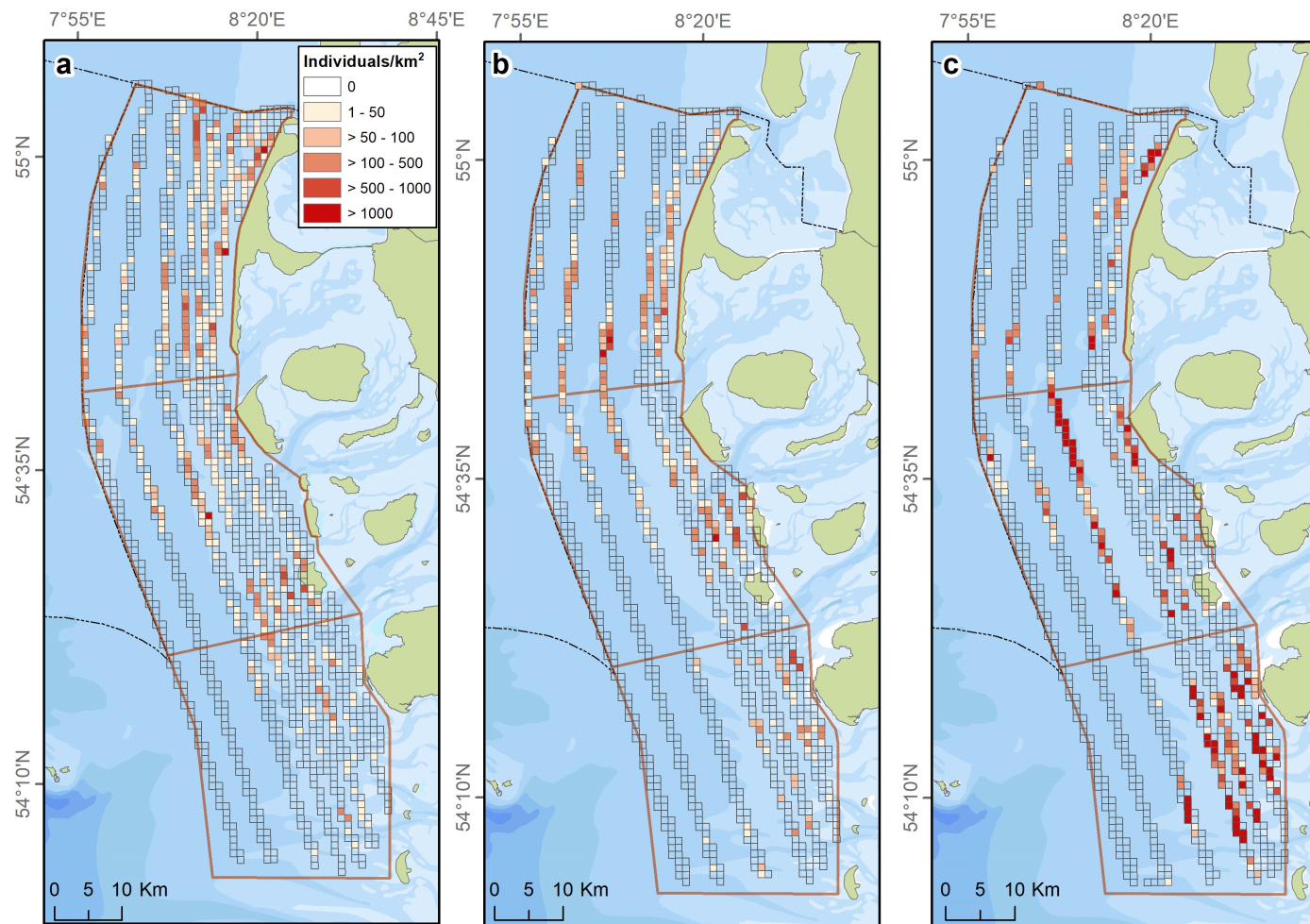
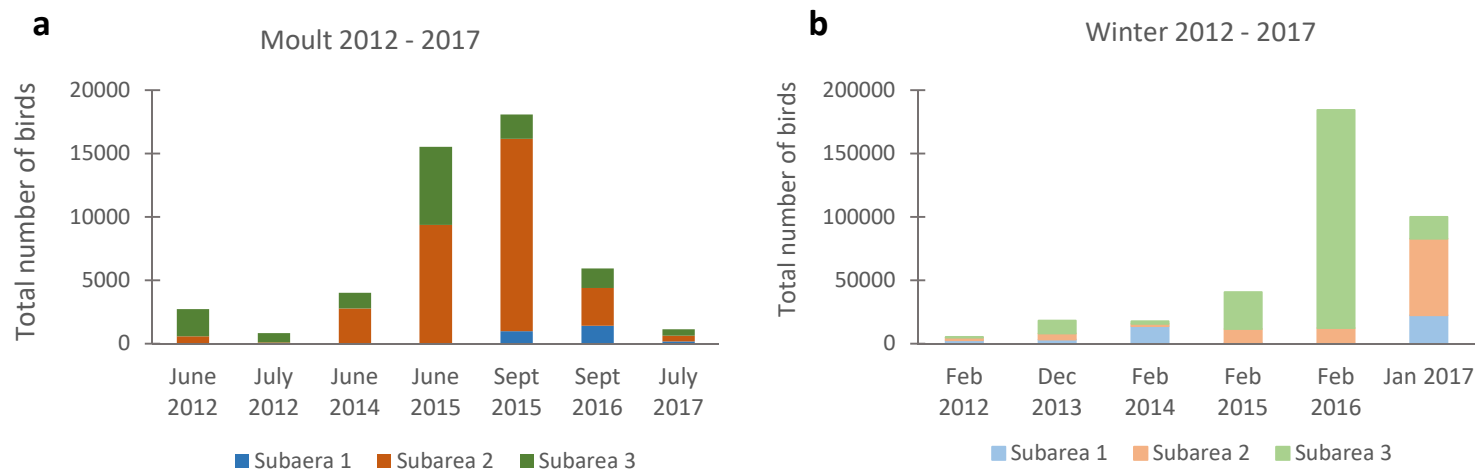**Fig. 3** Distribution patterns of wintering Common Scoter during the years **(a)** 2006-2010, **(b)** 2012-2014 and **(c)** 2015-2017.

Fig. 4 Graphs showing the overall occurrence of Common Scoter in each subarea during 2010-2017 for **(a)** the moulting and **(b)** the wintering period.
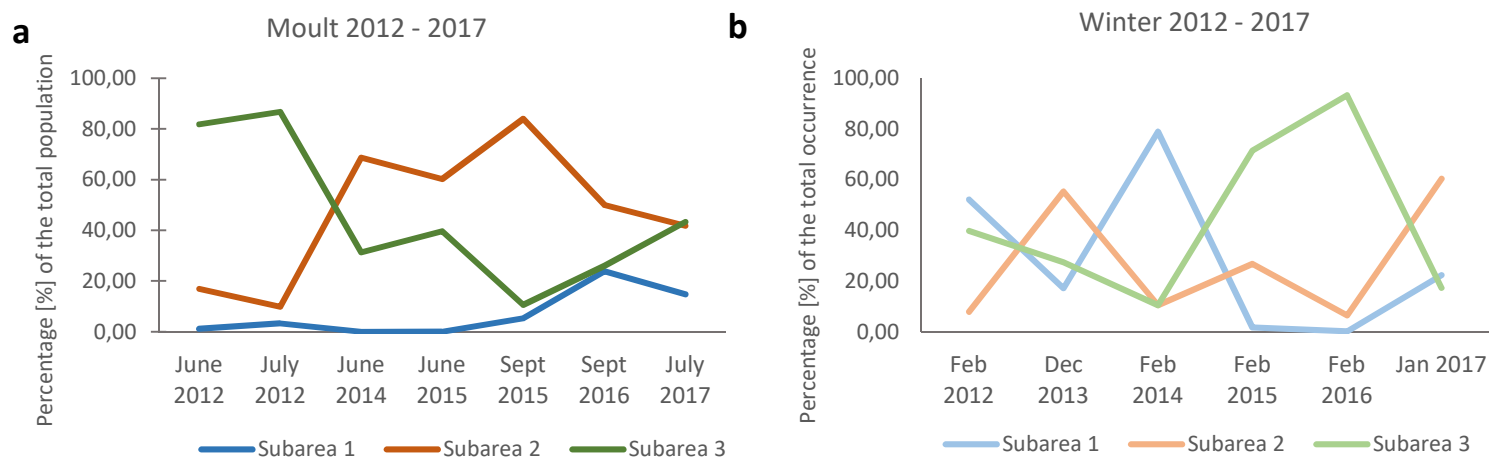

Fig. 5 Graphs showing the percentage of the overall occurrence of Common Scoter in each subarea for **(a)** the moulting and **(b)** the wintering period during the years 2010-2017.

Table 2 Summary of the number of observed Common Scoter counted, the proportion of the overall occurrences (%) and the distance travelled (km) during each survey year and each period for each subarea.

	Survey date	Subarea 1			Subarea 2			Subarea 3		
		Birds observed	Proportion [%]	Distance [km]	Birds observed	Proportion [%]	Distance [km]	Birds observed	Proportion [%]	Distance [km]
MOULT	23.07.2008	37.8	18.26	176.63	97.2	49.96	164.78	72	34.78	165.61
	19.06.2012	36	1.13	177.86	2610	81.92	121.75	840	16.95	125.80
	25.07.2012	27	3.30	134.16	711	86.81	130.26	81	9.89	130.78
	27.06.2014	0	0	136.02	1260	31.32	147.86	2763	68.68	145.24
	12.06.2015	0	0	152.64	6159.6	36.69	174.42	9360	60.31	177.49
	28.09.2015	972	5.38	143.64	1926	10.65	153.77	15183	83.97	159.79
	07.09.2016	1419	23.91	382.65	1548	26.09	385.38	2967	50.00	389.72
	06.07.2017	167.7	14.83	323.71	490.20	43.35	328.93	473	41.83	338.60
WINTER	14.02.2009	15265.8	59.82	174.24	7930.8	31.08	164.92	2323.8	9.11	153.96
	04.02.2012	2736	52.23	159.56	414	7.90	171.03	2088	39.86	171.9
	02.12.2013	3132	17.26	125.16	10044	55.36	136.60	4968	27.38	143.52
	11.02.2014	13878	78.92	149.74	1854	10.54	171.51	1854	10.54	161.95
	12.02.2015	675	1.66	165.95	10917	26.82	177.95	29106	71.52	177.83
	28.02.2016	344	0.19	419.36	11997	6.51	388.00	172043	93.31	367.41
	17.01.2017	22360	22.34	404.72	60415	60.35	432.24	17329	17.31	424.65

Discussion

Our study confirmed that Common Scoter consistently use the waters along the Schleswig-Holstein North Sea coast during their moulting and wintering period. During moult, Common Scoter generally aggregated close to the coast in water depths of < 10m and during winter they occurred further offshore in deeper waters. While large numbers of individuals were observed at water depths of < 10 m during the winter as well, several individuals were also found in areas varying between 10 and 20 m water depth. Our results showed a general increase over time in the overall number of birds present (most dramatically in moulting numbers, but with strikingly high numbers in the winters of 2016 and 2017) as well as a southbound shift in their distribution patterns during both seasons. Numbers of Common Scoter increasingly concentrated in the central (subarea 2) and southern parts (subarea 3) of the study area close to the Eiderstedt peninsula during the moulting and the wintering period. We hypothesise that this shift is likely the result of an increase in the abundance of prey species, particularly the American Razor Clam *Ensis leei* (M. Huber, 2015). This invasive bivalve occurs in high densities west of the North Frisian Islands (Schwemmer *et al.* 2019.), but has been shown to be present in even higher densities west of the Eiderstedt peninsula (Kottsieper *et al.* 2019). Schwemmer *et al.* (2019) modelled the distribution of Common Scoters in relation to the distribution of *E. leei* in the central eastern German North Sea and found that the abundance of this alien bivalve explained scoter dispersal to a high degree. By analysing stomach prey compositions of dead Common Scoter, they could show that 35 % of these contained *E. leei* fragments. Dannheim and Rumohr (2012) described the successful settlement and reproduction of this bivalve species along the coast of Schleswig-Holstein with high abundances west of Sylt and the Eiderstedt peninsula. These studies highlight that the American Razor Clam likely is an important (and reliable) prey item for Common Scoters.

During the moulting season, when individuals simultaneously replace flight feathers and are therefore flightless, Common Scoter aggregated close to the coast in shallow waters. During the winter, they spread across larger areas and moved to deeper waters further offshore. Fox *et al.* (*under review*) recently confirmed this pattern for Common Scoter in the German North and the Danish Baltic Sea. When moulting, Common Scoter distribute in shallow waters with easily accessible rich prey resources first and thereby minimise their foraging costs while maximising their nutritional and energetic intake rates. With more individuals arriving as the winter progresses they move to deeper waters, distributing themselves across wider areas and further offshore.

Despite the overall increase in moulting and wintering birds, our data showed some fluctuations with between year numbers sometimes drastically decreasing or increasing. This might be accounted for by the difficulty to record Common Scoters as they occur far offshore and have long flush distances (e.g

Berndt and Busche 1993, Hennig and Eskildsen 2001, Schwemmer *et al*. 2011, Fliessbach *et al*. 2019). Moreover, it is assumed that individuals move within as well as between German, Dutch and Danish North and Baltic Sea areas (Berndt and Busche 1993, Hennig and Eskildsen 2001, Sonntag *et al.* 2004). Thus, individuals change locations on a broad spatial scale and might therefore cause some of the described fluctuations in observed numbers. In recent years, more Common Scoter were observed beyond the 12 nm border with water depths ranging between 20 to 30 m. Since these areas are not covered by the current transect design, individuals further offshore were probably missed during the counts analysed in this study.

The consistent long-term use of the waters between the Schleswig-Holstein North Sea coast and the 12 nm zone highlights the importance of this area for Common Scoter. A recent study could show that the numbers of Common Scoter are increasing in the German Baltic Sea as well (Markones et al. *in preparation*). These results suggest that German waters are progressively becoming increasingly important habitats for moulting and wintering Common Scoter. The study area in the German North Sea falls within special protected areas designated by the EU Habitats Directive, the EU Birds Directive and the Ramsar Convention. Our study reinforces the importance of these areas along the Schleswig-Holstein North Sea coast as protected areas for the Common Scoter (and other seabird species).

So far, only a few studies have attempted to analyse factors influencing habitat selection of Common Scoter in the German North Sea (e.g. Deppe 2003, Kaiser *et al.* 2006, Schwemmer *et al.* 2019). Schwemmer *et al.* (2019) were not only able to show that Common Scoter distribution is influenced by the distribution of *E. leei*. They could also show that it is possible to model the distribution of an avian species in relation to a selection of environmental parameters (including for example water depth and bed shear stress). Thereby, they characterised a statistical tool, which can be used to predict bird's dispersal with regard to their chosen habitat. If this approach can be applied to a larger spatial scale, it could be a useful future tool to identify the most influential habitat characteristics for Common Scoter. Despite these previous studies, the reason why Common Scoters consistently uses particularly the areas along the Schleswig-Holstein North Sea coast during the moulting and wintering season still remains poorly understood. Understanding the influence of e.g. environmental parameters, which can impact scoter distribution, is not only necessary to increase our understanding about how they distribute themselves. It is also important to enhance and specify future protection strategies. Therefore, more detailed knowledge on the impact of environmental parameters such as prey accessibility and availability in relation to seasonal variation, water depth and disturbance is needed.

Acknowledgments

References

Banks AN, Sanderson WG, Hughes B, Cranswick PA, Smith LE, Whitehead S, Musgrove AJ, Haycock B, Fairney NP (2008) The Sea Empress oil spill (Wales, UK): Effects on Common Scoter *Melanitta nigra* in Carmarthen Bay and status ten years later. Marine Pollution Bulletin 56:895–902

Berndt RK., Busche G (1993). Vogelwelt Schleswig-Holsteins. Bd. 4: Entenvögel II. Karl Wachholtz Verlag, Neumünster.

BirdLife International (2015) Species factsheet: *Melanitta nigra*. Downloaded from http://www.birdlife.org on 15/06/2015

Dannheim J, Rumohr H, (2012) The fate of an immigrant: *Ensis directus* in the eastern German Bight. Helgoland Mar. Res. 66, 307–317. https://doi.org/10.1007/s10152-011-0271-2

Deppe L, (2003) Die Trauerente (*Melanitta nigra*) in der deutschen Bucht–GIS-basierte Bewertung räumlicher und zeitlicher Parameter. Dipl-Arbeit, Universität Hamburg.

Environmental Systems Research Institute (ESRI) 2013 ArcGIS Desktop Release Version 10.2.1, https://www.esri.com/de-de/arcgis/about-arcgis/overview

Fliessbach KL, Borkenhagen K, Guse N, Markones N, Schwemmer P, Garthe S (2019) A ship traffic disturbance vulnerability index for Northwest European seabirds as a tool for marine spatial planning. Frontiers in Marine Science 6:192, https://doi.org/10.3389/fmars.2019.00192

Fox AD, Kottsieper J, Petersen IK, Markones N, Schwemmer P, Garthe S Large-scale depth-related sesonal dispersal patterns of a benthic-feeding sea duck in two contrasting marine systems. Marine Ecological Progress Series *under review*

Garthe S, Hüppop O, Weichler T (2002) Anleitung zur Erfassung von Seevögeln auf See von Schiffen. Seevögel 23:47–55

Glutz von Blotzheim UN, Bauer KN (1990) Handbuch der Vögel Mitteleuropas, 2. durchges. Aufl. Aula-Verlag, Wiesbaden

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A Global Map of Human Impact on Marine Ecosystems. Science 319:948–952

Hennig V, Eskildsen K (2001) Notwendigkeit ungestörter Mausergebiete für die Trauerente (Melanitta nigra). Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer (Eds.): Wattenmeermonitoring 70–71.

Kaiser MJ, Galanidi M, Showler DA, Elliott AJ, Caldow RWG, Rees EIS, Stillman RA, Sutherland WJ (2006)

Distribution and behaviour of Common Scoter *Melanitta nigra* relative to prey resources and environmental parameters. Ibis 148:110-128.

Kottsieper J, Schwemmer P, Markones N, Fox AD, Garthe S (2019) An invasive alien bivalve apparently provides a novel food source for moulting and wintering benthic feeding sea ducks. Helgoland Marine Research 73 (1)

Krause J, Wollny-Goerke K, Boller F, Hauswirth M, Heinicke K, Herrmann C, Körber P, Narberhaus I, Richter-Kemmermann A (2011) The German Marine Protected Areas in the North Sea and Baltic Sea. *Natur und Landschaft* 86: 397.

Markones N, Garthe S (2011) Monitoring von Seevögeln im Offshore-Bereich der schleswig-holsteinischen Nordsee im Rahmen von NATURA 2000 in den Jahren 2004 bis 2009. Corax 22:11–50

Mendel B, Sonntag N, Wahl J, Schwemmer P, Dries H, Guse N, Müller S, Garthe S (2008) Profiles of seabirds and waterbirds of the German North and Baltic Seas: Distribution, ecology and sensitivities to human activities within the marine environment. Naturschutz und Biologische Vielfalt 61. Bundesamt für Naturschutz, Bonn - Bad Godesberg

Schwemmer P, Mendel B, Sonntag N, Dierschke V, Garthe S (2011) Effects of ship traffic on seabirds in offshore waters: implications for marine conservation and spatial planning. Ecological Applications 21:1851–1860

Schwemmer P, Volmer H, Enners L, Riemers HC, Binder K, Horn S, Eskildsen K, Adler S, Fox AD, Garthe S (2019) Modelling summer distribution patterns of common scoters (*Melanitta nigra*) by its most important prey species, the razor clam (*Ensis directus*), and hydrodynamic parameters. Estuar Coast Shelf Sci 225

Sonntag N, Engelhard O, Garthe S (2004) Sommer- und Mauservorkommen von Trauerenten Melanitta nigra und Samtenten M. fusca auf der Oderbank

CHAPTER II

Comparison of bivalve communities between moulting and wintering areas used by Common Scoter *Melanitta nigra* in the German North Sea

Johanna Kottsieper, Ulrike Schückel, Philipp Schwemmer, Anthony D. Fox, Stefan Garthe

© Johanna Kottsieper

Comparison of bivalve communities between moulting and wintering areas used by Common Scoter *Melanitta nigra* in the German North Sea

Johanna Kottsieper[a]*, Ulrike Schückel[b], Philipp Schwemmer[a], Anthony D. Fox[c], Stefan Garthe[a]

[a]*Research and Technology Centre (FTZ), Kiel University, Hafentörn 1, 25761 Büsum, Germany*

[b]*Schleswig-Holstein Agency for Coastal Defence, National Park and Marine Conservation, National Park Authority, 25832 Tönning, Germany*

[c]*Department of Bioscience, Aarhus University, Grenåvej 14, 8410 Rønde, Denmark*

* Corresponding author, Email: kottsieper@ftz-west.uni-kiel.de

Abstract

The Common Scoter (*Melanitta nigra*) is a common sea duck, which predominantly feeds on sedentary benthic bivalve prey and occurs in large late-summer moulting concentrations in the German North Sea in areas which differ from those used by later wintering concentrations. Assuming scoters distribute in response to prey accessibility, abundance and profitability, we hypothesis that their contrasting distribution during moult compared to winter potentially reflects differences in prey type and distribution. We compared benthic bivalve community composition, abundance, ash-free dry mass and flesh-to-shell ratios between both areas to investigate factors influencing the seasonal difference in areas used by scoters. The American Razor Clam (*Ensis leei*) was the most common bivalve in the moulting area (mean abundance 1004 ± 1681 ind. m^{-2}, mean ± SD) with the highest flesh-to-shell ratio (0.341 g m$^{-2} \pm 0.729$ g m^{-2}), whereas the American Piddock (*Petricolaria pholadiformis*) showed the highest ash-free dry mass (0.635 g m$^{-2} \pm 0.392$ g m^{-2}). In the wintering area, the most common bivalve was the Bean-like Tellin (*Fabulina fabula,* 13 ± 17 ind. m^{-2}), *Spisula solida* had the highest ash-free dry mass (1.639 g m$^{-2} \pm 1.262$ g m^{-2}) and *F. fabula* and *Abra alba* had the highest flesh-to-shell ratios. Overall benthic species community composition differed considerably between moulting and wintering area, with fewer species and lower abundance in the wintering area. The high abundance and food quality (flesh-to-shell ratios) of *E. leei* (an invasive alien to the German North Sea since the 1980s) in the moulting area suggests its relative importance and potentially explains the seasonal differences of Common Scoter distributions.

Introduction

Seabirds at Sea surveys conducted since the 1990s have shown that German North Sea coasts are important late summer habitats for moulting Common Scoters *Melanitta nigra* (Linneaus, 1758) replacing flight feathers and subsequently for larger wintering aggregations (e.g. Nehls, 1998, Hennig and Hälterlein, 2000, Markones and Garthe, 2011). Up to a quarter of the Western Palearctic flyway population can be found in the German North (and Baltic) Sea (Mendel et al., 2008) from late July until mid-October (Mendel et al., 2008) aggregating in shallow waters (Deppe, 2003). Higher numbers occur in winter (December - late February) when Scoters move into deeper waters further offshore (Markones and Garthe, 2011, Mendel et al., 2008). Common Scoters consistently utilised different moulting areas in the German North Sea compared to their wintering distributions (FTZ unpublished data). These distributions are thought to be a response to the distribution of their prey (e.g. Madsen, 1954, Meissner and Bräger, 1990, Degraer et al., 1999 and Kaiser et al., 2006), although their aggregative responses to food supplies throughout the annual cycle have yet to be demonstrated (Nehls, 1998, Hennig and Hälterlein, 2000, Deppe, 2003).

Birds tend to distribute themselves to maximise nutritional and energetic intake rates while simultaneously minimising their feeding costs and predation risk (e.g. MacArthur and Pianka, 1966). The profitability of feeding areas could therefore be defined as the energy gained from prey species minus the costs spend foraging. Thus, we infer that Common Scoters select areas where prey organisms are most abundant, most profitable and accessible with least energy expenditure. Scoters dive to feed on abundant sedentary bivalve molluscs, accessible in upper marine sediment layers, preferentially selecting species such as *Abra alba*, *Cerastoderma edule*, *Limecola balthica* or *Spisula subtruncata* (for taxonomical authorities see Table 1) of size classes 5-20 mm, and up to 40 mm (Madsen, 1954, Fox, 2004). Additionally, Common Scoters prefer to feed in water depths of 2-7 metres (but also down to 20 metres, Madsen, 1954, Cramp and Simmons, 1977) confirmed by modelled distribution patterns in relation to water depth (Schwemmer et al. 2019a, this issue).

One explanation for Common Scoters using different moulting and wintering areas in the German North Sea could relate to differences in benthic communities with regard to prey species accessibility, composition, spatial distribution, densities and profitability (since Common Scoters prefer feeding in shallow waters and sandy substrates, Fox, 2004). Furthermore, Common Scoters likely deplete prey resources in the moulting areas, potentially making deeper water areas with less favoured substrates and prey relatively more profitable as the winter progresses.

In this study, we compare bivalve benthic communities sampled from two separate areas known consistently for their use by Common Scoters during moult and winter, looking for differences in benthic prey species in terms of species composition and abundance. To determine the profitability of

bivalve species, we calculated ash-free dry mass as a measure of organic matter and flesh-to-shell-ratio in both areas for all bivalve species. Since environmental parameters influence distribution and species composition of benthic communities (e.g. Kunitzer et al., 1992, Ellingsen, 2002), we incorporated selected environmental parameters into our analyses. Finally, based on these differences, we looked for explanations for the differences in scoter use of the two areas at different stages of the annual cycle to gain greater insight into how food supply may influence scoter distribution patterns.

Based on the differences in Common Scoter moulting and wintering distributions, we raised the following hypotheses:

1. Benthic bivalve species community compositions differ between moulting and wintering areas.
2. We predict higher abundances of more profitable prey items among benthic bivalves in the moulting compared to the wintering region.
3. Biomass (ash-free-dry mass) and profitability (flesh-to-shell ratio) of benthic bivalve species are more profitable in moulting versus wintering areas.
4. The spatial distribution of benthic bivalve species varies with several environmental parameters (e.g. sediment characteristics, water depth, bed shear stress).
5. Common scoter distribution matches the distribution of their preferred prey items (which in turn are linked to environmental parameters).

Material and Methods

2.1 Study area

The two defined study areas were previously identified as core moulting and wintering areas for Common Scoter in the coastal sublittoral German North Sea within the twelve nautical mile zone (Markones and Garthe, 2011, see Fig. 1). The moulting area covered 860 km^2 in the southern German North Sea, extending from Westerheversand (54°23'N, 8°33'E) on the Eiderstedt peninsula to Friedrichskoog (54°2'N, 8°34'E) in the south, extending 23 km off the coast and ranging from 1 to 16 m water depth (Fig. 1). The wintering area was located west of the island of Sylt, covered an area of 490 km^2 with water depths ranging from 5 to 17 m and extending from Lister Deep to Hörnum Deep 20 km off the coast (Fig. 1).
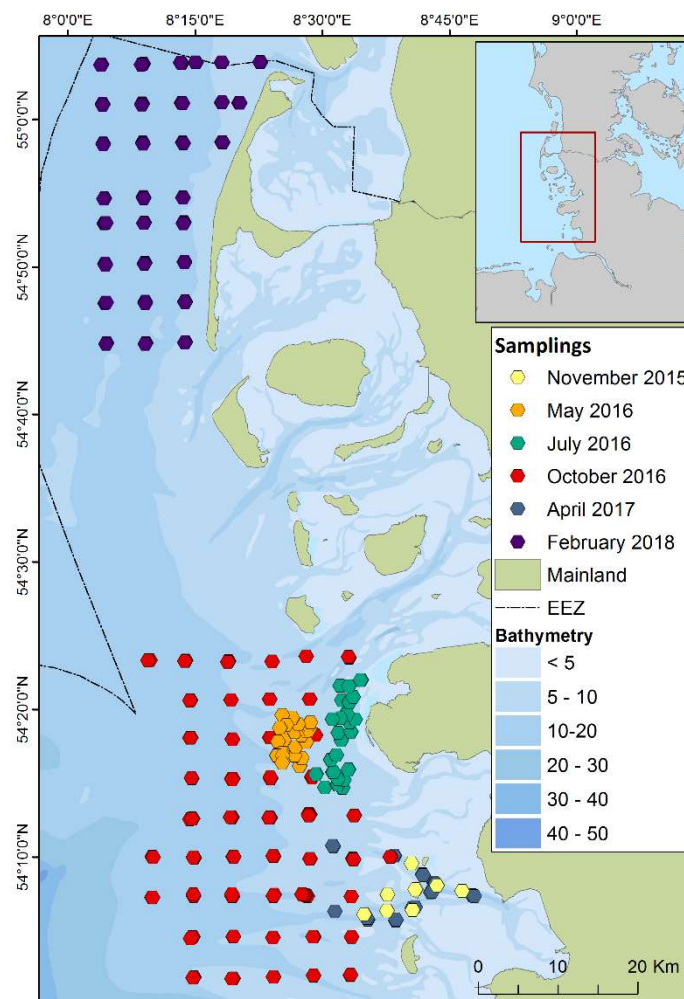

Fig. 1. Location of benthos sampling survey areas in the German North Sea, showing sampling stations and dates in the Common Scoter northern wintering area and the more southerly moulting area. Samples collected during May/July 2016 and April 2017 represent the pre-moult season, samples collected during November 2015 and October 2016 represent the post-moult season. The wintering season is represented by samples of February 2018.

2.2 Benthos and sediment sampling

In total, 263 benthos and 107 sediment samples were collected with a 0.1 m^2 Van Veen grab during five cruises performed between 2015 and 2017 in the moulting area and 56 benthos and 30 sediment samples during one cruise in the wintering area (2018).

In the moulting region, three cruises were conducted before (May and July 2016, April 2017) and two after the moulting season (November 2015, October 2016). In October 2016, samples were taken based on a 5x5 km grid to ensure consistent coverage of both areas (Gray and Elliott, 2009). Samples in May and July 2016 were taken in collaboration with the Kiel University Geology Department investigating gradients in sediment distribution based on a random stratified design. In November 2015 and April 2017, bad weather restricted sampling to two tidal inlets close to Büsum harbour (Fig. 1). The wintering area was sampled in February 2018 based on a 5x5 km grid (Fig. 1).

We took three replicates at each sampling station, each sieved through a 2 mm mesh and retrieved bivalves were stored in zip lock bags and frozen at -20°C for subsequent analysis. To describe the full benthic community, additional replicates taken in October 2016 were sieved through a 1 mm mesh, the full results of which are reported in Margeritis et al. (this issue). This study focuses on bivalve species, since they are the main prey items of Common Scoters. Sediment samples were taken from the first replicate, stored in zip lock bags and frozen at -20°C for further analysis.

2.3 Bivalve species analysis

All bivalve specimens were identified to species (see Table 1), counted and measured by callipers to the nearest 0.1 mm (length, width and height). Individual ash free dry weight (ash-free dry mass, given in g m^{-2}) was determined based on the loss on ignition method (Kramer et al., 1992). Flesh-to-shell ratio was calculated based on dry weights. Flesh was removed from complete shells, with flesh and shells dried separately in porcelain crucibles at 50°C for 24 hours and weighed. To determine ash content, flesh fractions were combusted in a muffle furnace at 560°C for 12 hours and subsequently reweighed. Cumulative individual ash free dry weights were used to calculate species ash-free dry mass per sample. Individuals where separation of flesh and shell was impossible (e.g. if shells were broken or individuals were too small) were excluded from further analysis. Due to of variable abundances, only bivalve species with a minimum of 26 (moulting area) and 7 (wintering area) sampled specimen were considered for further analyses. Species abundances, ash-free dry mass and flesh-to-shell ratio of all species collected are given as mean ± SD shown in Appendix Table A.1.

Some moulting area samples contained large numbers of two bivalve species, *E. leei* and *L. balthica* (for taxonomical authorities see Table 1), so only subsamples were subject to the loss on ignition method. Remaining individuals were either measured with a calliper (*L. balthica*) or separated into 5

mm size classes (from >0 to 110 mm) by placing them on graph paper (*E. leei*). Based on the ash free dry weight (y)/shell length (x) relationship of processed specimens, the following linear regressions models were fitted to determine the ash-free dry mass of the measured individuals: $y = 3E\text{-}07x^{3.2144}$ ($R^2 = 0.93$ for *E. leei*) and $y = 2E\text{-}07x^{4.2294}$ ($R^2 = 0.91$ for *L. balthica*).

2.4 Sediment analysis

Sediment samples were dried at 100°C for 6-8 hours, weighed and treated with a 10% hydrogen peroxide (H_2O_2) solution for 12-24 hours to oxidize all organic constituents. Samples were subsequently rinsed with freshwater through sieves of 2 mm and 63 µm mesh size until the water was clear. Particulate matter >2 mm (gravel, stones, shells etc.) was separated, dried together with the washed samples at 100 °C for 6-8 hours and weighed. To analyse grain size distribution, a subsample of 50 to 80 g was sieved in ¼ Phi fractions for 10 minutes with twenty-one sieves ranging from 63 µm to 2 mm mesh (modified in accordance with Buchanan, 1984). Grain size statistics (e.g. mean, mode, sorting etc.) were calculated using GRADISTAD using their terminology (Blott and Pye, 2001).

2.5 Bivalve species community analysis

Bivalve species data (abundance and ash-free dry mass) were standardized to m^{-2} and $g\ m^{-2}$ respectively and abundance, ash-free dry mass and flesh-to-shell ratio are given as means ± standard deviation. All statistical analyses were performed with R (R Core Team, 2017), except for simple linear regression (performed in Microsoft Excel 2013). All maps were produced with ArcGIS (ESRI, Version 10.2.1, 2013). Bivalve species composition was tested for differences within each area and between areas. Abundance, ash-free dry mass and flesh-to-shell ratio data were tested for normality and homogeneity of variances. Ash-free dry mass and flesh-to-shell ratio of all bivalves were tested for potential significant differences in population variances. Significant differences of ash-free-dry mass and flesh-to-shell ratio means were determined via *post hoc* tests (USERFRIENDLYSCIENCE package, Peters, 2018).

Bivalve species communities in the samples from the moulting and wintering areas combined were classified in terms of species abundance (ind. m^{-2}) using a cluster analysis based on Bray-Curtis dissimilarities (VEGAN package, Oksanen et al., 2018). The potential influence of the variables "year" (2015 – 2018), "season" (moult or winter) or "month" (Feb, Apr, May, Jul, Oct, Nov) on the hierarchical clustering was tested with nested PERMANOVA analysis using the Adonis function in VEGAN (Oksanen et al., 2018, modified by Martinez Arbizu, 2017). To contrast the seasonally different distributions of moulting and wintering scoters, we defined two clusters *a priori*: one representing the moulting and the second representing the wintering area. Differences in bivalve communities between those clusters were assessed *post hoc* by a multilevel pairwise comparison (PERMANOVA) using the Adonis function in VEGAN (Oksanen et al., 2018, modified by Martinez Arbizu, 2017). The most dominant

species separating different communities were specified using similarity percentage analysis (SIMPER, Warton et al., 2012). We used multilevel pattern analysis (INDICSPECIES, De Caceres and Legendre, 2009) to determine the strength and significance of the association between species occurrence and communities.

Relationships between bivalve species abundance or ash-free dry mass and environmental variables were examined using Spearman or Pearson rank correlations (depending on whether data was normally distributed or not), using only bivalve species occurring at > five stations. Environmental variables were assigned to the benthos data by spatially joining them in ArcGIS. Selected parameters were different sediment characteristics (sediment type, sorting, sorting [μm], mean, median, mode 1), mud content [%], water depth [m], distance to coast [km] and bed sheer stress [N m^{-2}]. All values referring to sediment characteristics, mud content and water depth were taken from data we recorded during surveys (water depth) or determined by sample analysis (sediment characteristics, mud content). Distance to coast of sampling stations was calculated based on data provided by the national park administration for Schleswig-Holstein (NPV Schleswig-Holsteinisches Wattenmeer). Bed shear stress values were calculated from the numerical model by Kösters and Winter (2014). Environmental data were initially analysed for collinearity by using variance inflation factor (VIF) analysis (Zuur et al., 2009). The bioenv function was used to identify the best subset of environmental variables with the maximum rank correlation (VEGAN, Oksanen et al., 2018). Correlations between community and environmental dissimilarity matrices were calculated using the mantel function (VEGAN, Oksanen et al., 2018).

Results

3.1 Moulting area

3.1.1 Bivalve species composition and characterisation

In total, 16 different bivalve species were found in the moulting area. Due to strongly varying abundances, only 10 species were considered for further analyses. Total abundance of those bivalves varied between 10 and 4740 ind. m^{-2} (mean 550 ± 833 ind. m^{-2}) per sample. Mean abundance for each bivalve species is given in Table 1.

Samples from the moulting area were numerically dominated by *Ensis leei* (93%), followed by *Limecola balthica* (4%), *Abra alba* (1.5%) and *Petricolaria pholadiformis* (1%), contributing 99.5% of the total bivalve species abundance; their distribution and relative abundance are shown in Fig. 2. Study sites sampled during pre-moult (May and July 2016, April 2017) were dominated by *E. leei* (92%), followed by *L. balthica* (6%) and *P. pholadiformis* (1.7%), which together represented 99.7% of total bivalve species abundance. Post-moult, *E. leei* (95%) again dominated, followed by *A. alba* (2%) and *L. balthica* (1%), which together represented 98% of total bivalve species abundance.

3.1.2 Ash-free dry mass and flesh-to-shell ratio

Of the nine analysed bivalve species, *P. pholadiformis* had the highest ash-free dry mass (mean 0.635 ± 0.392 g m^{-2}), followed by *E. leei* (mean ash-free dry mass 0.341 ± 0.729 g m^{-2}) and *L. balthica* (mean ash-free dry mass 0.293 ± 0.458 g m^{-2}). Mean ash-free dry mass of *A. alba* was relatively low (0.054 ± 0.030 g m^{-2}). Ash-free dry mass and flesh-to-shell ratio for all bivalve species are shown in Table 1.

While *E. leei* dominated the bivale community in terms of abundance during pre- and post-moult, *P. pholadiformis* had the highest ash-free dry mass among pre-moult samples and *L. balthica* among post-moult samples (see Appendix Table 2).

Significant differences in ash-free dry mass were found between *E. leei* and *A. alba*, the Furrow Shell (*Abra prismatica)*, the Striped Venus (*Corbula gibba)* and the Banded Wedge Shell (*Donax vittatus,* Fig. 3a). *L. balthica* showed significant differences in ash-free dry mass to all species except the Common Nutclam (*Nucula nitidosa*) and *P. pholadiformis*. *N. nitidosa* showed significant differences to all species except *D. vittatus* and *F. fabula*. *P. pholadiformis* showed significant differences to all species.

E. leei had the highest flesh-to-shell ratio (mean 0.407 ± 0.708), followed by *L. balthica* (mean 0.244 ± 1.632), *A. alba* (mean 0.205 ± 0.097) and *P. pholadiformis* (mean 0.197 ± 0.045).

Significant differences in flesh-to-shell ratio were found between *E. leei* and *A. prismatica*, *C. gibba*, *D. vittatus*, *F. fabula* and *N. nitidosa* (Fig. 3b). *F. fabula* showed significant differences to *A. alba*, *C. gibba*, *D. vittatus*, *N. nitidosa* and *P. pholadiformis*.
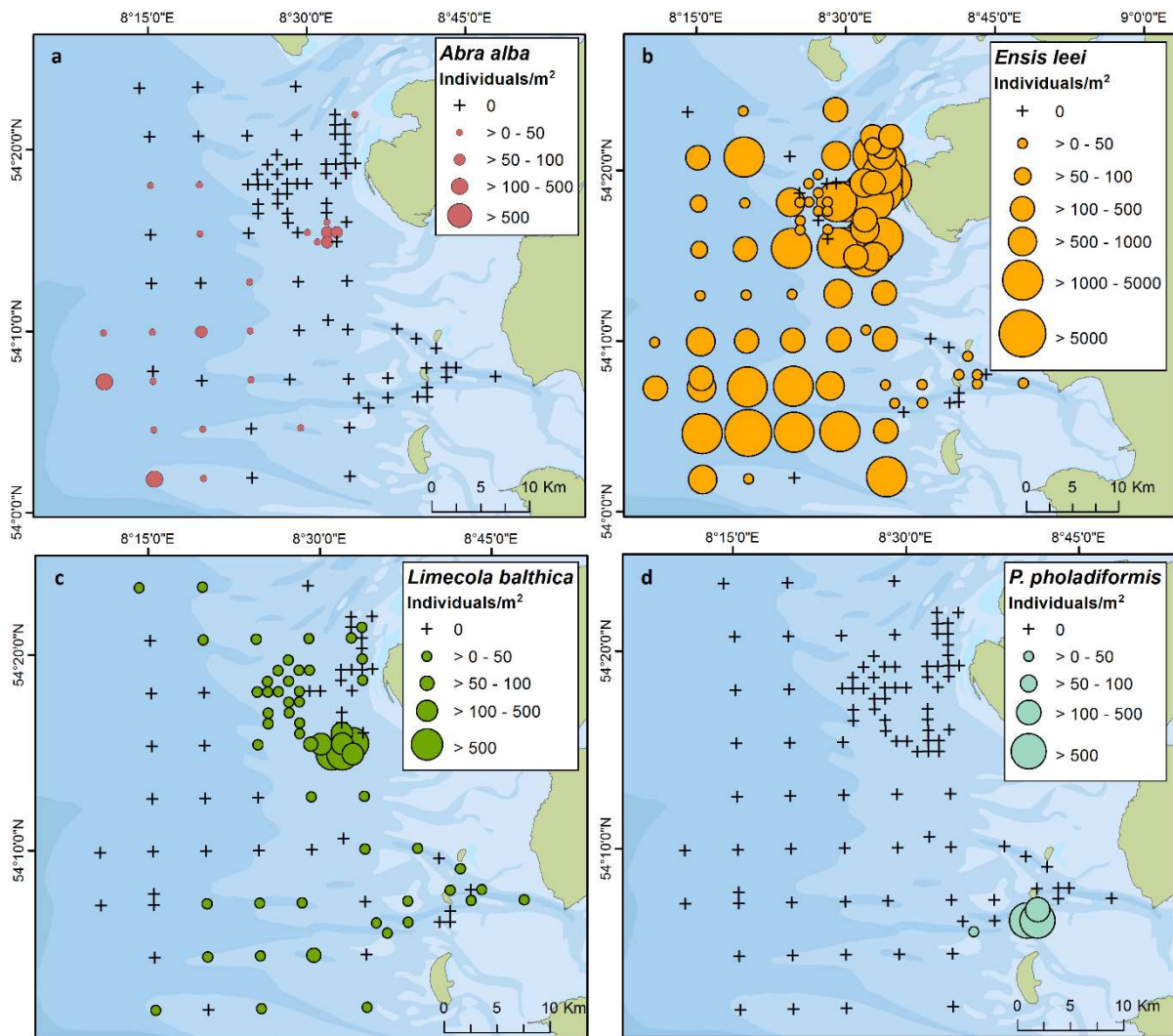
Fig. 2. Spatial distribution and abundance (ind. m^{-2}) of (**a**) *Abra alba*, (**b**) *Ensis leei*, (**c**) *Limecola balthica* and (**d**) *Petricolaria pholadiformis* in the Common Scoter moulting area. Samples were collected during November 2015, May/July/October 2017 and April 2017.
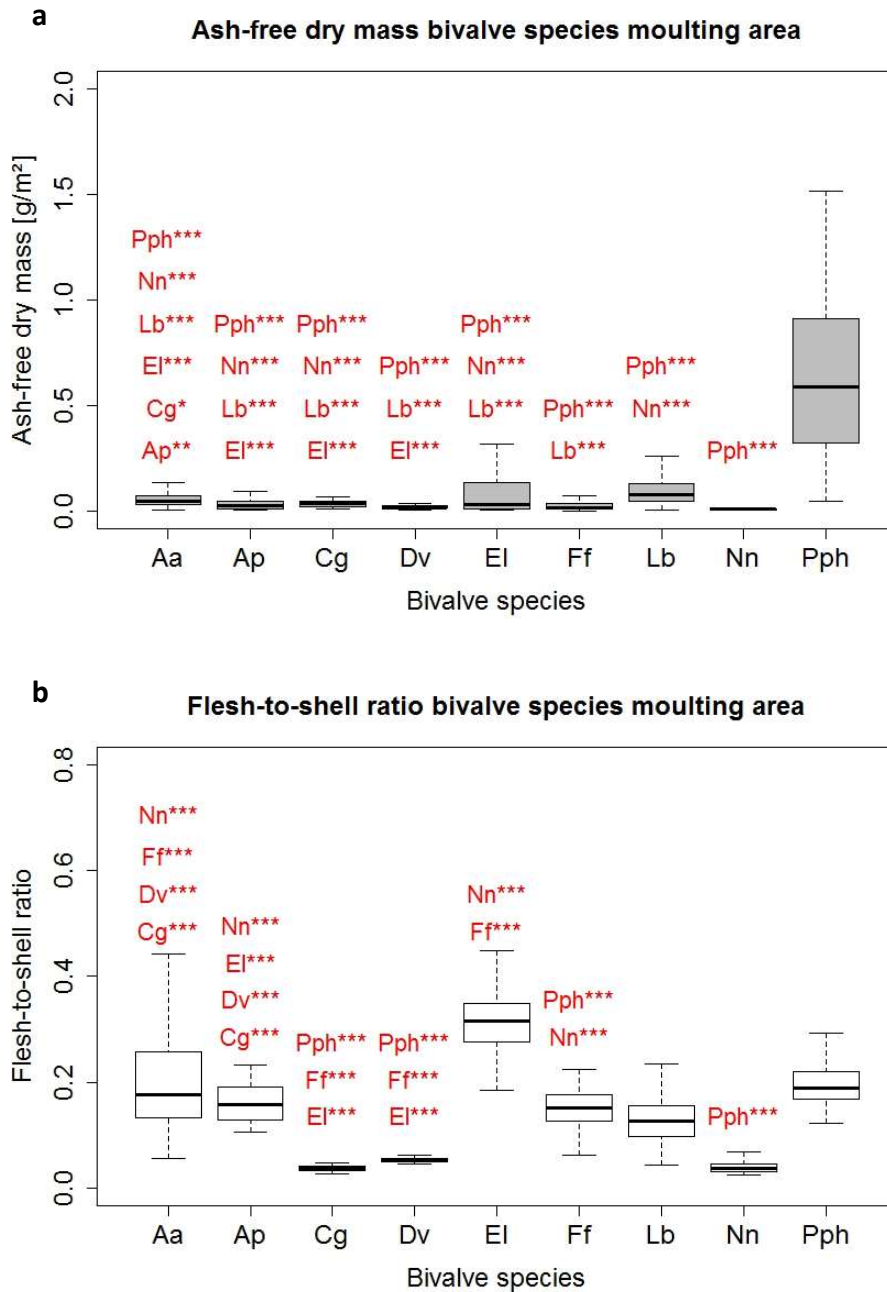
Fig. 3. Boxplots showing (**a**) the ash-free dry mass and (**b**) the flesh-to-shell ratio of the most abundant bivalve species found in the Common Scoter moulting area. Significant differences in means in ash-free dry masses and flesh-to-shell ratio between species according to Games-Howell *post hoc* testing are indicated by species codes in red above the boxplot. Significance levels <0.001 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1, 1. **Aa** *Abra alba*, **Ap** *Abra prismatica*, **Cg** *Corbula gibba*, **Dv** *Donax vittatus*, **El** *Ensis leei*, **Ff** *Fabulina fabula*, **Lb** *Limecola balthica*, **Nn** *Nucula nitidosa*, **Pph** *Petricolaria pholadiformis*

3.1.3 Size classes of *E. leei* and *L. balthica*

Pre-moult, 99.7% of *E. leei* individuals fell in size classes >10 and <15 mm (Fig. 4a), with 0.3% >30 and <60 mm and single individuals >90–95 mm and >100–105 mm. Post-moult, 91.5% fell in size classes >10 and <35 mm, with 8.5% in size classes >35 and <60 mm (Fig. 4b). No individuals >60 mm were found. During both periods, no individuals <10 mm were found.

Pre-moult, 85.6% of *L. balthica* individuals ranged from >5 to 15 mm and 14.4% >15 to 30 mm (Fig. 4c). No individuals >30 mm were found. Post-moult, 72.3% fell intos size classes >5 and <15 mm, and another peak of 27.7% in size classes >15 and <25 m (Fig. 4d). No individuals >25 mm were found. During both periods, no individuals <5 mm were found.
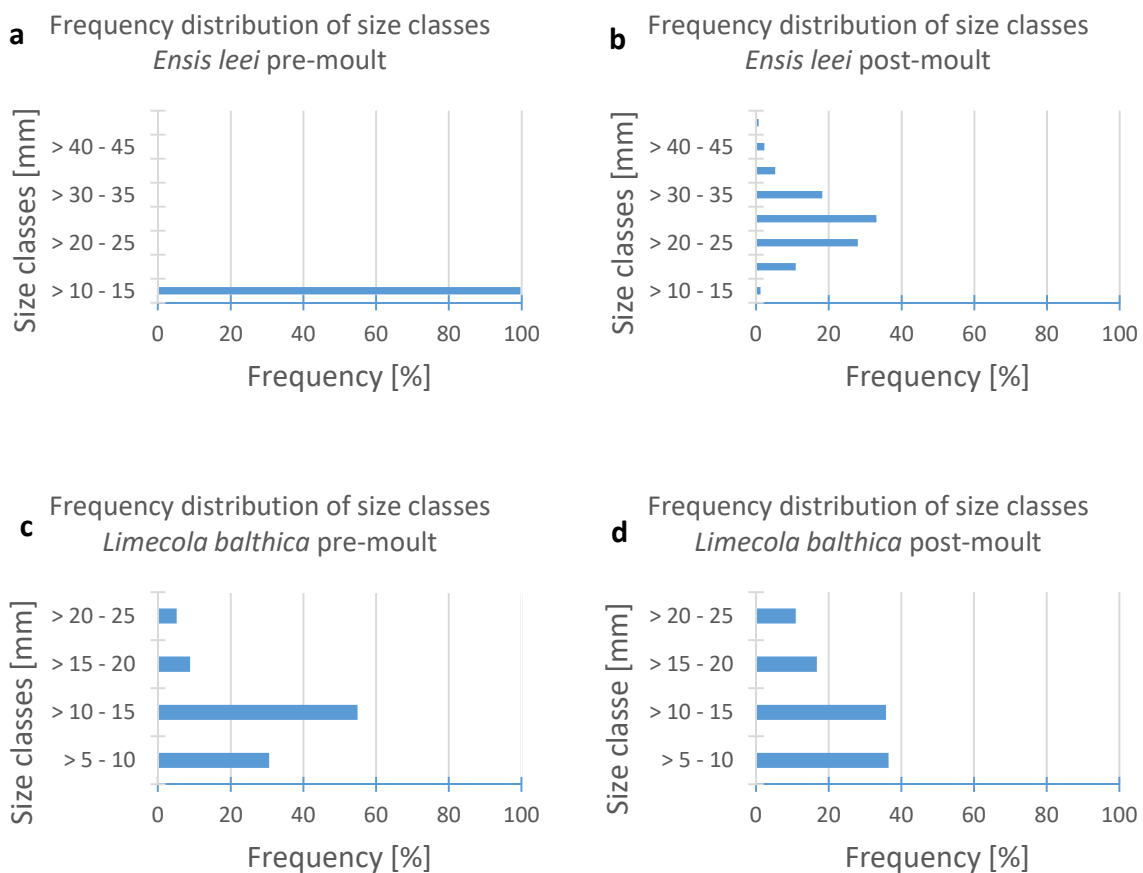

Fig. 4. Frequency distribution of individual size classes [mm] for *Ensis leei* (**a** pre-moult, **b** post-moult) and *Limecola balthica* (**c** pre-moult, **d** post-moult). Pre-moult samples were collected during May/July 2016 and April 2017. Post-moult samples were collected during November 2016 and October 2016.

3.1.4 Sediment characteristics

Sediment types varied from very fine (27% of all samples), fine (57%) and medium sand (8%) to coarse (1%) and very coarse silt (6%). Sediment grains varied from very well sorted to very poorly sorted, with a mean of 1.78 ± 0.84 µm. Mud content [%] in samples ranged from 0.8 to 81.8% (mean 13.2 ± 16%).

3.2 Wintering area

3.2.1 Bivalve species composition and characterisation

Nine different bivalve species occurred across all samples. Due to strongly varying abundances, only five were considered for further analyses (Table 1). Total abundance of all bivalve species varied between 10 and 70 ind. m^{-2} (mean 22 ± 16 ind. m^{-2}) per sample.

F. fabula dominated (44%), followed by *S. solida* (20%), *E. leei* (10%), *A. alba* (10%), and the Cut-Through Shell (*Spisula subtruncata*, 4%), which together represented 89% of total bivalve species abundance. Their distribution and relative abundance are shown in Fig. 5.

3.2.2 Ash-free dry mass and flesh-to-shell ratio

Of the five analysed bivalve species in the wintering area, *S. solida* had the highest ash-free dry mass (mean 1.639 ± 1.262 g m^{-2}, Table 1), followed by *L. balthica* (mean ash-free dry mass 0.233 ± 0.503 g m^{-2}) and *A. alba* (mean ash-free dry mass 0.200 ± 0.080 g m^{-2}). Ash-free dry mass of *F. fabula* was comparatively low (mean 0.047 ± 0.084 g m^{-2}).

Significant differences in ash-free dry mass were found between *S. solida* and all species, and between *A. alba* and *F. fabula* (Fig. 6a).

F. fabula had the highest flesh-to-shell ratio (mean 0.182 ± 0.038), followed by *A. alba* (mean 0.180 ± 0.032) and *L. balthica* (mean 0.132 ± 0.036). The flesh-to-shell ratio of *S. solida* was comparatively low (mean 0.056 ± 0.007).

Significant differences in flesh-to-shell ratio were found between *L. balthica* and all species, as well as between *S. solida* and all species (Fig. 6b). *S. subtruncata* likewise showed significant differences to all species.

3.2.3. Sediment characteristics

Sediment types varied between fine (73% of all samples), medium (13%) and coarse sand (13%). Sediment grains varied from very well to moderately sorted, with a mean of 1.45 ± 0.12 µm. Mud content [%] in samples ranged from 1.2 to 33.7% (mean 4.2 ± 6.5%).

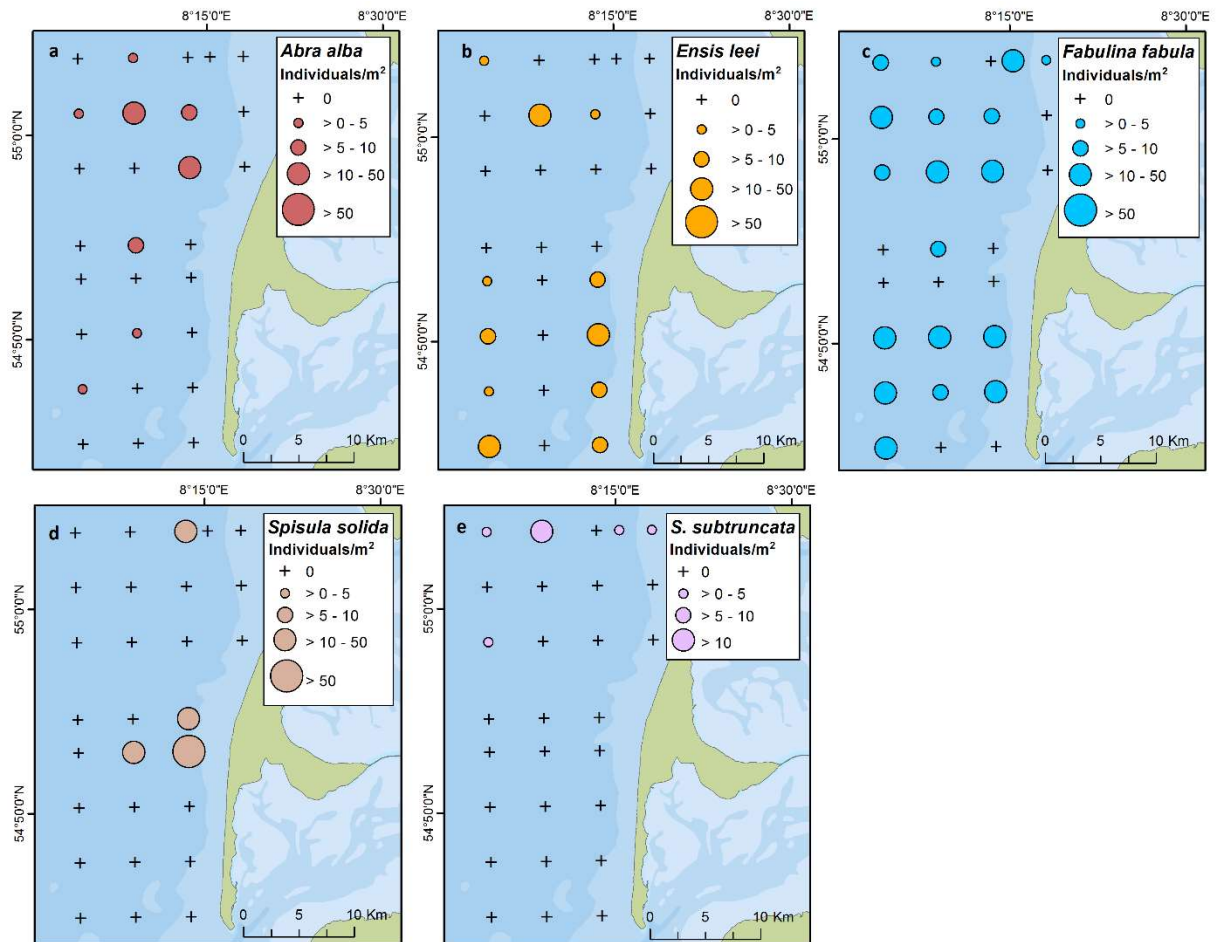**Fig. 5.** Spatial distribution and abundance (ind. m^{-2}) of (**a**) *Abra alba*, (**b**) *Ensis leei*, (**c**) *Fabulina fabula*, (**d**) *Spisula solida* and (**e**) *Spisula subtruncata* in the Common Scoter wintering area. Samples were collected during February 2018.
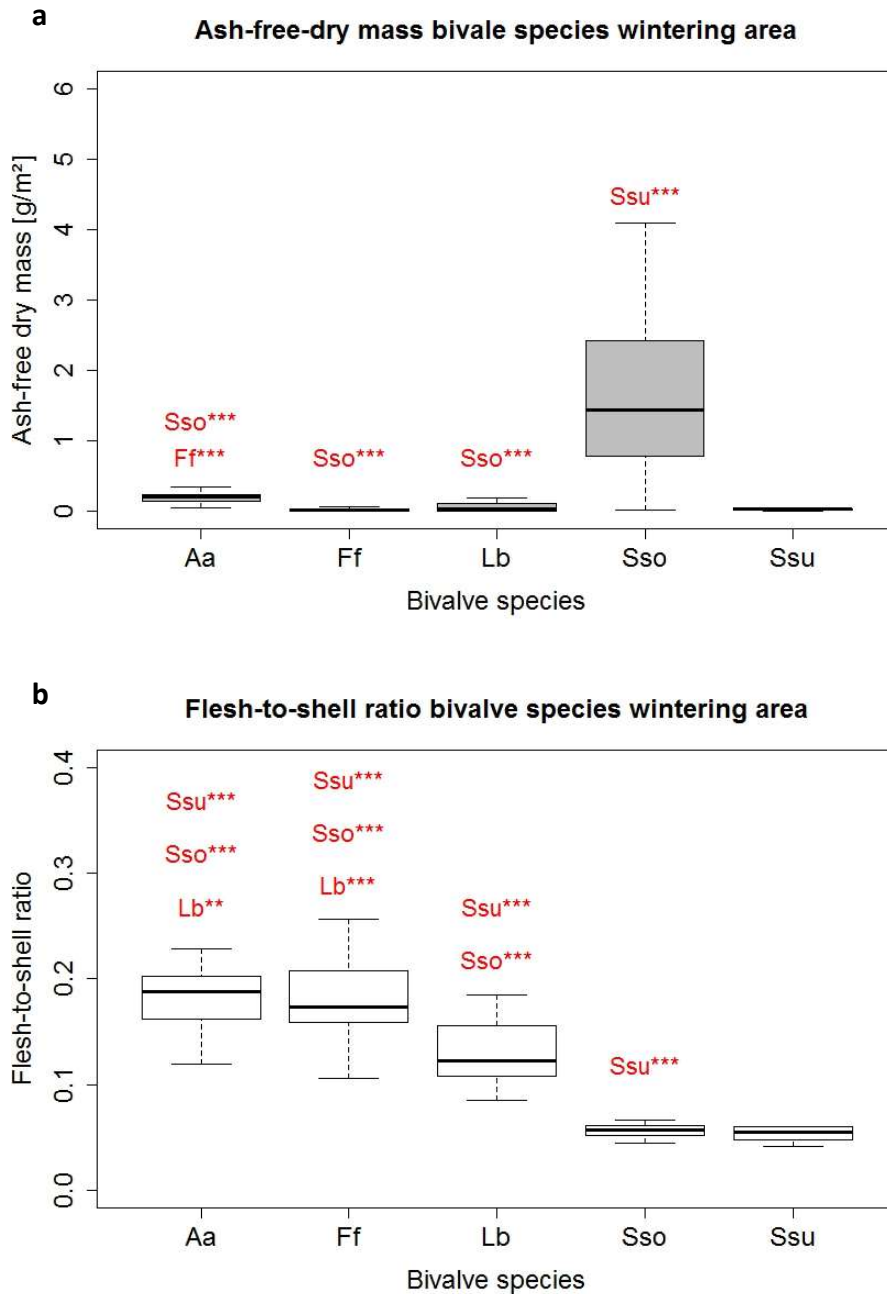
Fig. 6. Boxplots showing (**a**) the ash-free dry mass and (**b**) the flesh-to-shell ratio of the most abundant bivalve species found in the wintering area. Significant differences in means in ash-free dry masses and flesh-to-shell ratio between species according to Games-Howell and Tukey's HSD *post hoc* testing are indicated by species codes in red above the boxplot. Significance levels <0.001 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1, 1. **Aa** *Abra prismatica*, **Ff** *Fabulina fabula*, **Lb** *Limecola balthica*, **Sso** *Spisula solida*, **Ssu** *Spisula subtruncata*

Table 1. Abundance (ind. m^{-2}), ash-free dry mass (g m^{-2}) and flesh-to-shell ratio for each species in each area given as mean ± standard deviation. Species with the highest abundance, ash-free dry mass and flesh-to-shell ratio are given in bold. The data represents results for collected bivalves of all sampling cruises (November 2015, May/July/October 2016, April 2017 and February 2018).

Species	Abundance [ind. m^{-2}]		Ash-free dry mass [g m^{-2}]		Flesh-to-shell ratio	
	Moulting area	Wintering area	Moulting area	Wintering area	Moulting area	Wintering area
Abra alba (Wood, 1802)	14.2 ± 58.2	3 ± 7	0.054 ± 0.030	0.200 ± 0.080	0.205 ± 0.097	0.180 ± 0.032
Abra prismatica (Montagu, 1808)	1.8 ± 17.3		0.035 ± 0.028		0.166 ± 0.046	
Corbula gibba (Olivi, 1792)	1.1 ± 8.8		0.038 ± 0.020		0.038 ± 0.007	
Donax vittatus (da Costa, 1778)	1.1 ± 9.1		0.030 ± 0.048		0.062 ± 0.030	
Ensis leei (M. Huber, 2015)	**1003.9 ± 1680.7**		0.341 ± 0.729		**0.407 ± 0.708**	
Fabulina fabula (Gmelin, 1791)	2.6 ± 14.5	**13.4 ± 17.1**	0.059 ± 0.114	0.047 ± 0.084	0.157 ± 0.058	**0.182 ± 0.038**
Limecola balthica (Linnaeus, 1758)	38.8 ± 123.3	1.4 ± 4.4	0.293 ± 0.458	0.233 ± 0.503	0.244 ± 1.632	0.132 ± 0.036
Nucula nitidosa (Winckworth, 1930)	1.2 ± 10.8		0.010 ± 0.004		0.040 ± 0.012	
Petricolaria pholadiformis (Lamarck, 1818)	9.4 ± 100		**0.635 ± 0.392**		0.197 ± 0.045	
Spisula solida (Linnaeus, 1758)		6.2 ± 18.1		**1.639 ± 1.262**		0.056 ± 0.007
Spisula subtruncata (da Costa, 1778)	0.3 ± 2.3	1.2 ± 3.8	0.297 ± 0.284	0.161 ± 0.335	0.092 ± 0.033	0.060 ± 0.020

Cluster analysis and correlations with environmental parameters

To compare benthic bivalve communities between the moulting and the wintering area, we defined both as two separate clusters *a priori*. The pairwise multilevel comparison (Adonis) showed a significant separation between them (P = 0.001). We could not detect an influence of sampling year, season or month (see Appendix Table A.3).

E. leei and *L. balthica* were the characteristic species in the moulting area cluster with *E. leei* alone contributing >90 % to Bray-Curtis dissimilarities (Table 2). Six different bivalve species were identified as characteristic in the wintering area cluster contributing > 90% to Bray-Curtis dissimilarities: *F. fabula*, *S. solida*, *E. leei*, *A. alba*, *L. balthica* and *S. subtruncata* (Table 2).

The SIMPER and INDICSPECIES analysis both showed that the moulting area cluster was dominated by *E. leei* and *L. balthica* with both species being significantly associated to this cluster as well (*E. leei P*= 0.001 and *L. balthica P*= 0.001). *F. fabula* (*P*= 0.001), *S. solida* (*P*= 0.008) and *S. subtruncata* (*P*= 0.022) were the dominating and significantly associated species in the wintering area cluster.

According to the Variance inflation factor (VIF) analyses, only mean particle size showed autocorrelation (see Appendix Table A.4). Against all expectations, no significant correlations were found between clusters and environmental parameters (Table 3). Regarding bivalve species, only *E. leei* showed a significant correlation with the environmental variables median particle size and sorting (P = 0.001).

Table 2. Characterisation of the two clusters described by the occurrence of their characteristic species.

	Cluster moulting area		Cluster wintering area	
Characterstic species (Contribution [%])	*Ensis leei* ***	90.11	*Fabulina fabula* ***	43.43
	Limecola balthica ***	5.61	*Spisula solida* **	20
	Abra alba	1.85	*Ensis leei*	13.14
			Abra alba	9.71
			Limecola balthica	4.57
			Spisula subtruncata *	4

Species dominating each cluster are given in bold. Species significantly associated with a cluster are indicated with an asterisks. Statistical significance codes: <0.001 '***' 0.001 '**' 0.01 '*'.

Table 3. Summary of the correlations between environmental parameters and clusters as well as species.

	Parameters for best model	r^2	*P*
Cluster moulting area	Sorting [µm], Mud content [%]	0.05	0.863
Cluster wintering area	Sediment type	0.27	0.678
Abra alba	Water depth [m]	0.12	0.357
Abra prismatica	Sorting	0.47	0.591
Ensis leei	Median, Sorting	0.25	**0.001 ****
Fabulina fabula	Bed shear stress, Distance to coast [km], Mode 1	0.09	0.945
Limecola balthica	Distance to coast [km], Water depth [m]	0.11	0.989
Spisula solida	Sorting	0.64	0.568
Spisula subtruncata	Bed shear stress, Sorting [µm], Water depth [m]	0.32	0.705

Spearman's/Pearson's correlation coefficient r^2 and the P-value are given for each correlation. Significant P-values are given in bold. Statistical significance codes: <0.001 '***' 0.001 '**' 0.01 '*'

Discussion

4.1 Benthic bivalve communities

Multivariate classification of benthic bivalve communities revealed significant differences in terms of species composition between scoter moulting and wintering areas. Overall, 19 bivalve species were collected, only six were present in both areas (*A. alba*, the Striped venus (*Chamelea striatula*), *E. leei*, *F. fabula*, *L. balthica* and *S. subtruncata*). The total bivalve abundance and species richness were much higher in the moulting compared to the wintering area. Based on the differences in the distribution of moulting and wintering scoters, we separated our data into two different clusters (moulting vs. wintering area). However, we would expect benthic species community characteristics to underlie seasonal influences. The fact that we could not find an impact of sampling year, month or season on the data is likely caused by insufficient sampling coverage across years in both study areas. Therefore, we need more detailed data to verify our findings in terms of spatial and seasonal variability.

The frequency distribution of *E. leei* size classes in the moulting area suggested the majority were juveniles (>20-60 mm) and spawn (<20 mm), most likely from 2015 (juveniles) and 2016 (spawn, see Kenchington et al., 1998 and Armonies and Reise, 1999 for size class data). This indicates a reproduction and recruitment peak in the two years prior to the survey. Other studies have reported increasing *E. leei* abundance elsewhere in the North Sea (Houziaux et al., 2011, Dekker and Beukema, 2012, Troost et al., 2017) and German Bight (Armonies and Reise, 1999, Dannheim, 2002, Dannheim and Rumohr, 2012). In Belgian waters, important recruitment events have taken place since at least 2007 (Houziaux et al., 2011). In Dutch waters, recruitment peaks were observed starting in 2004/05 (Dekker and Beukema, 2012). Our findings suggest continuous successful reproduction and recruitment in the North Sea contributes to the increasing distribution and abundance of this alien species. Which factors (e.g. environmental parameters such as temperature during the winter or reproductive period) are contributing to these recruitment peaks remains to be verified (Houziaux et al., 2011, Dekker and Beukema, 2012).

Explaining lower bivalve abundance and species richness in the wintering area remains challenging. We cannot exclude the contribution of seasonal declines in densities to the lower abundance and species richness in the wintering area (sampled during a single survey in February) compared to the moulting area (sampled in summer/early winter). Reiss and Kröncke (2005) demonstrated that seasonal variability of benthic communities in the German Bight was influenced by an interaction of food availability, water temperature, predation and hydrodynamic stress. Armonies et al. (2001) demonstrated severe winters could lead to increased mortality in several different bivalve species. Severe winters in the North Sea are often accompanied by easterly winds, which might displace bivalves into deeper waters, reducing abundance closer to the coast. Hostile environmental conditions,

such as the strong currents in the wintering area, may inhibit the settlement of juvenile benthic organisms into the sediment. Conversely, higher water temperatures can enhance energy expenditure, reducing energetic investment in gamete production (Honkoop and Beukema, 1997, Beukema et al., 1985, 2001, 2009, 2014) affecting abundance in subsequent years. The 2016/17 and 2017/18 winters were comparatively mild, which might have contributed to low bivalve reproduction rates. Our study results suggest that this could be the case for all bivalve species except *E. leei*. Dekker and Beukema (2012) previously suggested that *Ensis* recruitment might be less susceptible to changes in water temperature compared to other bivalve species.

4.2 Cluster analysis and correlations with environmental parameters

The differentiation between the two clusters was distinct. Performing a community analysis without the *a priori* definition also confirmed a discrete differentiation of clusters between both areas. This indicates that the species composition of each cluster was strongly characteristic for either the moulting or the wintering area. However, as our samplings did not cover all seasons in both areas, we need more data to verify our findings and determine whether the differences in bivalve communities between both areas are based on either spatial or seasonal variations. Due to its abundance at large spatial scales, *E. leei* had a substantial influence on the cluster in the moulting area. In the wintering area, where *E. leei* was less frequent, the cluster was characterised by the two most abundant bivalve species, in this case *F. fabula* and *S. solida*. Dannheim and Rumohr (2012) reported that *E. leei* integrated into the existing communities along the Frisian coast without suppressing any other species. Schwemmer et al. (2019b, this issue) found that modelling the distribution of *E. leei* in the north-eastern German Wadden Sea revealed an overlap with native benthic species causing potential competition for resources. Our results demonstrate how the high abundance of this non-native species influences benthic coastal communities, although the abundance of traditionally dominant *L. balthica* and *F. fabula* have apparently been stable on a long term basis (e.g. Racher and Nehmer, 2003, Kröncke et al., 2011).

Only in the case *of E. leei* did we find a correlation with median particle size and sediment sorting. Except for the spatial dominance of one or more bivalve species, the cluster differences could not be explained by any of the environmental variables we incorporated in our explanatory models. This might be caused by insufficient seasonal coverage or the sampling of inappropriate environmental parameters. Water temperature, chlorophyll a concentration or other factors might be of greater importance in explaining bivalve distribution and abundance, but such data were not available at sufficient spatial and temporal resolution to be incorporated in these analyses. Some of the sampled environmental parameters (e.g. sediment characteristics) were very uniform in both areas, which might explain the lack of correlations. Alternatively, biotic interactions between bivalve benthic species

might be more decisive at small spatial scales (Reiss et al., 2009) and influence species community composition. On larger spatial scales, gradients in environmental parameters (such as water depth, sediment or bed shear stress) can be crucial to the composition of benthic communities (Reiss and Kröncke, 2005, Kröncke et al, 2011). At smaller spatial scales, gradients in these parameters are less likely and therefore interactions between benthic species could be of greater importance. Unfortunately, we could not incorporate this feature into our analysis as we only sampled bivalves, not the complete benthic community.

4.3 Relationship between bivalve communities and Common Scoter distributions

Despite distinct difference in benthic communities, bivalve species present in both areas had similar mean ash-free dry masses and flesh-to-shell ratios in moulting and wintering areas, suggesting both regions are equally profitable to foraging bivalve predators. This might also compensate for their reduced abundance, especially in the wintering area. Even if bivalve species were less numerous, they still provide a profitable energy resource. Despite *P. pholadiformis* having the highest ash-free dry mass, it is not a species Common Scoters forage on as it prefers consolidated, peaty sediment. All bivalve species, which were listed as important prey items for scoters (e.g. *A. alba*, *C. edule*, *L. balthica*) in a review of Fox (2004) were found in both study areas. Common Scoters are believed to prefer shallow waters and sandy substrates, in which they can easily access their prey (Madsen, 1954). They preferentially select individuals scaling between 5 and 20 mm in length, sometimes up to 40 mm (Madsen, 1954, Fox, 2004). Particularly the numerous *E. leei* individuals found in the moulting area match these shell lengths very well. Additionally, prey depletion in areas of shallowest water may simply force birds to forage for the same prey at similar densities in progressively deeper water as the winter progresses. Regions with the shallowest water depths were precisely the areas, where we also found the highest *E. leei* (and *L. balthica)* densities. Dannheim and Rumohr (2012) found high densities of *E. leei* in the moulting and wintering area as long ago as 2000/2001. Schwemmer et al (2019b, this issue) reported high abundances of *E. leei* along the North Frisian Islands throughout the year. Seabirds at Sea surveys indicate an increase in scoter densities in the moulting and wintering areas in recent years (FTZ unpublished data). The consistent successful reproduction and recruitment of *E. leei* (especially in the moulting area) might have contributed to providing profitable energy resources and thus might support increasing scoter numbers with a reliable food resource for longer periods across seasons. Nevertheless, we need more data on bivalve communities (especially in the wintering area) across seasons to verify our findings.

Conclusions

Our results showed that two areas characterised by their differences in seasonal use by Common Scoter displayed strong differences in the benthic bivalve communities, abundance and species

richness they supported. Food profitability and ash-free dry mass did not differ between study areas, suggesting early season moulting Common Scoter select to feed in the moulting area due to the greater abundance of bivalves, especially the extremely abundant and profitable invasive alien *E. leei.* Although environmental parameters did not explain differences in bivalve community compositions, the consistent difference seems likely to explain why Common Scoters first forage in the moulting areas and continue to do so through the winter. Later, they spread into more northerly areas where the food resource would appear less profitable. Based on the results of our study, we conclude that the factor mostly influencing the distribution patterns of Common Scoters was the abundance of their bivalve prey, likely moderated by water depth and other factors affecting food availability (such as disturbance from shipping). In order to get deeper insight into the relations of Common Scoter distribution, not only the location and dispersal of their prey needs to be considered. Environmental parameters, such as water depth, bed shear stress and sediment characteristics, need to be incorporated as well, as these also have an influence on bivalve distribution. However, we still need to know a great deal more about the seasonal and inter-annual changes in benthic bivalve species abundance, age-class distributions and community composition before we can better understand the numerical responses of the Common Scoter on the surface to their food supply in the sediment below.

Funding

Declaration of interest

None

Acknowledgments

References

Armonies, W., Reise, K., 1999. On the population development of the introduced razor clam *Ensis americanus* near the island of Sylt (North Sea). Helgoland Mar. Res. 52, 291. https://doi.org/10.1007/BF02908903

Armonies, W., Herre, E., Sturm, M., 2001. Effects of the severe winter 1995/96 on the benthic macrofauna of the Wadden Sea and the coastal North Sea near the island of Sylt. Helgoland Mar. Res. 55, 170–175. https://doi.org/10.1007/s101520100077

Beukema, J., Dekker, R., Jansen, J., 2009. Some like it cold: populations of the tellinid bivalve *Macoma balthica* (L.) suffer in various ways from a warming climate. Mar. Ecol. Prog. Ser. 384, 135–145. https://doi.org/10.3354/meps07952

Beukema, J., Drent, J., Honkoop, P., 2001. Maximizing lifetime egg production in a Wadden Sea population of the tellinid bivalve *Macoma balthica*: a trade-off between immediate and future reproductive outputs. Mar. Ecol. Prog. Ser. 209, 119–129. https://doi.org/10.3354/meps209119

Beukema, J.J., Cadée, G.C., Dekker, R., Philippart, C.J.M., 2014. Annual and spatial variability in gains of body weight in *Macoma balthica* (L.): Relationships with food supply and water temperature. J. Exp. Mar. Bio. Ecol. 457, 105–112. https://doi.org/10.1016/j.jembe.2014.04.003

Beukema, J.J., Knol, E., Cadbe, G.C., 1985. Effects of temperature on the length of the growing season in the tellenid bivalve *Macoma balthica* (L.) living on tidal flats in the Dutch Wadden Sea. J. Exp. Mar. Bio. Ecol. 90, 129-144.

Blott, S.J., Pye, K., 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surf. Proc. Land. 26, 1237–1248. https://doi.org/10.1002/esp.261

Buchanan, J.B., 1984. Sediment analysis, in: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the Study of Marine Benthos. Blackwell Scientific Publications, Oxford, UK, pp. 41–635.

Cramp, S. (Ed.), 1994. Ostrich to ducks, Handbook of the birds of Europe, the Middle East and North Africa. Reprinted. ed, Oxford Univ. Press, Oxford.

Dannheim, J., 2002. Zur Biologie von *Ensis directus* und *Spisula solida* (Mollusca: Bivalvia) in den Küstengewässern der östlichen Nordsee, Dipl.-Arbeit, Institut für Meereskunde, Universität Kiel.

Dannheim, J., Rumohr, H., 2012. The fate of an immigrant: Ensis directus in the eastern German Bight. Helgoland Mar. Res. 66, 307–317. https://doi.org/10.1007/s10152-011-0271-2

De Caceres, M., Legendre, P. 2009. Associations between species and groups of sites: indices and statistical inference. Ecology, URL http://sites.google.com/site/miqueldecaceres/

Degraer, S., Vincx, M., Meire, P., Offringa, H., 1999. The macrozoobenthos of an important wintering area of the common scoter (*Melanitta nigra*). J. Mar. Biol. Assoc. U.K. 79, 243–251. https://doi.org/10.1017/S0025315498000277

Dekker, R., Beukema, J.J., 2012. Long-term dynamics and productivity of a successful invader: The first three decades of the bivalve *Ensis directus* in the western Wadden Sea. J. Sea Res. 71, 31–40. https://doi.org/10.1016/j.seares.2012.04.004

Deppe, L., 2003. Die Trauerente (*Melanitta nigra*) in der deutschen Bucht–GIS-basierte Bewertung räumlicher und zeitlicher Parameter. Dipl-Arbeit, Universität Hamburg.

Ellingsen, K., 2002. Soft-sediment benthic biodiversity on the continental shelf in relation to environmental variability. Mar. Ecol. Prog. Ser. 232, 15–27. https://doi.org/10.3354/meps232015

Environmental Systems Research Institute (ESRI), 2013. ArcGIS Desktop Release Version 10.2.1, https://www.esri.com/de-de/arcgis/about-arcgis/overview

Fox, A.D., 2004. Diet and habitat use of scoters *Melanitta* in the Western Palearctic - a brief overview. Wildfowl 54, 163–182.

Gray, J.S., Elliott, M., 2009. Ecology of Marine Sediments: From Science to Management. Oxford University Press.

Hennig, V., Hälterlein, B., 2000. Trauerente–Erfassungsschwierigkeiten einer Offshore-Vogelart.

Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer (Eds.): Wattenmeermonitoring 20–23.

Honkoop, P.J., Beukema, J., 1997. Loss of body mass in winter in three intertidal bivalve species: an experimental and observational study of the interacting effects between water temperature, feeding time and feeding behaviour. J. Exp. Mar. Biol. Ecol. 212, 277–297. https://doi.org/10.1016/S0022-0981(96)02757-8

Houziaux J.S., Craeymeersch J., Merckx, B., Kerckhof, F., van Lancker, V., Courtens, W., Stienen, E., Perdon, J., Goudswaard, P.C., van Hoey, G., Vigin, L., Hostens, K., Vincx, M., Degraer, S., 2011. 'EnSIS' - Ecosystem Sensitivity to Invasive Species. Final Report. Brussels : Belgian Science Policy Office 2012 – Research Programme Science for a Sustainable Development. 105 pp.

Kaiser, M.J., Galanidi, M., Showler, D.A., Elliott, A.J., Caldow, R.W.G., Rees, E.I.S., Stillman, R.A., Sutherland, W.J., 2006. Distribution and behaviour of Common Scoter Melanitta nigra relative to prey resources and environmental parameters. Ibis 148, 110–128. https://doi.org/10.1111/j.1474-919X.2006.00517.x

Kenchington, E., Duggan, R., Riddell, T., 1998. Early Life History Characteristics of the Razor Clam, Ensis directus, and the Moonsnails, Euspira Spp., with Applications to Fisheries and Aquaculture. Department of Fisheries & Oceans, Science Branch, Maritimes Region, Invertebrate Fisheries Division, Bedford Institute of Oceanography.

Kösters, F., Winter, C., 2014. Exploring German Bight coastal morphodynamics based on modelled bed shear stress. Geo-Mar. Lett. 34, 21–36. https://doi.org/10.1007/s00367-013-0346-y

Kramer, K.J., Brockmann, U.H., Warwick, R.M., 1992. Manual of sampling and analytical procedures for tidal estuaries. TNO Institute of Environmental Sciences, Laboratory of Applied Research.

Kröncke, I., Reiss, H., Eggleton, J.D., Aldridge, J., Bergman, M.J.N., Cochrane, S., Craeymeersch, J.A., Degraer, S., Desroy, N., Dewarumez, J.-M., Duineveld, G.C.A., Essink, K., Hillewaert, H., Lavaleye, M.S.S., Moll, A., Nehring, S., Newell, R., Oug, E., Pohlmann, T., Rachor, E., Robertson, M., Rumohr, H., Schratzberger, M., Smith, R., Berghe, E.V., van Dalfsen, J., van Hoey, G., Vincx, M., Willems, W., Rees, H.L., 2011. Changes in North Sea macrofauna communities and species distribution between 1986 and 2000. Estuar. Coast. Shelf Sci. 94, 1–15. https://doi.org/10.1016/j.ecss.2011.04.008

Kunitzer, A., Basford, D., Craeymeersch, J.A., Dewarumez, J.M., Dorjes, J., Duineveld, G.C.A., Eleftheriou, A., Heip, C., Herman, P., Kingston, P., Niermann, U., Rachor, E., Rumohr, H., de Wilde, P.A.J., 1992. The benthic infauna of the North Sea: species distribution and assemblages. I.C.E.S. J. Mar. Sci. 49, 127–143. https://doi.org/10.1093/icesjms/49.2.127

MacArthur, R.H., Pianka, E.R., 1966. On Optimal Use of a Patchy Environment. Am. Nat. 100, 603–609. https://doi.org/10.1086/282454

Madsen, F.J., 1954. On the food habits of the diving ducks in Denmark. Dan. Rev. Game Biol. 2(3), 157-266.

Margaritis, D., Schückel, U., Kottsieper, J., Eskildsen, K., Scheu, S., 2019. Comparison of trophic structure and function of different food webs in the subtidal of the Wadden Sea by using Ecological Network Analysis. Estuar. Coast. Shelf Sci. Under review

Markones, N., Garthe, S., 2011. Monitoring von Seevögeln im Offshore-Bereich der schleswig-holsteinischen Nordsee im Rahmen von NATURA 2000 in den Jahren 2004 bis 2009. Corax 22, 11–50.

Martinez Arbizu, P., 2017. pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.0.1. https://github.com/pmartinezarbizu/pairwiseAdonis

Meissner, J., Bräger, S., 1990. The feeding ecology of wintering eiders Somateria mollissima and

common scoters *Melanitta nigra* on the Baltic Sea coast of Schleswig-Holstein, FRG. Wader Study Group Bull. 58, 10–12. Microsoft Excel, Microsoft Office Professional Plus 2013

Mendel, B., Sonntag, N., Wahl, J., Schwemmer, P., Dries, H., Guse, N., Müller, S., Garthe, S., 2008. Artensteckbriefe von See-und Wasservögeln der deutschen Nord-und Ostsee: Verbreitung, Ökologie und Empfindlichkeiten gegenüber Eingriffen in ihren marinen Lebensraum. Bundesamt f. Naturschutz.

Nehls, G., 1998. Untersuchungen zu Bestand und Verbreitung von Eiderente, Trauerente und Brandente im Nationalpark Schleswig-Holsteinisches Wattenmeer. Gutachten im Auftrag des Landesamtes für den Nationalpark Schleswig-Holsteinisches Wattenmeer.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2018. vegan: Community Ecology Package. R package version 2.5-2. https://CRAN.R-project.org/package=vegan

Peters, G., 2018. userfriendlyscience: Quantitative analysis made accessible, R package version 0.7.1, <URL: https://userfriendlyscience.com>, URL: http://doi.org/10.17605/osf.io/txequ.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rachor, E., Nehmer, P., 2003. Erfassung und Bewertung ökologisch wertvoller Lebensräume in der Nordsee. Abschlußbericht für das F+E-Vorhaben *„Erfassung und Bewertung ökologisch wertvoller Lebensräume in der Nordsee"*. Bundesamt für Naturschutz. FKZ 89985310.

Reiss, H., Kröncke, I., 2005. Seasonal variability of infaunal community structures in three areas of the North Sea under different environmental conditions. Estuar. Coast. Shelf Sci. 65, 253–274. https://doi.org/10.1016/j.ecss.2005.06.008

Reiss, H., Greenstreet, S., Sieben, K., Ehrich, S., Piet, G., Quirijns, F., Robinson, L., Wolff, W., Kröncke, I., 2009. Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. Mar. Ecol. Prog. Ser. 394, 201–213. https://doi.org/10.3354/meps08243

Schwemmer, P., Volmer, H., Enners, L., Riemers, H.C., Binder, K., Horn, S., Eskildsen, K., Adler, S., Fox, A.D., Garthe, S., 2019a. Modelling summer distribution patterns of common scoters (*Melanitta nigra*) by its most important prey species, the razor clam (*Ensis directus*), and hydrodynamic parameters. Estuar. Coast. Shelf Sci. *in press*

Schwemmer P., Adler S., Enners L., Volmer H., Kottsieper J., Ricklefs K., Stage M., Schwarzer K., Wittbrodt K., Reimers HC., Binder K., Asmus R., Asmus H., Horn S., Schückel U., Kohlus J., Eskildsen K., Klingbeil K., Gräwe U., Garthe, S., 2019b. Modelling and predicting habitats for the neobiotic American razor clam Ensis leei in the north-eastern Wadden Sea – a matter of spatial scale-. Estuar. Coast. Shelf Sci. *under review*

Troost, K., Perdon, K.J., Zwol, J. van, Jol, J., van Asch, M., 2017. Schelpdierbestanden in de Nederlandse kustzone in 2017 (No. 17.014). Stichting Wageningen Research, Centrum voor Visserijonderzoek (CVO), IJmuiden.

Tulp, I., Craeymeersch, J., Leopold, M., van Damme, C., Fey, F., Verdaat, H., 2010. The role of the invasive bivalve *Ensis directus* as food source for fish and birds in the Dutch coastal zone. Estuar. Coast. Shelf Sci. 90, 116–128. https://doi.org/10.1016/j.ecss.2010.07.008

Warton, D.I., Wright, T.W., Wang, Y., 2012. Distance-based multivariate analyses confound location and dispersion effects. *Methods Ecol. Evol* 3, 89–101.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. New York, NY: Spring Science and Business Media.

Appendices

Glossary

Aa	*Abra alba*	White Furrow shell
Ap	*Abra prismatica*	Furrow shell
Cg	*Corbula gibba*	Basket shell
Dv	*Donax vittatus*	Banded Wedge shell
El	*Ensis leei*	American Razor clam
Ff	*Fabulina fabula*	Bean-like Tellin
Lb	*Limecola balthica*	Baltic Tellin
Nn	*Nucula nitidosa*	Nutclam
Pph	*Petricolaria pholadiformis*	American Piddock
Sso	*Spisula solida*	Surf Clam
Ssu	*Spisula subtruncata*	Cut-Through shell

Table A.1. Abundance (ind. m^{-2}), ash-free dry mass (g m^{-2}) and flesh-to-shell ratio for all species in both sampling areas given as mean ± standard deviation. The data represents results for collected bivalves of all sampling cruises (November 2015, May/July/October 2016, April 2017 and February 2018).

Species	Abundance [ind. m^{-2}]		Ash-free dry mass [g m^{-2}]		Flesh-to-shell ratio	
	Moulting area	Wintering area	Moulting area	Wintering area	Moulting area	Wintering area
Abra alba (Wood, 1802)	14.2 ± 58.2	3 ± 7	0.054 ± 0.030	0.200 ± 0.080	0.205 ± 0.097	0.180 ± 0.032
Abra prismatica (Montagu, 1808)	1.8 ± 17.3		0.035 ± 0.028		0.166 ± 0.046	
Barnea candida (Linnaeus, 1758)	0.15 ± 1.9		1.379 ± 0.817		0.530 ± 0.231	
Cerastoderma edule (Linnaeus, 1758)	0.12 ± 1.1		3.445 ± 2.793		0.072 ± 0.025	
Chamelea striatula (da Costa, 1778)	0.12 ± 1.4	0.53 ± 2.3	0.250 ± 0.089	0.296 ± 0.394	0.051 ± 0.006	0.043 ± 0.014
Corbula gibba (Olivi, 1792)	1.1 ± 8.8		0.038 ± 0.020		0.038 ± 0.007	
Donax vittatus (da Costa, 1778)	1.1 ± 9.1		0.030 ± 0.048		0.062 ± 0.030	
Ensis leei (M. Huber, 2015)	1003.9 ± 1680.7	4.1 ± 7.3	0.341 ± 0.729	6.301	0.407 ± 0.708	
Fabulina fabula (Gmelin, 1791)	2.6 ± 14.5	13.4 ± 17.1	0.059 ± 0.114	0.047 ± 0.084	0.157 ± 0.058	0.182 ± 0.038
Limecola balthica (Linnaeus, 1758)	38.8 ± 123.3	1.4 ± 4.4	0.293 ± 0.458	0.233 ± 0.503	0.244 ± 1.632	0.132 ± 0.036
Mactra stultorum (Linnaeus, 1758)	0.6 ± 3.1		2.410 ± 1.909		0.207 ± 0.049	
Macomangulus tenuis (da Costa, 1778)		0.18 ± 1.3		0.566		
Mya truncata (Linnaeus, 1758)	0.08 ± 0.9		3.184 ± 3.981		0.393 ± 0.085	
Mytilus edulis (Linnaeus, 1758)	0.09 ± 1.1		0.222 ± 0.171		0.124 ± 0.084	
Nucula nitidosa (Winckworth, 1930)	1.2 ± 10.8		0.010 ± 0.004		0.040 ± 0.012	
Phaxas pellucidus (Pennant, 1777)		0.9 ± 4.4		0.280 ± 0.034		
Petricolaria pholadiformis (Lamarck, 1818)	9.4 ± 100		0.635 ± 0.392		0.197 ± 0.045	
Spisula solida (Linnaeus, 1758)		6.2 ± 18.1		1.639 ± 1.262		0.056 ± 0.007
Spisula subtruncata (da Costa, 1778)	0.3 ± 2.3	1.2 ± 3.8	0.297 ± 0.284	0.161 ± 0.335	0.092 ± 0.033	0.060 ± 0.020

Table A.2. Abundance (ind. m^{-2}), ash-free dry mass (g m^{-2}) and flesh-to-shell ratio for each species during pre- and post-moult period given as mean ± standard deviation. Species with the highest abundance, ash-free dry mass and flesh-to-shell ratio are given in bold. Pre-moult samples were collected during May/July 2016 and April 2017. Post-moult samples were collected during November 2015 and October 2017.

Species	Abundance [individuals m^{-2}]		Ash-free dry mass [g m^{-2}]		Flesh-to-shell ratio	
	Pre moult	Post moult	Pre moult	Post moult	Pre moult	Post moult
Abra alba	7.42 ± 24.48	20.22 ± 76.06	0.059 ± 0.028	0.053 ± 0.030	0.34 ± 0.08	0.16 ± 0.05
Abra prismatica		3.53 ± 23.62		0.035 ± 0.028		0.17 ± 0.05
Corbula gibba		1.99 ± 12.04		0.038 ± 0.020		0.04 ± 0.01
Donax vittatus		2.06 ± 12.48		0.030 ± 0.048		0.06 ± 0.03
Ensis leei	**1093.25 ± 1633.48**	**925.15 ± 1723.56**	0.022 ± 0.091	0.154 ± 0.201	**0.54 ± 0.95**	**0.37 ± 0.61**
Fabulina fabula	0.33 ± 1.80	4.63 ± 23.79	0.462 ± 0.113	0.032 ± 0.041	0.27 ± 0.05	0.15 ± 0.05
Limecola balthica	70.49 ± 173.62	10.81 ± 21.6	0.198 ± 0.340	**0.257 ± 0.536**	0.16 ± 0.06	0.35 ± 2.47
Nucula nitidosa		2.35 ± 14.67		0.010 ± 0.004		0.04 ± 0.01
Petricolaria pholadiformis	20.08 ± 145.72		**0.635 ± 0.392**		0.20 ± 0.04	

Table A.3. Pairwise multilevel comparison of the potential influence of sampling year, season or month for data collected in the moulting area.

Year/Season/Month	F. Model	R^2	P-value	P adjusted
2015 vs 2016	NaN	1	NA	NA
2015 vs 2017	NaN	1	NA	NA
2016 vs 2017	NaN	1	NA	NA
Pre-moult vs Post-moult	NaN	1	NA	NA
Apr vs May+Nov	8.663	0.896	0.333	1
Apr vs July+Oct	7.484	0.882	0.333	1
May+Nov vs Jul+Oct	12.04	0.857	0.333	1

Codes to identify levels of statistical significance: <0.001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1"

Table A.4 Variance inflation factors for the environmental parameters used in the correlation. **VIF** Variance inflation factor

Parameter	VIF
Bed shear stress	1.20
Distance to coast [km]	2.69
Mean	20.22
Median	5.33
Mode 1	13.37
Mud content [%]	4.13
Sediment type	1.44
Sorting	5.08
Sorting [μm]	10.18
Water depth [m]	2.06

CHAPTER III

An invasive alien bivalve apparently provides a novel food source for moulting and wintering benthic feeding sea ducks

Johanna Kottsieper, Philipp Schwemmer, Nele Markones, Anthony D. Fox, Stefan Garthe

© Johanna Kottsieper

© Johanna Kottsieper
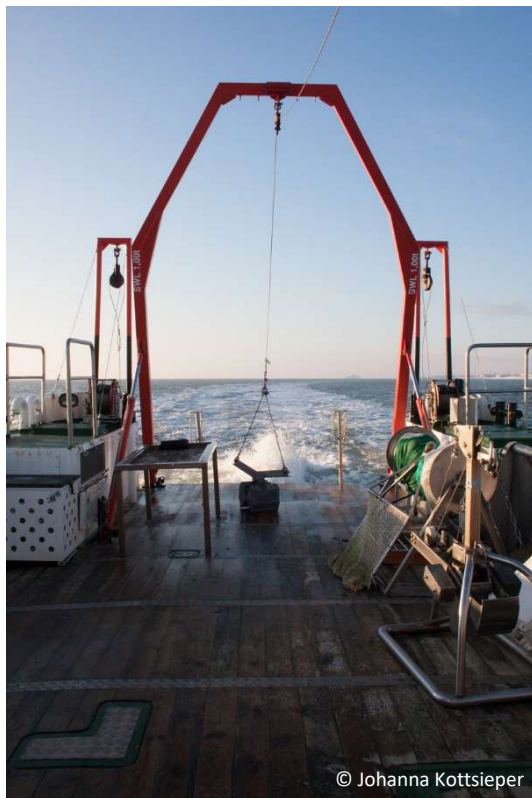
An invasive alien bivalve apparently provides a novel food source for moulting and wintering benthic feeding sea ducks

Johanna Kottsieper[1*], Philipp Schwemmer[1], Nele Markones[1], Anthony D. Fox[2], Stefan Garthe[1]

[1] Research and Technology Centre (FTZ), Kiel University, Buesum, Germany

[2] Department of Bioscience, University of Aarhus, Rønde, Denmark

Johanna Kottsieper kottsieper@ftz-west.uni-kiel.de, ORCID 0000-0002-1875-2994

Philipp Schwemmer schwemmer@ftz-west.uni-kiel.de, ORCID 0000-0002-3930-2845

Nele Markones markones@ftz-west.uni-kiel.de

Anthony D. Fox tfo@bios.au.dk, ORCID 0000-0001-8083-7633

Stefan Garthe garthe@ftz-west.uni-kiel.de, ORCID 0000-0003-0548-9346

* Corresponding author

Abstract

Since its introduction from North America in the 1970s, the American razor clam *Ensis leei* (M. Huber, 2015) has successfully spread throughout North Sea coasts from Spain to Norway and the United Kingdom to the Western Baltic. We investigated the distribution and abundance of this non-indigenous bivalve species as a potential novel food resource for common scoter *Melanitta nigra* (Linnaeus, 1758) along the eastern German North Sea coast. Highest densities of flightless moulting and wintering common scoters coincided with areas of high *E. leei* abundance. Other European studies showed common scoters extensively feed on *E. leei*. Even with these findings, it remains difficult to demonstrate convincingly that *E. leei* constitutes a major food source for common scoter in the German North Sea during their non-breeding season. However, our study suggests that *E. leei* has become an important prey item for internationally important concentrations of common scoters at large spatial scales, including within EU Birds Directive protected areas designated for the species. This finding is unusual for an abundant marine invasive alien species.

Keywords: American razor clam · *Ensis leei* · common scoter · German Bight · *Melanitta nigra* · subtidal benthos

Introduction

Invasive species constitute one of the most serious threats to global marine biological diversity (Molnar et al. 2008) potentially affecting ecosystem function, goods and services (Bax et al. 2003). Being less susceptible, for instance, to endemic competitors, predators, diseases or parasites, they can become extremely abundant and dominate host systems (e.g. Grosholz et al. 2000). However, it is known that some avian predators make use of aquatic alien bivalve species as novel food resources (e.g. Cadee 2001 or Werner et al. 2005).

Of several marine alien species introduced to the German North Sea since the early 18th century, some now only persist within limited ranges whereas others have become widespread (Gollasch 2006; AquaNis 2015). The American razor clam (*Ensis leei*, see caption of Fig. 2 for taxonomic authorities) was first recorded in the German North Sea in 1979 (Cosel et al. 1982), but now it occurs from Spain to Norway, the UK and the Western Baltic Sea (Gollasch et al. 2015). It has rapidly increased in abundance and biomass over the last three decades in the Dutch (Dekker and Beukema 2012) and more recently in the German North Sea (Dannheim and Rumohr 2012; Kottsieper et al. 2018, unpublished). Being common and highly abundant, *E. leei* potentially offers a profitable food resource for other species, such as benthic feeding fish and birds (Tulp et al. 2010).

The common scoter (*Melanitta nigra*) is a sea duck species found in large numbers along the German North Sea coasts during moulting (July-September) and wintering seasons (October-March; Mendel et al. 2008). Its distribution patterns are regularly monitored along the Dutch, German and Danish Wadden Sea coasts (e.g. Markones and Garthe 2011; Pihl et al. 2015; Fijn et al. 2017). Scoters predominantly feed on sedentary bivalve prey, which are highly abundant and easily accessible at any given site. They select mostly individuals ranging between 5 and 20 mm, and sometimes up to 40 mm, in length (Madsen 1954; Fox 2004). Recent studies report sea ducks such as common scoters actively feed on *E. leei* (e.g. Leopold and Wolf 2003; Leopold et al. 2007; Tulp et al. 2010). However, although the local distribution patterns of both common scoters and *E. leei* have been described, few studies have attempted to demonstrate large-scale connections between distributions of these avian predators and their benthic bivalve prey. Furthermore, few authors have demonstrated a direct connection by investigating the dietary contributions of *E. leei* by analysing stomach contents of dead scoters (but see Freudendahl and Jensen 2006; Leopold et al. 2007; Schwemmer et al. 2018 unpublished).

To investigate the importance of *E. leei* as a food resource, we studied its distribution pattern in the German Bight. We also mapped the distribution patterns of moulting (i.e. flightless) and wintering common scoter. Based on these distributions, we raised the following hypotheses:

1. High(est) densities of common scoters are found in areas with high(est) densities of *E. leei*.

2. Where present, *E. leei* is more abundant compared to other native bivalve species and can thus contribute a major share to common scoter diets.

Material and Methods

2.1 Study areas

The study areas were located in the sublitoral German North Sea along the coast of Schleswig-Holstein (see Fig. 1). These areas were consistently used by moulting and wintering common scoter (FTZ unpublished data). The moulting area covered 860 km^2 in the southern German North Sea extending from Friedrichskoog (54°2'N, 8°34'E) to Westerheversand (54°23'N, 8°33'E) with water depths ranging from 1 to 16 m. The wintering area was located west of the island Sylt covering 490 km^2 with water depths ranging from 5 to 17 m. Both areas were within the twelve nautical mile zone. Both regions are located in protected areas designated by the Habitats Directive and the Birds Directive, as well as being listed as Ramsar sites (Krause et al., 2011).

2.2 *Ensis leei* distribution

Overall, 319 benthos samples were taken with a 0.1 m^2 van Veen grab in both areas. 263 samples were collected in the moulting area during five cruises in 2015-2017 and 56 samples were collected in the wintering area during one cruise in 2018. Samples were taken based on grids (either a 5x5 km grid or a random stratified design) with three replicates at each sampling station. Collected bivalves were sieved through a 2 mm mesh and frozen in zip lock bags at -20°C for subsequent analysis. *E. leei* individuals were measured with callipers to the nearest mm and their numbers were converted to density (number of individuals per m^2 expressed as means ± standard deviation). To test for statistical differences in *E. leei* frequencies between sampling stations and areas, a chi-square test was performed in R (R Core Team 2017).

2.3 Common scoter distribution

Data from ship and aerial Seabirds at Sea (SAS) surveys conducted by the Research and Technology Centre (FTZ) during the moulting and wintering periods of common scoter were used to generate distribution patterns and calculate common scoter densities (individuals per km^2 summarised for all surveys and rastered by 5 x 5 km grid squares). The surveys were implemented by the FTZ within a regular offshore seabird monitoring on behalf of the Schleswig-Holstein Agency for Coastal Defence, National Park and Marine Conservation-National Park Authority. Surveys were carried out following internationally standardized Seabirds at Sea methods (Camphuysen at al. 2004) based on line transect methodology including distance sampling (Buckland et al. 2015). All aerial surveys had a fixed design with seven nearly N-S transects parallel to the coast. The four innermost transects were spaced at a 3

km interval, the remaining three had a 6 km interval. Surveys were performed from a high-winged twin-engine Partenavia P-68 with bubble windows at a flight altitude of 76m (250 feet) and a cruising speed of 185km/h (100 knots). The occurrence of birds was recorded within 388m wide transects running parallel to the flight route of the observation platform. Ship based counts were either conducted parallel to the benthos sampling cruises or data were taken from regular ship based monitorings. Birds were recorded within a 300m wide transect running parallel to the keel line of the observation vessel. Due to gaps in data, caused by either bad weather conditions or unavailability of ship/aircraft, data from 2015-2017 was combined. To match the benthos sampling areas, distribution maps are shown for the Schleswig-Holstein North Sea coast.

Results

3.1 *Ensis leei* distribution

E. leei was more widespread and occurred at higher densities in the southern study area (1003.9 ± 1680.7 ind/m^2, exceeding 10000 ind/m^2 in some samples) than in the northern study area (4.1 ± 7.3 ind/m^2). A chi-square test revealed statistically significant differences in the distribution between both areas (p=<0.001). *E. leei* densities for all sampling stations in both areas are shown in Fig. 1. *E.leei* was present at almost all sampling stations in the southern study area (see Fig. 2a), but was less prominent (p=<0.001) in the northern study area (Fig. 2b). Where present, *E. leei* dominated the benthic species composition in almost every single sample in the southern study area.
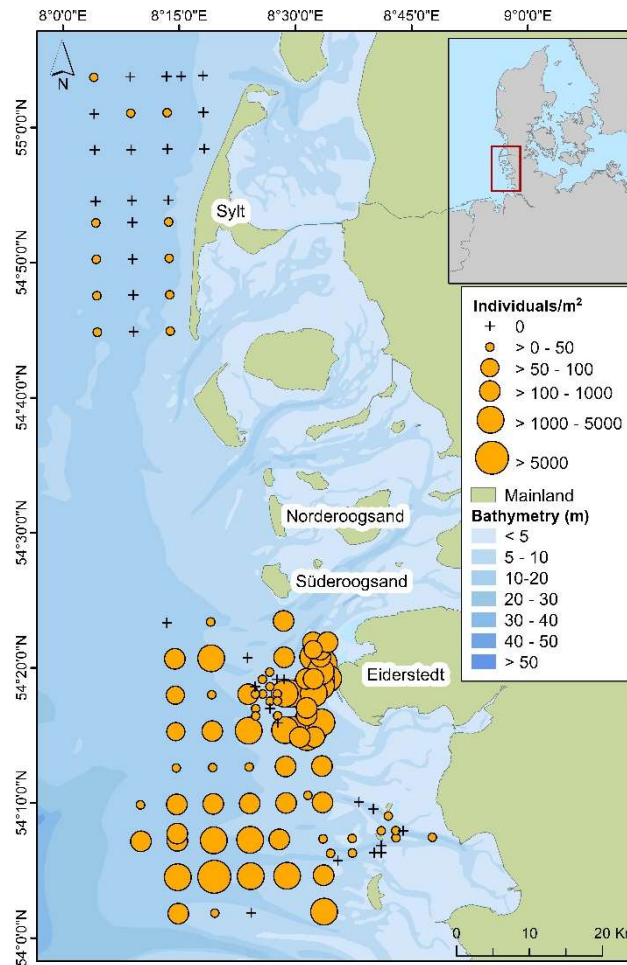
Fig. 1 Distribution and densities of *Ensis leei* determined from 319 benthos samples taken during 2015-2017 in the moulting (south) and the wintering (north) area in the eastern German North Sea, which are consistently used by moulting and wintering common scoters *Melanitta nigra*
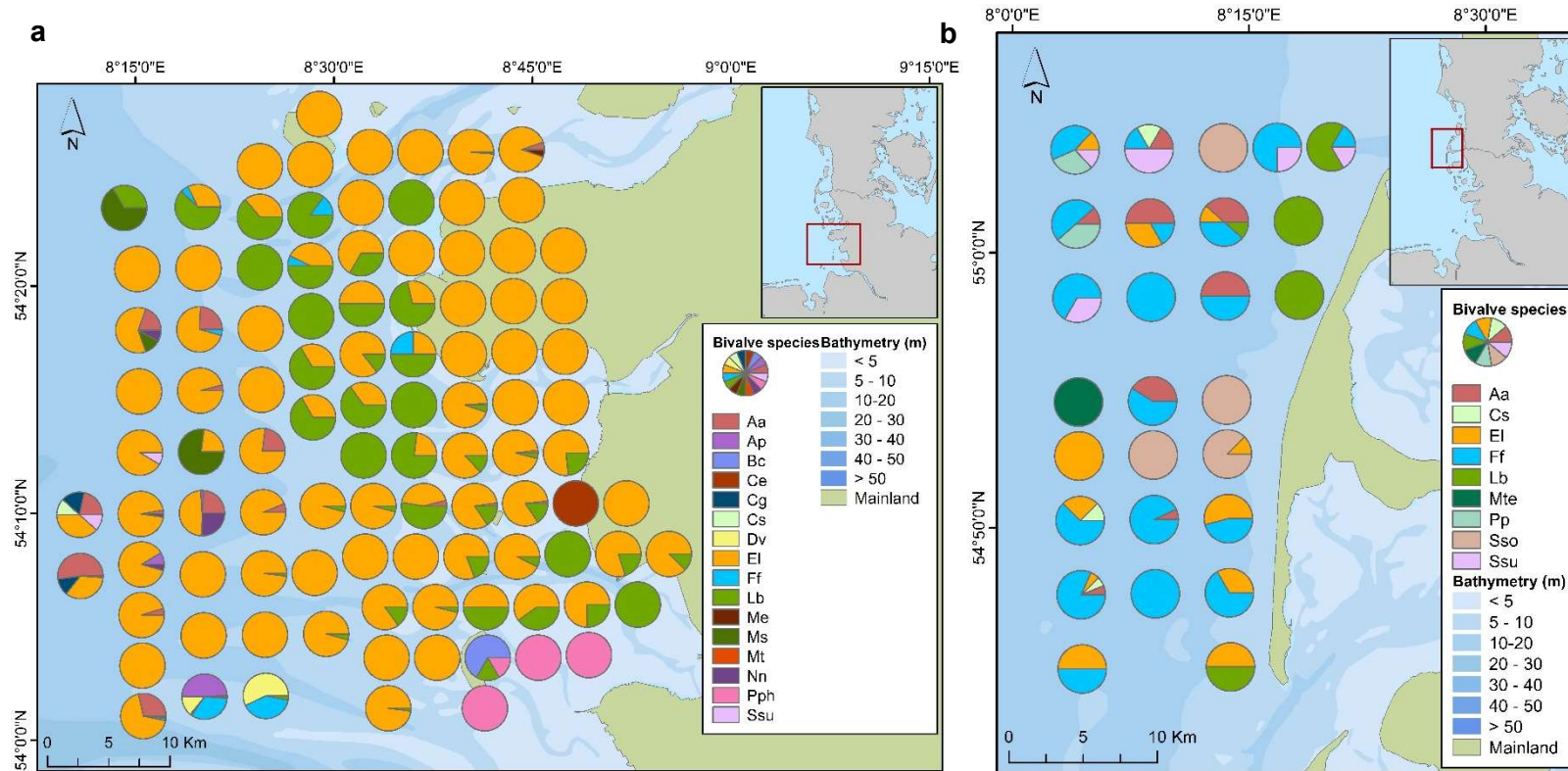
Fig. 2 Bivalve species composition for each sampling station in (**a**) the moulting and (**b**) the wintering area. **Aa** *Abra alba* (Wood, 1802), **Ap** *Abra prismatica* (Montagu, 1808), **Bc** *Barnea candida* (Linnaeus, 1758), **Ce** *Cerastoderma edule* (Linnaeus, 1758), **Cg** *Corbula gibba* (Olivi, 1792), **Cs** *Chamelea striatula* (da Costa, 1778), **Dv** *Donax vittatus* (da Costa, 1778), **El** *Ensis leei* (M. Huber, 2015), **Ff** *Fabulina fabula* (Gmelin, 1791), **Lb** *Limecola balthica* (Linnaeus, 1758), **Me** *Mytilus edulis* (Linnaeus, 1758), **Ms** *Mactra stultorum* (Linnaeus, 1758), **Mt** *Mya truncata* (Linnaeus, 1758), **Mte** *Macomangulus tenuis* (da Costa, 1778), **Nn** *Nucula nitidosa* (Winckworth, 1930), **Pp** *Phaxas pellucidus* (Pennant, 1777), **Pph** *Petricolaria pholadiformis* (Lamarck, 1818), **Sso** *Spisula solida* (Linnaeus, 1758), **Ssu** *Spisula subtruncata* (da Costa, 1778)

3.2 Common scoter distribution

During the time of moulting, common scoters occurred in small numbers along the entire eastern German North Sea coast with highest densities west of the islands Süderoogsand (810 ind/km^2) and south west of the Eiderstedt peninsula (219 ind/km^2, Fig. 3). Fewest individuals were observed in the northern parts west of the island of Sylt and in offshore areas. This distribution corresponded closely with areas of highest *E. leei* abundance, including areas where this species dominated the benthic community. Additionally, areas of highest scoter abundance were observed at the sites with the highest densities of small (< 2 cm in length) *E. leei* individuals.

During winter, common scoters were more dispersed along the eastern German North Sea coast and located further offshore (Fig. 4). Higher densities were observed west of Sylt, particularly along the northern end and highest densities were found southwest of the Eiderstedt peninsula (618 ind/km^2) and close to Süderoogsand (560 ind/km^2). Again, the occurrence of scoters west of the Eiderstedt peninsula matched the locations with highest *E.leei* abundance.
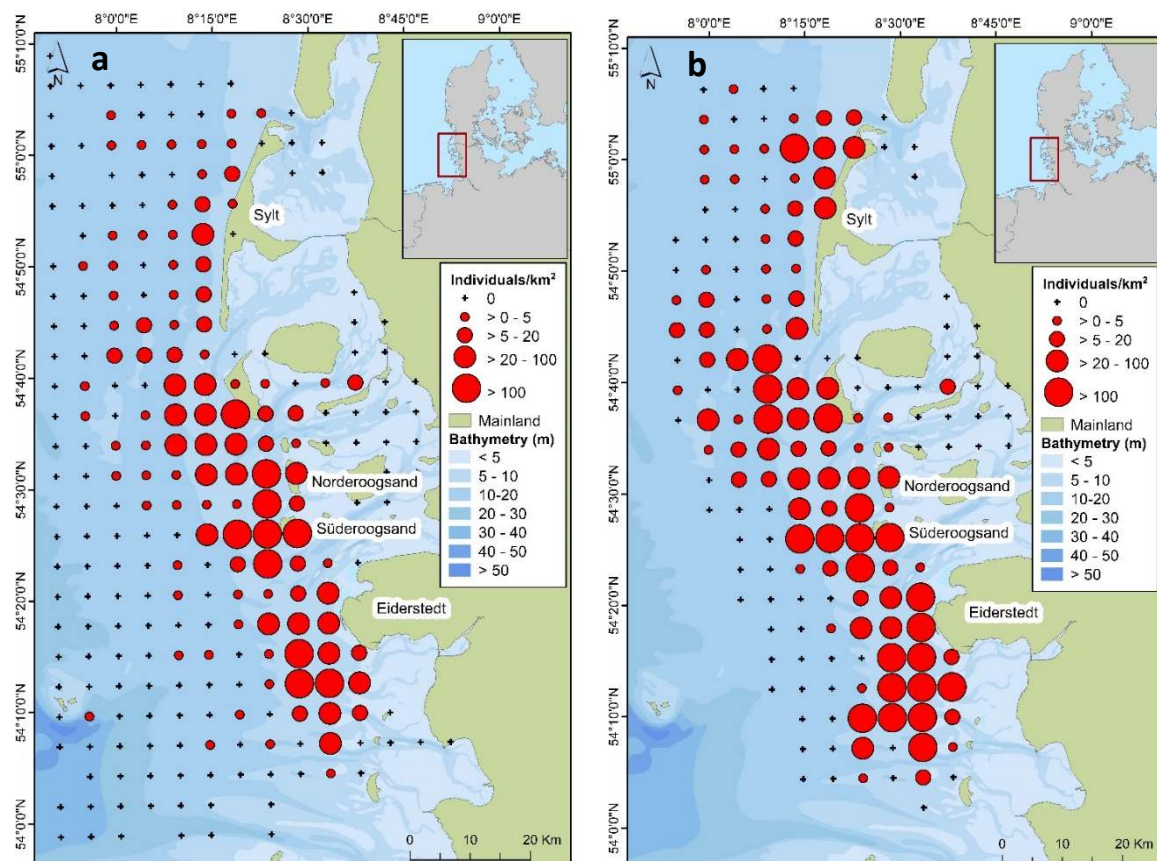

Fig. 3 Distribution patterns of common scoter *Melanitta nigra* in the German North Sea during a) the moulting and b) the wintering season given as individuals/km^2. The map shows data from June to

September (moult) and December to February (winter) in the years 2015-2017. To calculate densities, the number of birds was summed for all surveys

Discussion

Our findings show that common scoters occur along the German North Sea coast in areas where *E. leei* is extremely abundant. This pattern is particularly evident during the moulting period when these birds cannot fly and therefore their surveyed distributions reflect their feeding grounds. Highest scoter abundances during moult and winter occurred in the southern German North Sea, corresponding to areas of highest *E. leei* densities based on our benthos sampling. Common scoter typically feed on bivalves <60 mm long (Fox 2004), although single scoters have been regularly observed feeding on *E.leei* individuals >90 mm as well (I.K. Petersen *personal communication*). Kottsieper et al. (2018, unpublished) found that the *E. leei* individuals sampled in both the moulting and wintering areas matched these size classes. Particularly in the moulting area, high densities of small *E. leei* specimens were detected. The dominance, extent and available size class distribution of *E. leei* throughout the German North Sea in areas with moulting and wintering common scoters suggests this species could potentially provide a profitable food resource to this sea duck species in these areas.

Leopold and Wolf (2003) were the first to describe that scoters actively feed on the American razor clam. Prior to this study, *Abra alba*, *Cerastoderma edule*, *Limecola balthica*, *Mya arenaria*, *Mytilus edulis* and *Spisula subtruncata*, amongst others, were listed as the most important prey items (Fox 2004). Studies from the German North Sea, however, showed that all these species had lower flesh to shell ratios compared to *E. leei*, so this species is not just most abundant but also of superior food quality compared to native bivalves in the area (Kottsieper et al. 2018, unpublished). A recent study from Fijn et al. (2017) stated that common scoters residing in the Dutch Wadden Sea preferably feed on *Spisula subtruncata*, yet the high abundances of *E. leei* provides enough resources to fall back on. Freudendahl and Jensen (2006) reported that all 26 common scoters shot at Horns Rev in the Danish North Sea had been feeding on *E. leei*. In a more recent study, Schwemmer et al. (2018, unpublished) analysed >100 stomachs of scoters found dead along the German North Sea coast, showing that *E. leei* was the most common species in all stomachs. However, assessing the importance of a prey by analysing stomach contents can be difficult. Stomachs from birds found dead on the shore inevitably originate from weakened individuals that have died of disease or were in poor condition and likely have emptied their stomachs long before being washed ashore. Collecting birds by shooting does not necessarily resolve this issue. Thirty wintering common scoter shot in the Wadden Sea and 59 moulting specimens shot in Aalborg Bugt (Denmark) had nearly empty stomachs, suggesting that birds may potentially feed most actively at night (Fox et al. 2008; Skov et al. 2008).

It is extremely challenging to prove that common scoters have switched from native prey to aggregate during moult and winter periods in a feeding response to *E. leei* density and abundance along German North Sea coasts. Sampling of benthos occurs at a scale (<1 m^2) which is inappropriate to explain the distribution and abundance of common scoter that assort themselves in many thousands of individuals throughout more than 3000 km^2 of marine habitat off the German Wadden Sea. As discussed above, there are limitations and challenges associated with analysing the stomach contents of dead birds to assess the relative importance of *E. leei* in the moult and wintering diet of individuals and the population as a whole. The flesh to shell ratio of *E. leei* is superior to most other sympatric bivalve species (Kottsieper et al. 2018, unpublished) making it highly suitable prey for scoters. However, its attractiveness as prey is dependent on its abundance and size class distribution relative to other molluscs in the same sediment and the depth of the water column through which the sea ducks have to dive to obtain their prey (which determines the energetic costs of obtaining such prey). Spat settlement, mass die-offs and predation by fish and sea ducks all affect bivalve abundance and size class distributions within and between seasons. In tidal marine systems, therefore, it is impossible to demonstrate a meaningful aggregative response of common scoters to *E. leei.* However, we would contend that based on data presented here, moulting (and therefore largely immobile) common scoters occur in very high densities over substrates where the benthos is composed almost exclusively of *E. leei.* We therefore assume that this highly profitable species contributes a major share to the scoter diet. The distribution and abundance of *E. leei* likely explains the distribution and abundance of the common scoters in their moulting and wintering areas at the present time. Modelling the distribution of common scoter in connection with the *E. leei* distribution would give us more insight into the relationship between both species.

E. leei also likely explains the distribution of common scoters elsewhere and at greater geographical scales. Houziaux et al. (2011) reported high recruitment of juvenile *E. leei* in spring 2007 in the Belgian Wadden Sea and annual monitoring shows the species has been increasing in the Dutch Wadden Sea since 2010 (Troost et al. 2017). In the German North Sea, Schwemmer et al. (2018, unpublished) found high densities along the North Frisian Island coasts. In a previous study, Dannheim and Ruhmohr (2012) found high densities west of Sylt and Amrum as well as Eiderstedt. All these regions support common scoters and in many areas their numbers are increasing. Results from detailed benthos studies in German North Sea common scoter moulting areas demonstrated remarkably high abundances of *E. leei* (Kottsieper et al. 2018, unpublished), which have correlated with increasing densities of moulting and wintering scoter numbers in this area during the last three years (FTZ unpublished data).

Common scoter distribution and abundance are regularly monitored throughout the annual cycle along Wadden Sea coasts (e.g. Markones and Garthe 2011). However, we lack spatially and temporally

explicit monitoring of benthic communities and the seasonal size class distributions of their components to help interpret their attractiveness and relative importance to feeding common scoters. Annual benthos monitoring occurs only in the Netherlands (e.g. Troost et al. 2017) and the few studies of *E. leei* distributions in the German North Sea have restricted spatial scales (e.g. Dannheim and Rumohr 2012). However, Schwemmer et al. (2018, unpublished) and Kottsieper et al. (2018, unpublished) have contributed new and more detailed information of recent years. Nevertheless, demonstrating the importance of *E. leei* as food for common scoters remains difficult as long as aerial seabird and benthos surveys are not performed simultaneously or at similar spatial scales that can account for shifts in patterns and seasonal differences. More detailed information on the dietary composition (including oesophagus, gizzard and gut contents) is needed to improve our understanding of common scoter diets. The results presented here confirm other studies showing that along North Sea coasts, *E. leei* has become an important element of the diet of common scoters during the critical moult and winter periods at large (i.e. thousands of square kilometres) spatial scales, including within EU Birds Directive protected areas designated for internationally important aggregations of this sea duck species.

Acknowledgments

Funding

Competing interests

The authors declare that they have no conflict of interest.

Consent for publication

Not applicable.

Ethics approval and consent to participate

Not applicable.

Availability of data and materials

All data analysed and used in this study are published in this article as well as in" Comparison of bivalve communities between moulting and wintering areas used by Common Scoter *Melanitta nigra* in the German North Sea" by Kottsieper J, Schueckel U, Schwemmer P , Fox AD, Garthe S (2019) published in Estuar Coast Shelf Sci (*under review).* Since this study is part of a still ongoing PhD thesis by the first author data used and analysed in this study is only available from the corresponding author on reasonable request.

Author's contribution

JK and PS were responsible for planning and conducting the study. JK carried out sample and data analysis and drafted the manuscript. NM is responsible for the Seabirds at Sea monitoring. All authors read and approved the final version of the manuscript.

References

AquaNIS Editorial Board (2015) Information system on Aquatic Non-Indigenous and Cryptogenic Species. World Wide Web electronic publication. www.corpi.ku.lt/databases/aquanis. Version 2.36+. Accessed 2018-07-30.

Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. Mar Policy 27:313-323. https://doi.org/10.1016/S0308-597X(03)00041-1

Buckland ST, Rexstad EA, Marques TA, Oedekoven CS (2015) Distance sampling: methods and applications. Springer

Cadee GC (2001) Herring gulls learn to feed on a recent invader in the Dutch Wadden Sea, the Pacific Oyster Crassostrea gigas. Basteria 65(1-3):33-42. http://natuurtijdschriften.nl/download?type=document&docid=643840

Camphuysen CJ, Fox AD, Leopold MF, Petersen IK (2004). Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the U.K. COWRIE-Report BAM-02-2002. Royal Netherlands Institute for Sea Research, Texel

Cosel R, Dörjes J, Mühlenhardt-Siegel U (1982) Die Amerikanische Schwertmuschel *Ensis directus* (Conrad) in Der Deutschen Bucht: I. Zoogeographie Und Taxonomie Im Vergleich Mit Den Einheimischen Schwertmuschel-Arten [The American Jackknife Clam *Ensis directus* (Conrad) in the German Bight: I. Zoogeography and Taxonomy in Comparison with the Native Jackknife and Razor Clams'] Senckenberg Marit 3/4:147-173. http://www.vliz.be/en/imis?refid=115578.

Dannheim J, Rumohr H (2012). The Fate of an Immigrant: *Ensis directus* in the Eastern German Bight. Helgoland Mar Res 66:307–17. https://doi.org/10.1007/s10152-011-0271-2.

Dekker R, Beukema JJ (2012) Long-Term Dynamics and Productivity of a Successful Invader: The First Three Decades of the Bivalve *Ensis directus* in the Western Wadden Sea. J Sea Res 71:31–40. https://doi.org/10.1016/j.seares.2012.04.004.

Fijn RC, Leopold MF, Dirksen S, et al (2017) Een onverwachte concentratie van Zwarte Zee-eenden in de Hollandse kustzone in een gebied met hoge dichtheden van geschikte schelpdieren. Limosa 90:97–117

Fox AD (2004) Diet and Habitat Use of Scoters *Melanitta* in the Western Palearctic - a Brief Overview.

Wildfowl 54: 163–182.

Fox AD, Hartmann P, Petersen IK (2008) Body mass and organ size change during wing moult in Common Scoter. J Avian Biol 39:35-40. https://doi.org/10.1111/j.2007.0908-8857.04135.x

Freudendahl AS, Jensen KT, 2006. Population dynamics of the American razor clam (*Ensis americanus*) at Horns Rev. Report by University of Aarhus, Department of Marine Ecology.

Gollasch S (2006) Overview on Introduced Aquatic Species in European Navigational and Adjacent Waters. Helgoland Mar Res 60:84–89. https://doi.org/10.1007/s10152-006-0022-y.

Gollasch S, Kerckhof F, Craeymeersch J, Goulletquer P, Jensen K, Jelmert A, Minchin D (2015) Alien Species Alert: *Ensis directus*. Current Status of Invasions by the Marine Bivalve *Ensis directus*. ICES Coop Res Rep 323:1–36.

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG (2000) The impacts of a nonindigenous marine predator in a California Bay. Ecology 81:1206-1224. https://doi.org/10.1890/0012-9658(2000)081[1206:TIOANM]2.0.CO;2

Houziaux JS, Craeymeersch J, Merckx B, Kerckhof F, van Lancker V, Courtens W, Stienen E, Perdon J, Goudswaard PC, van Hoey G, Vigin L, Hostens K, Vincx M, Degraer S (2011). *'EnSIS' - Ecosystem Sensitivity to Invasive Species.* Final Report. Brussels: Belgian Science Policy Office 2012 – Research Programme Science for a Sustainable Development. 105 pp.

Kottsieper J, Schueckel U, Schwemmer P , Fox AD, Garthe S Comparison of bivalve communities between moulting and wintering areas used by Common Scoter *Melanitta nigra* in the German North Sea. Estuar Coast Shelf Sci *under review*

Krause J, Wollny-Goerke K, Boller F, Hauswirth M, Heinicke K, Herrmann C, Körber P, Narberhaus I, Richter-Kemmermann A (2011) The German Marine Protected Areas in the North Sea and Baltic Sea. *Natur Und Landschaft* 86 (9): 397.

Leopold MF, Wolf P (2003) Zee-Eenden Eten Ook Ensis. Nieuwsbrief Nederlandse Zeevogelgroep 4: 5.

Leopold MF, Spannenburg PC, Verdaat HJP, Kats RKH (2007) Identification and Size Estimation of *Spisula subtruncata* and *Ensis americanus* from Shell Fragments in Stomachs and Faeces of Common Eiders *Somateria mollissima* and Common Scoters *Melanitta nigra*. Pp. 63-85. In: Common Eiders *Somateria mollisssima* in the Netherlands The rise and fall of breeding and wintering populations in relation to the stocks of shellfish. Kats, R.K.H., Groningen: Rijksuniversiteit Groningen (Scientific Contributions 19)

Madsen FJ (1954) On the Food Habits of the Diving Ducks in Denmark. Dan Rev Game Biol 2:159-266.

Markones N, Garthe S (2011) Monitoring von Seevögeln Im Offshore-Bereich Der Schleswig-Holsteini-Schen Nordsee Im Rahmen von NATURA 2000 in Den Jahren 2004 bis 2009. Corax 22:11–50.

Mendel B, Sonntag N, Wahl J, Schwemmer P, Dries H, Guse N, Müller S, Garthe S (2008) Artensteckbriefe von See- und Wasservögeln Der Deutschen Nord- und Ostsee: Verbreitung, Ökologie Und Empflindlichkeiten Gegenüber Eingriffen in Ihren Marinen Lebensraum. Bundesamt f. Naturschutz.

Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. Front Ecol Environ 6:485-492. https://doi.org/10.1890/070064

Pihl S, Holm TE, Clausen P, Petersen IK, Nielsen RD, Laursen K, Bregnballe T, Søgaard B (2015) Fugle 2012-2013 NOVANA. Videnskabelig Rapport 125 fra DCE-Nationalt Center for Mijø og Energi. Aarhus Universitet, Denmark.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rodriguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and why

these impacts occur. Biol. Invasions 8:927-939. https:/doi.org/10.1007/s10530-005-5103-3

Schwemmer P, Volmer H, Enners L, Riemers HC, Binder K, Horn S, Eskildsen K, Adler S, Fox AD, Garthe S (2019) Modelling summer distribution patterns of common scoters (*Melanitta nigra*) by its most important prey species, the razor clam (*Ensis directus*), and hydrodynamic parameters. Estuar Coast Shelf Sci 225

Skov H, Durinck J, Erichsen A, Kloster RM, Møhlenberg F, Leonhard SB (2008) Horns Rev II Offshore Wind Farm Food Basis for Common Scoter: Baseline Studies 2007-08. Final Report by Orbicon/DHI/Marine Observers to DONG Energy A/S, Copenhagen.

Troost K, Perdon KJ, van Zwol J, Jol J, van Asch M (2017) Schelpdierbestanden in de Nederlandse kustzone in 2017. IJmuiden: Stichting Wageningen Research, Centrum voor Visserijonderzoek (CVO), 2017. https://library.wur.nl/WebQuery/wurpubs/526296.

Tulp I, Craeymeersch J, Leopold M, van Damme C, Fey F, Verdaat H (2010). The Role of the Invasive Bivalve *Ensis directus* as Food Source for Fish and Birds in the Dutch Coastal Zone. Estuar. Coast Shelf Sci 90:116–28. https://doi.org/10.1016/j.ecss.2010.07.008.

Werner S, Moertl M, Bauer HG, Rothhaupt KO (2005) Strong impact of wintering waterbirds on zebra mussel (*Dreissena polymorpha*) populations at Lake Constance, Germany. Freshw Biol 50:1412-1426. https://doi.org/10.1111/j.1365-2427.2005.01411.x

CHAPTER IV

Large-scale depth-related seasonal dispersal patterns of a benthic-feeding sea duck in two contrasting marine systems

Anthony D. Fox, Johanna Kottsieper, Ib K. Petersen, Nele Markones, Philipp Schwemmer, Stefan Garthe

© Johanna Kottsieper

Large-scale depth-related seasonal dispersal patterns of a benthic-feeding sea duck in two contrasting marine systems

Anthony D. Fox[1*], Johanna Kottsieper[2], Ib K. Petersen[1], Nele Markones[2], Philipp Schwemmer[2], Stefan Garthe[2]

[1]Department of Bioscience, Aarhus University, 8410 Rønde, Denmark

[2]Research and Technology Centre (FTZ), Kiel University, 25761 Büsum, Germany

Corresponding author: *tfo@bios.au.dk

Running page head: Seasonal sea duck dispersal

Abstract

The Common Scoter *Melanitta nigra*, a benthos-feeding marine diving duck, aggregates at important moulting and wintering areas along the Schleswig-Holstein North Sea coast, in the German Bight and in Aalborg Bugt, Denmark at the entrance into the Baltic. In Aalborg Bugt, Common Scoter occur in relatively sheltered areas subject to restricted tidal influence, contrasting the tidal, more exposed waters used off German North Sea coasts. Despite these differences, we predicted that birds would distribute themselves in similar ways, aggregating to moult in shallowest waters with most accessible prey in July, gradually dispersing to deeper (i.e. comparatively less profitable) waters through the season as numbers increase and (potentially) as prey is depleted. To test this hypothesis, we used multiple aerial survey count data to study Common Scoter distribution patterns in Aalborg Bugt and the German Bight. Common Scoter displayed similar distribution patterns in both areas, showing significant increases in mean water depth (from 6.3 m in July to 9.8 m in March in Denmark, 6.5 m to 10.3 m in Germany), number of flock units (432 to 1614; 48 to 581) and the percentage of 3 x 3 km grid squares occupied by birds as the season progressed (15% to 44% of 628 grid cells; 1% to 39% of 408 grid cells). These results support the hypothesis that these predatory birds distribute themselves to maximise their nutritional and energetic intake while minimising costs of gaining food in two contrasting marine environments.

KEY WORDS: Common Scoter · Diving depth · Entropy · *Melanitta nigra* · Wintering distribution

Introduction

Common Scoter *Melanitta nigra* are benthic bivalve-feeding diving sea ducks (Fox 2004), which breed in the tundra and sub-arctic boreal and winter in large numbers around European coasts (Kear 2005). Recent suspected declines in their wintering numbers have raised concerns about their future conservation (Skov et al. 2011), focusing attention on the need to understand factors affecting their distribution and abundance, especially with regard to the provision of cohesive protected area networks for the effective protection of their favoured habitats. Key moulting (late summer) and wintering areas for this species exist in the Danish Aalborg Bugt (56°55'N 11°00'E, in the relatively sheltered moderately tidal Kattegat, see Fig. 1) and in the German North Sea (54°15'N 8°15'E, in strongly lunar tidal, more saline exposed waters off the Wadden Sea, see Fig. 2). Both sites are known to support moulting males from June onwards (which are flightless while replacing wing feathers *e.g.* Fox et al. 2008), as well as increasing numbers of females and first winter birds arriving from breeding areas to aggregate in the same areas to winter (Spalke et al. 2013, 2014, Holm et al. 2018). Up to 220,000 Common Scoters also occur on the Odra Bank in the southern German Baltic Sea (54°27'N 14°21'E), including moulting birds (Sonntag et al. 2004), but here we only present data from the German North Sea to contrast a moulting area in the more sheltered non-tidal Kattegat with one in the more exposed tidal North Sea.

Predators of sedentary prey should assort themselves in relation to prey density (the aggregative response), a response mediated by intake rate in relation to prey density (the functional response, Holling 1959). Since increasing prey densities support greater intake rates, predators should gather at patches of highest densities to maximize long-term intake-rates (Stephens & Krebs 1986). In reality, predators disperse between patches of different profitability due to foraging costs, predation risk, interference competition and imperfect knowledge of available resource densities (Goss-Custard 1980, Bernstein et al. 1991, Bautista et al. 1995, Piersma et al. 1995). Since Common Scoters wintering in European waters are exposed to few known predators, it seems likely that the relatively low levels of predation risk to which they are exposed are evenly distributed, so this factor is unlikely to determine major patterns in feeding distribution. Depth-dependent differences in the energy required to descend through the water column result in foraging costs increasing rapidly with the depth of the water column (Lovvorn et al. 1991, Lovvorn & Jones 1991, Lovvorn 1994). Hence, food size and the locomotor costs of diving largely determine the feeding profitability of diving sea ducks feeding on benthic prey. Simultaneously, factors such as water temperature, food dispersal, search and handling time have relatively little additional influence on the relative costs and benefits (Lovvorn & Gillingham 1996). Common Scoter only seem to aggregate in large numbers in association with abundant bivalve stocks, often consisting of only one species, where the density of biomass can support large numbers of these

predators (Fox 2004, Kottsieper et al. submitted 2018a). Although bivalve stocks can be affected by cold winters, storms and mass starvation events, it is generally the case that these organisms are sedentary and have only one reproductive pulse in the year (Gosling 2015). Hence, their availability as prey is likely to be more or less constant through the period when Common Scoters feed upon them, affected largely only by prey depletion from birds and other predators. In the case of the Common Scoter in the German North Sea and Danish Aalborg Bugt, we would hypothesise that the arriving moulting birds initially disperse themselves in the shallowest water areas within their regular wintering areas with an abundant food supply. As the season progresses and more birds arrive, we would predict that the birds increasingly disperse in deeper waters (because of prey depletion and intraspecific competition), where prey densities may be similar, but costs of access in deeper water are greater. Finally, we would predict the greatest dispersal at the end of the winter, when bird densities and prey depletion combine to disperse Common Scoter over the largest areas, fragmented into smallest groups. Based on this hypothetical framework, we make four predictions for the development in the pattern of dispersal of the species in both areas in the course of the season. These are that:

(i) the mean water depth used by Common Scoter would increase from June to March/April.

(ii) the area of habitat occupied by the birds would increase.

(iii) the large predator aggregations associated with the densest food concentrations will deplete these resources and may contribute to force birds to disperse into smaller flocks through the winter, resulting in:

(iv) greater entropy as their distribution becomes more even.

In this analysis, we use sequential aerial surveys within and between years from both areas to find support for these predictions.

Methods

2.1 Aerial survey techniques

In the Danish Aalborg Bugt, Common Scoter were counted from high-winged twin-engine Parternavia P-68 Observer aircraft flying at 76 m (250 feet altitude) and approximately 185 km h^{-1} (100 knots). Trained observers identified and counted all waterbird species encountered and assigned them to three bands at successive distances from the flight line (46-163 m, 164-432 m, and 433-1500 m determined by the observers' use of a clinometer set to predetermined angles from the horizontal). A band extending 46 m to either side of the flight line could not be observed adequately below, and birds observed in this band were disregarded. As observations were "binned" in this way, it was not possible to assign Common Scoters to true flocks, but in this analysis, the separation of groups along the axis of flight are used to define discrete blocks of birds, which we hereafter refer to as spatially explicit "flock

units". Bird behaviours (sitting on water, diving, flushing or diving) and numbers were continuously recorded directly onto a Dictaphone, assigning all flock units or individuals to a distance band and a time; all these forms of registrations are considered here. The aircraft flew between waypoints entered into the navigation system and a computer logged the flight track from a differential GPS device accurate to 2 m at five-second intervals. This provided the position and time stamp to link subsequently transcribed bird observations to a geographical position (considered accurate to within 4 seconds), geographically spread left or right of the track line according to observers side of the aircraft and out to a distance perpendicular to the track line according to the transect bin. Encountering very dense flock units rarely grouped observations over 10 seconds, so we consider positional longitudinal accuracy was within less than 206 m of reality, occasionally 515 m. Although these observation methods do not strictly record flock size (since this was not a design objective), we consider this method of capturing spatial observations standardises our recording of separate blocks of birds. Surveys were never carried out when conditions of severe sun glare, poor light or wind speeds > 6 m s^{-1} occurred (see Petersen et al. 2003 for full details). The Aalborg Bugt study area was covered from 30 N-S parallel transects flown at 3 km intervals eastwards from the east Jutland coast in the west to east of Læsø and Anholt (as shown in Fig. 1b).

In the German North Sea, aerial surveys were carried out as part of a regular national monitoring programme, surveying the waters along 7 roughly N-S parallel transects between the Schleswig-Holstein coast and the 12 nm zone at least twice per year during summer and winter (Fig. 2b). Transects were spaced 3 km apart for the innermost four flight lines closest to the coast, but at 6 km intervals between the outer most three transects. The same type of aircraft, altitude and data collection protocols were used as for the Aalborg Bugt study area, but see Markones & Garthe (2011) for detailed descriptions.

The same fixed transect design was repeated for each survey in both study areas, ensuring consistent coverage of the same overall area for each flight. We here present data from 11 surveys carried out intensively in two season in Aalborg Bugt between 12 August 1999 and 23 March 2000 and between 5 September 2000 and 16 April 2001, as well as data from 26 surveys in the German Bight carried out between 22 January 2006 and 6 July 2017. This provided us with detailed within-year data from just two seasons from Aalborg Bugt and a more comprehensive long-term database across many years from the German Bight. The individual surveys generated between 18,460 and 90,219 bird detections in Aalborg Bugt and between 61 and 49,774 in the German Bight survey area. The full list of flight details and summary of the raw data are given in Supplementary Material Tables S1 and S2.

Distribution maps were generated using ArcGIS (ESRI, Version 10.2.1, 2013 and 10.4.1, 2015). To map the distribution patterns in the German North Sea, four aerial surveys from 2011-2014 were chosen for each period (July-September, October-November and December-March, for survey dates see Supplementary Material Table S2). Due to the limited amount of surveys during October and November, two November surveys from 2006 and 2009 were chosen to illustrate the early winter period, identified in the caption of Fig. 2.

2.2 Environmental parameters and analyses

To test the hypothesis that Common Scoter progressively foraged in deeper water through the season, we determined the mean water depth (m) at the point of observation of each scoter flock unit and weighted the average for each survey according to the number of individuals recorded at each point. The mean water depth (m) was identified by spatially joining each observation to a bathymetry layer. In Aalborg Bugt, depth information was received in the form of a multi-beam based ASCII file supplied by the Danish Coast Guard, transformed into an ArcGIS TIN (triangular irregular networks) layer. In the German North Sea, depth data based on one metre intervals were received in the form of an ArcGIS shape file provided by the Federal Maritime and Hydrographic Agency (BSH, Germany, Asprion et al. 2013). To test the prediction that Common Scoter would disperse into more flock units due to resource depletion as the season progresses, we calculated the number of flock units encountered by the observers in each flight. To analyse the spatial dispersal of the birds during the course of the season, we established a 3 x 3 km polygon grid cell layer for both survey areas to calculate the number of grid cells containing Common Scoter observations per survey (628 cells in Aalborg Bugt, 408 in the German Bight). We then used the successional occupation (i.e. simple presence/absence in each grid square at each survey, expressed as the percentage of occupied grid cells) to see if the Common Scoter spread out progressively through the course of the season. Finally, we measured the entropy of their dispersal, using the Shannon index (*H'*, Shannon & Weaver 1964) as a measure of inequality in the distribution of Common Scoter. This we expressed as:

$$H' = -\sum_{i=1}^{R} pi \ln pi$$

where p_i represents the proportion of Common Scoter occurring in the *i*th grid square out of R grid cells. We predicted that during moult, when clumped, *H'* will be less, but this measure will increase with the increasing evenness of the distribution as Common Scoter disperse through the season. All numerical data storage, processing and statistical analysis were carried out in Access and Excel (Microsoft Office 2016).

Results

In Aalborg Bugt, moulting Common Scoter aggregated in large flock units to the south of Læsø (Fig. 1b) and in areas off east Jutland and north Djursland (in the western and southern edges of Aalborg Bugt respectively). Large numbers of birds remained in these areas throughout the winter. However, they increasingly dispersed throughout the area through the winter (Fig. 1c, d), exploiting (based on weighted monthly average depths) deeper water through the season (mean 6.3 m in July to 9.8 m in March based on actual mean values for these months, Fig. 3a). Common Scoter assorted themselves in increasing numbers of flock units (432 in July to 1614 in March, Fig. 3b), dispersed over greater areas of sea, being detected in 93 grid cells out of 628 (15%) in July 2000 compared to 275 (44%) in March 2000 and 243 (39%) in March 2001 (Fig. 3c) resulting in increasingly even dispersal (as measured by entropy, Fig. 3d and see Supplementary Material Table S1).

In the German Bight, moulting Common Scoter mainly aggregated west of the Eiderstedt peninsula and Süderoogsand (southern German Bight, Fig. 2b) during July to September. Single flock units of moulting birds were also observed west of Amrum (central German Bight, Fig. 2b) and north of Sylt (northern German Bight, Fig. 2b). Large flock units remained west of the Eiderstedt peninsula throughout the winter (Fig. 2c, d). At the same time, the number of scoter flock units increased in the areas west of Sylt (northern German Bight, Fig. 2c, d) and Norderoogsand (central German Bight, Fig. 2c, d). In general, Common Scoter were located in increasingly deeper waters throughout the season (from a mean of 6.5 m solving the regression model for 15 July, to 10.3 solving for 18 March, Fig. 3e). As in Aalborg Bugt, the number of flock units increased (from 48 in July to 581 in March, Fig. 3f) and they dispersed over greater numbers of grid cells, being detected in four grid cells out of 408 (1%) in June 2010 compared to 158 (39%) in February 2014 (Fig. 3g). The dispersal became more even during the course of winter (Fig. 3h, see Supplementary Material Table S2), although due to some surveys with large numbers of flock units early on during the moulting season, the pattern of dispersal was not as even as in Aalborg Bugt. The maximum number of flock units and occupied grid cells were observed in the months of January and February (see Supplementary Material Table S2).
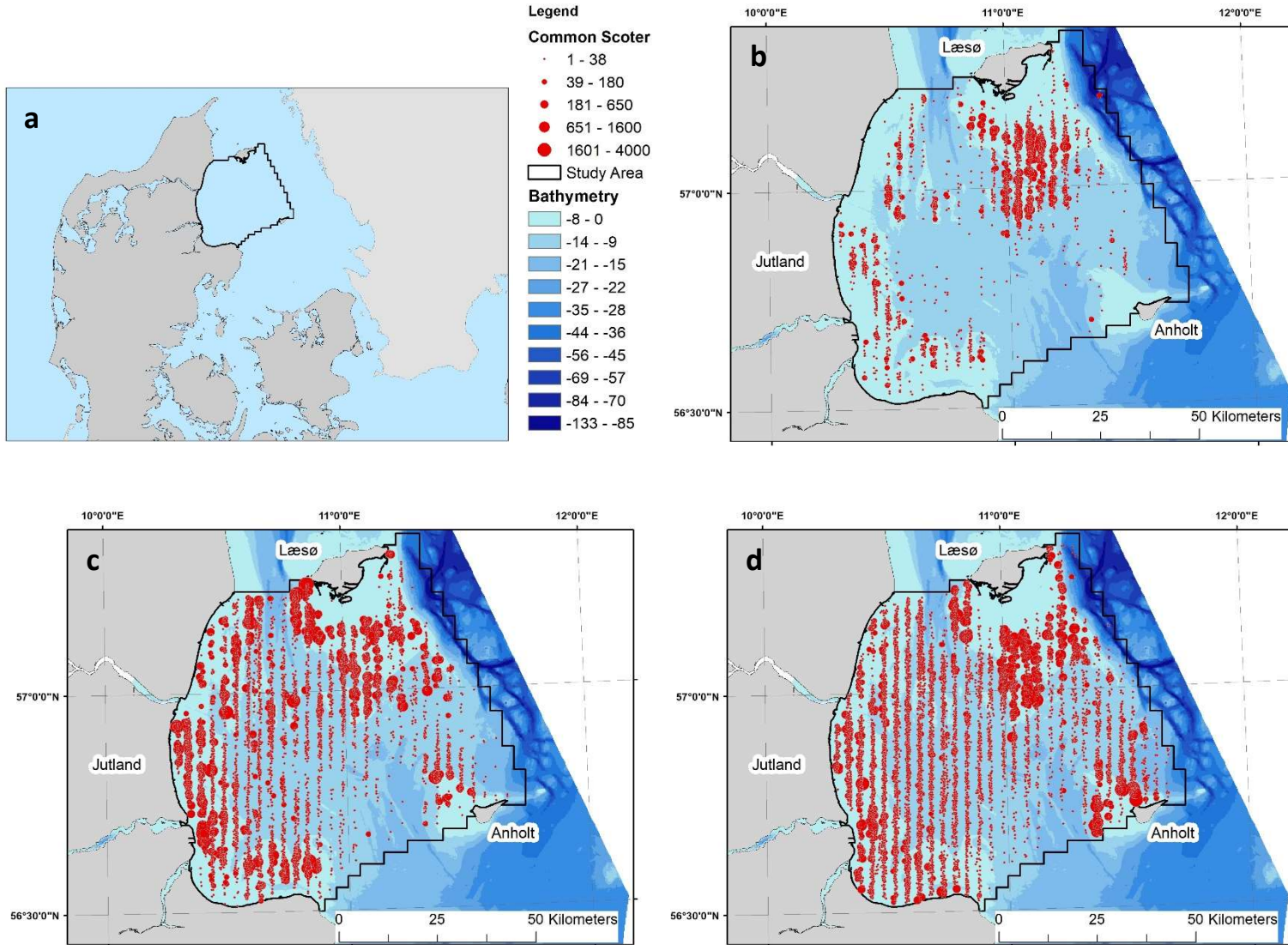
Fig. 1. Map of Common Scoter *Melanitta nigra* distribution in Aalborg Bugt, Denmark (showing location and legend (a)), during (b) the flightless moult period July-September, (c) the early winter October and November and (d) late winter December-March in the years 1999-2001. Red circles indicate discrete groups of birds, the size of which reflects the numbers present (see key for size class intervals).
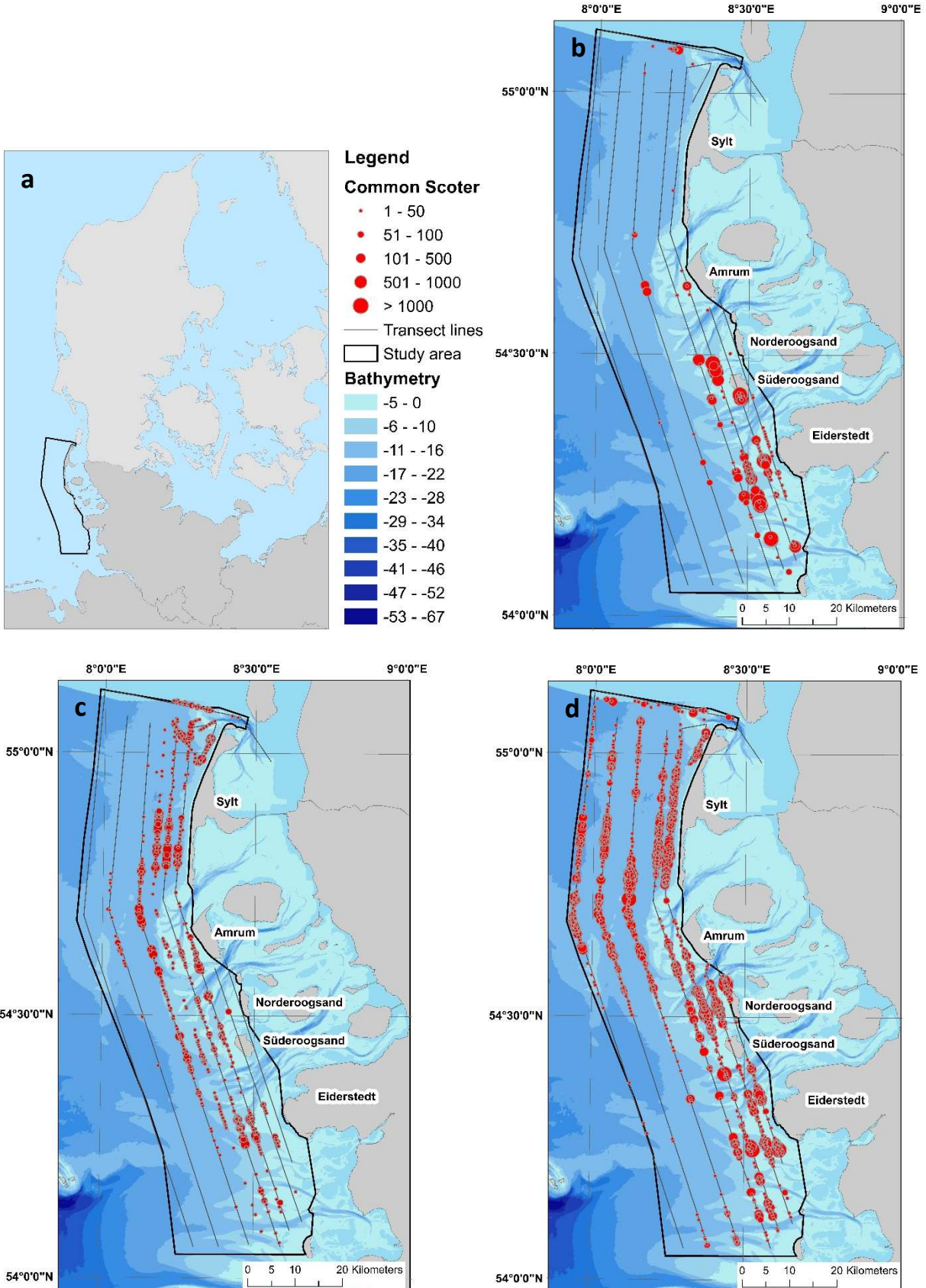
Fig. 2. Map of Common Scoter *Melanitta nigra* distribution in the German North Sea (showing location and legend (a)), during (b) the flightless moult period (surveys: 25 July and 19 August 2012, 16 July 2013 and 1 August 2014), (c) early winter October-November (surveys: 3 November 2006 and 10 November 2009) and (d) late winter December-March (surveys: 2 December 2013, 4 February 2012 and 11 February 2014). Red circles indicate flock units counted during the surveys, the size of each red circle reflects the numbers present (see key for size class intervals).
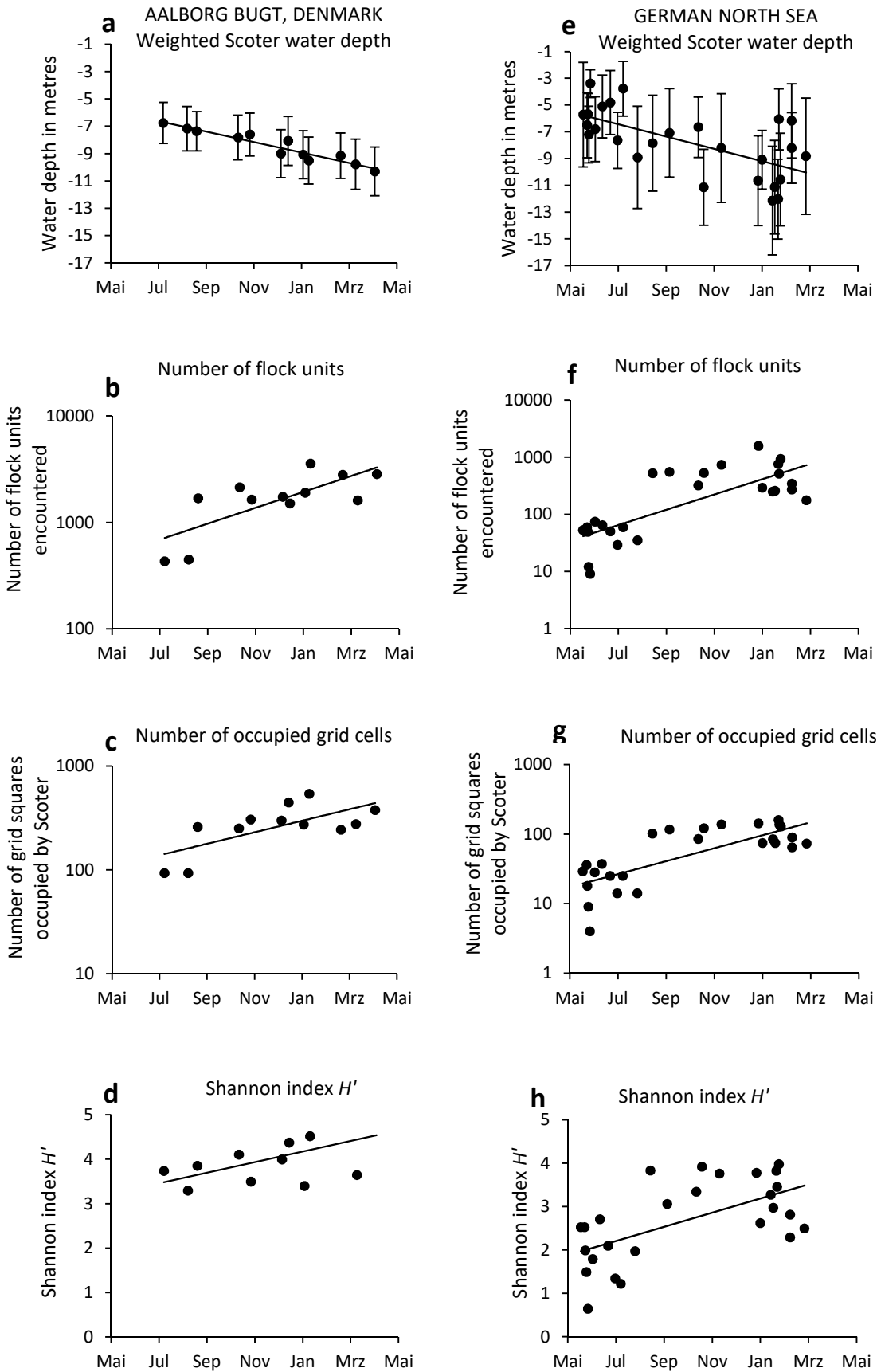
Fig. 3. Graphs of changes in (a), (e) mean water depth (± SD), (b), (f) number of flock units, (c), (g) number of occupied 3x3 km grid squares and (d), (h) entropy of Common Scoter *Melanitta nigra* from (a)–(d) Aalborg Bugt, Denmark and (e)-(h) the German North Sea from the moulting period in July to the end of winter in March. For Aalborg Bugt, the data originate from the years 1999-2000. For the German North Sea, the data originate from the years 2006-2017. Note $\log_{10}$ transformed y-axis in Figs 3b, 3c, 3f and 3g. See Supplementary Materials Table S3 for statistical details of fitted regression models, all of which were significant at least at $P < 0.05$

Discussion

The results of generating spatially explicit distributions of Common Scoter from aerial surveys showed very similar patterns of dispersal during the course of the year in Aalborg Bugt and the German Bight. Common Scoter increasingly used deeper waters, in greater numbers of individual flock units, distributed across greater areas and became more evenly dispersed as the season drew on (meeting all of our four predictions), despite the major differences in the nature of the two marine habitats investigated. The more brackish, relatively sheltered and less tidal Aalborg Bugt represents a very different marine environment to conditions in the more saline, exposed and strongly lunar tidal German Bight. Nevertheless, Common Scoters arrived to moult in both areas in June to aggregate in the shallowest areas and gradually dispersed into smaller, more numerous flock units in deeper water as the season progressed. Assuming that bivalve prey availability was reasonably evenly distributed from the start of each season throughout both two study areas, this pattern supports the hypothesis that birds distribute themselves to maximise nutritional and energetic intake while minimising costs of gaining food at the same time by foraging on the most abundant prey in the shallowest water (e.g. MacArthur & Pianka 1966). We consider this is a reasonable assumption, since substrate type and conditions are uniform through most of the Aalborg Bugt study area, although regrettably we lack benthos sampling from this study area. In the German Bight, an extensive survey has demonstrated that despite major differences in abundances and biomass of bivalves the food profitability throughout the core Common Scoter feeding areas used for moulting and wintering seems to be equal (Kottsieper et al. submitted 2018b). Hence, by exploiting shallowest waters initially, birds minimise energy expenditure, which is likely of particular significance during the flightless wing moult when birds are immobile while replacing flight feathers. As more birds (especially females and first autumn juveniles) arrive in autumn, we hypothesised that social interactions and depletion of prey resources potentially spread birds over larger areas to meet individual nutritional and energetic needs. Correspondingly, Common Scoter are most highly dispersed, distributed at lowest densities at the very end of winter, just prior to the time when they migrate back to breeding areas. Limited evidence from the German Bight study area suggests that Common Scoters are feeding on similar

bivalve communities in the same way throughout the period from moult to the end of winter (Kottsieper et al. 2018a, 2018b, submitted). The birds merely forage in deeper water depths on similar prey that occur at similar densities and of equally favourable food quality (especially the abundant invasive *Ensis leei* (M. Huber, 2015), Kottsieper et al. 2018a, 2018b, submitted). This bivalve species has successfully spread throughout North Sea coasts since its invasion in the 1970s to the extent it is now abundant along German North Sea coasts (Kottsieper et al. 2018a, 2018b, submitted). Dannheim and Ruhmohr (2012) could show that even in deeper waters further off the coast, the abundance of *E. leei* is high, which would ensure sufficient energy intake even though energy expenditure increases due to increasing diving depths. It is striking that intensive observations within two seasons in Aalborg Bugt and from 26 surveys spread less intensively over 10 seasons in German waters, both show the same pattern, namely increasing exploitation of successively deeper water at greater dispersal and reduced density. Despite the clarity of the results, we should be extremely prudent about interpreting the cause of the observed Common Scoter distribution patterns, given that we have no evidence of increasing agonistic interactions or of food depletion to specifically support these two potential explanations or their interaction. Hence, the next priority is to find evidence to support the food depletion and social spacing hypotheses to try to explain these patterns.

Although the patterns in the German North Sea (in relation to mean water depth (m), number of flock units and Shannon index *H'*) match those in the Baltic Sea, gathering data from 10 different seasons has inevitably introduced more background variance into the basic relationships. During the last 3 years, numbers of moulting Common Scoter have been increasing along Schleswig-Holstein coasts, while the number of wintering birds remaining in the moulting area have also been steadily growing as well (FTZ unpublished data). These patterns have potentially been explained by the increase in the abundance of one benthic prey species (*E. leei*) in the moulting area, the continuous availability of which seems to provide a reliable and high quality food source even during the winter (Kottsieper et al. 2018b, submitted). Hence, shifting abundance in the prey base of the German Bight might contribute to the potential explanation for some of the noise inherent in the relationships shown in Fig. 3.

It is extremely rare to be able to track the changes in distribution and dispersal of hundreds of thousands of marine predatory organisms feeding on their largely sedentary prey through the course of an annual cycle as was possible in this study. These results clearly show that Common Scoter sequentially exploit greater areas of shallow inshore waters in greater depths of water as the non-breeding period of their annual cycle progressed, compared to those to which they first aggregate during the moulting period. While it is clear that water depth affects the seasonal distribution of Common Scoters, we lack data to assess the contribution from human disturbance to explain these patterns, which is known to affect their distributions at sea and

may have particular effects on bird distributions during the flightless moult period (Kaiser et al. 2006, Schwemmer et al. 2011). We also have no knowledge of the degree of turnover of individuals, which occurs within these aggregations, to interpret individual decision-making about how, when and where to disperse within a season. However, the implication from these findings is that in order to fulfil their annual energetic and nutritional needs, the Common Scoter using both study areas are required to exploit all the areas in which they are found until their departure in spring. If late winter/early spring is a critical period for acquiring necessary stores for spring migration and investment in reproduction, the areas occupied by Common Scoter at lowest densities dispersed across the greatest areas in the entire winter, may represent equally important priorities for site safeguard as areas protected during the moult period and for mid-winter concentrations. These findings are therefore also a reminder that the existence of these patterns have implications for nature conservation strategies and site-safeguard networks for this species as well, requiring protection of habitats at times when birds are most dispersed in their non-breeding distributions, as well as at other, more aggregated, times of year.

Acknowledgements

References

Asprion U, Sbresny J, Griffel G, Elbracht J (2013) Die Bathymetrie der deutschen Nordsee–Erstellung der projektweiten Bezugsfläche. Report of the Geo-scientific Potential of the German North Sea (GPDN) Project. Federal Institute for Geosciences and Natural Resources (BGR), the State Authority for Mining, Energy and Geology of Lower Saxony (LBEG) and the Federal Maritime and Hydrographic Agency (BSH). www.gpdn.de

Bautista LM, Alonso JC, Alonso JA (1995) A Field Test of Ideal Free Distribution in Flock-Feeding Common Cranes. J Anim Ecol 64:747–757. https://www.jstor.org/stable/5853.pdf

Bernstein C, Kacelnik A, Krebs (1991) Individual Decisions and the Distribution of Predators in a Patchy Environment. II. The Influence of Travel Costs and Structure of the Environment. J Anim Ecol 60:205–225. https://www.jstor.org/stable/pdf/5455.pdf

Dannheim J, Rumohr H (2012) The Fate of an Immigrant: *Ensis directus* in the Eastern German Bight. Helgoland Mar Res 66:307–317. https://doi.org/10.1007/s10152-011-0271-2.

Fox AD (2004) Diet and habitat use of scoters *Melanitta* in the Western Palearctic – a brief overview. Wildfowl 54:163–182. https://wildfowl.wwt.org.uk/index.php/wildfowl/article/download/1165/1165

Fox AD, Hartmann P, Petersen IK (2008) Body mass and organ size change during wing moult in Common Scoter. J Avian Biol 39:35–40. https://doi.org/ 10.1111/j.2007.0908-8857.04135.x

Gosling EM (2015) Marine bivalve molluscs, Second edition. Wiley Blackwell, Chichester, West Sussex, UK ; Hoboken, NJ, USA

Goss-Custard JD (1980) Competition for food and interference amongst waders. Ardea 68:31–52. https://doi.org/10.5253/arde.v68.p31

Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can Entomol 91:293–320.

Holm TE, Clausen P, Nielsen RD, Bregnballe T, Petersen IK, Mikkelsen P, Bladt J (2018) *Fugle 2018 NOVANA.* Research report from Aarhus University/Danish Centre for the Environment and Energy, Aarhus, Denmark. (In Danish). Accessible at: http://dce2.au.dk/pub/SR261.pdf

Kaiser MJ, Galanidi M, Showler DA, Elliott AJ, Caldow RWG, Rees EIS, Stillman RA, Sutherland WJ (2006) Distribution and behaviour of Common Scoter *Melanitta nigra* relative to prey resources and environmental parameters. Ibis 148:110–128. https://doi.org/10.1111/j.1474-919X.2006.00517.x

Kear J (Ed.) (2005) Bird Families of the World: Ducks, Geese and Swans. University Press, Oxford, UK.

Kottsieper J, Schwemmer P, Markones N, Fox AD, Garthe S (submitted 2018a) An invasive alien bivalve apparently provides a novel food source for moulting and wintering Common Scoter *Melanitta nigra* in the German Bight. Helgoland Mar. Res.

Kottsieper J, Schückel U, Schwemmer P, Fox AD, Garthe S (submitted 2018b) Comparison of bivalve communities between moulting and wintering areas used by Common Scoter *Melanitta nigra* in the German North Sea. Estuar Coast Shelf Sci

Lovvorn JR (1994) Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks. Hydrobiologia 278/279:223–233. https://link.springer.com/content/pdf/10.1007/BF00027856.pdf

Lovvorn JR, Gillingham MP (1996) Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. Ecology 77:435–451. https://www.jstor.org/stable/pdf/2265620.pdf

Lovvorn JR, Jones DR (1991) Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.). Can J Zool 69:2879–2887. https://www.nrcresearchpress.com/doi/pdfplus/10.1139/z91-406

Lovvorn JR, Jones DR, Blake WR (1991) Mechanics of underwater locomotion in diving ducks: drag, buoyancy and acceleration in a size gradient of species. J Exp Biol 159:89–108. http://jeb.biologists.org/content/jexbio/159/1/89.full.pdf

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609.

Markones N, Garthe S (2011) Monitoring von Seevögeln Im Offshore-Bereich Der Schleswig-Holsteinischen Nordsee Im Rahmen von NATURA 2000 in den Jahren 2004 bis 2009. Corax 22:11–50.

Petersen IK, Fox AD, Clausager I (2003) Distribution and numbers of birds in Kattegat in relation to the proposed offshore wind farm south of Læsø - Ornithological impact assessment. Report to Elsam Engineering A/S. National Environmental Research Institute, Kalø, Denmark.

Piersma T, van Gils J, De Goeij P, van der Meer J (1995) Holling's Functional Response Model as a Tool to Link the Food-Finding Mechanism of a Probing Shorebird with its Spatial Distribution. J Anim Ecol 64:493–504. https://www.jstor.org/stable/pdf/5652.pdf

Schwemmer P, Mendel B, Sonntag N, Dierschke V, Garthe, S (2011) Effects of ship traffic on seabirds in offshore waters: implications for marine conservation and spatial planning. Ecol Appl 21:1851–1860. https://doi.org/10.1890/10-0615.1

Shannon C, Weaver W (1964) The Mathematical Theory of Communication. University of Illinois, Urbana, USA.

Skov H, Heinänen S, Zydelis R, Bellebaum J, Bzoma S, Dagys M, Durink J, Garthe S, Grishanov G, Hario M, Kieckbusch JJ, Kube J, Kuresoo A, Larsson K, Luigujoe L, Meissner W, Nehl HW, Nilsson L, Petersen IK, Roos MM, Pihl S, Sonntag N, Stock A, Stipniece A, Wahl J (2011) Waterbird Populations and Pressures in the Baltic Sea. Nordic Council of Ministers, Copenhagen.

Sonntag N, Engelhard O, Garthe S (2004) Sommer- und Mauservorkommen von Trauerenten *Melanitta nigra* und Samtenten *M. fusca* auf der Oderbank (südliche Ostsee). Vogelwelt 125:77–82

Spalke J, Diederichs A, Rassmus J, Dorsch M, Brandt MJ, Pieper V, Nehls G (2013) Fachliche Vorschläge für ein Management der Trauerente an der schleswig-holsteinischen Nordseeküste. Im Auftrag des Landesbetriebs für Küstenschutz, Nationalpark und Meeresschutz. Created by BioConsult SH, Husum & GFN, Kiel

Spalke J, Diederichs A, Grünkorn T, Rassmus J, Nehls G (2014) Trauerenten (*Melanitta nigra*) an der schleswig-holsteinischen Nordseeküste. Corax 22, no. Sonderheft 1 (2014): 12.

Stephens DW, Krebs JR (1986) *Foraging theory*. University Press, Princeton, USA

Supplementary material data tables

Table S1. Summary of the data used for the analysis from 12 aerial surveys of Common Scoter in Danish Aalborg Bugt.

Survey date	Mean depth (m.)	Number of flock units	Total number of birds	Grid cells covered (% out of 628)	Shannon index *H'*
25.07.2000	6.76	432	22605	93 (15%)	3.74
24.08.1999	7.19	449	18460	93 (15%)	3.30
05.09.2000	7.37	1683	36609	259 (42%)	3.86
27.10.2000	7.83	2137	90219	250 (40%)	4.11
11.11.1999	7.61	1643	54649	306 (49%)	3.50
20.12.2000	9.01	1740	88525	299 (48%)	4.00
29.12.1999	8.08	1514	73808	447 (71%)	4.38
17.01.2001	9.10	1902	48701	273 (43%)	3.40
24.01.2000	9.52	3559	74940	540 (86%)	4.52
04.03.2001	9.16	2799	34835	243 (39%)	5.00
23.03.2000	9.79	1614	52708	275 (44%)	3.65
16.04.2001	10.31	2846	35067	376 (60%)	5.02

Table S2. Summary of the data used for the analysis from 26 aerial surveys of Common Scoter in the German North Sea. Superscripts identify surveys used in the mapping of birds shown in Fig. 2 as follows: [1]July-September, [2]October-November and [3]December- March.

Survey date	Mean depth (m.)	Number of flock units	Total number of birds	Grid cells covered (% out of 408)	Shannon index H'
22.01.2006	9.09	291	10896	74 (18%)	2.62
28.02.2006	8.21	270	7273	64 (16%)	2.29
03.11.2006[2]	6.66	319	3133	85 (21%)	3.34
14.02.2009	10.58	926	16806	128 (31%)	4.00
10.11.2009[2]	11.15	525	12118	121 (30%)	3.92
07.02.2010	11.14	256	4805	74 (18%)	2.97
21.06.2010	3.40	9	554	4 (1%)	0.65
04.02.2012[3]	12.14	248	3861	84 (21%)	3.27
19.06.2012	7.20	12	2215	9 (2%)	1.49
25.07.2012[1]	7.65	29	762	14 (3%)	1.34
19.08.2012[1]	8.92	35	295	14 (3%)	1.97
17.06.2013	6.50	59	32965	36 (9%)	2.52
16.07.2013[1]	4.82	50	6420	25 (6%)	2.09
02.12.2013[3]	8.21	734	13879	137 (34%)	3.76
11.02.2014[3]	12.04	756	15928	158 (39%)	3.82
27.06.2014	6.81	74	5830	28 (7%)	1.79
01.08.2014[1]	3.78	59	3223	25 (6%)	1.22
12.02.2015	6.07	509	49774	136 (33%)	3.45
18.03.2015	8.83	176	18225	73 (18%)	2.49
12.06.2015	5.72	53	43842	29 (7%)	2.52
28.09.2015	7.09	547	25313	116 (28%)	3.06
28.02.2016	6.18	343	45150	89 (22%)	2.81
07.09.2016	7.86	523	3600	101 (25%)	3.83
17.01.2017	10.65	1562	29478	142 (35%)	3.78
18.06.2017	5.68	49	24165	18 (4%)	1.99
06.07.2017	5.11	64	6464	37 (9%)	2.71

Table S3. Summary statistics for fitted regression models shown in Figure 3.

Aalborg Bugt	Coefficient	r^2	F	P
Depth*	-0.01275	0.91	102.8	<0.0001
Log_{10} transformed number of flocks	0.0025	0.56	12.8	0.005
Log_{10} transformed occupied grid squares	0.0018	0.47	8.7	0.014
Entropy	0.0040	0.34	5.13	0.047
German Bight				
Depth*	-0.01494	0.41	20.9	<0.0001
Log_{10} transformed number of flocks	0.0044	0.51	31.4	<0.0001
Log_{10} transformed occupied grid squares	0.0030	0.44	23.4	<0.0001
Entropy	0.0053	0.31	13.5	0.0009

*weighted mean monthly depths were used in this regression model to track changes in this mean property with date, not the cumulative individual depth determinations. Regression models were solved for 12 June and 18 March to generate the values used in the Abstract and Results sections for German Bight.

CHAPTER V

Modelling the distribution of the Common Scoter *Melanitta nigra* in relation to environmental parameters in the eastern German North Sea

Johanna Kottsieper, Sven Adler, Philipp Schwemmer, Maria Stage, Klaus Ricklefs, Kerstin Wittbrodt, Klaus Schwarzer, Nele Markones, Anthony D. Fox, Stefan Garthe

© Johanna Kottsieper

Prepared for submission

Modelling the distribution of the Common Scoter *Melanitta nigra* in relation to environmental parameters in the eastern German North Sea

Johanna Kottsieper[1*], Sven Adler[2], Philipp Schwemmer[1], Maria Stage[1], Klaus Ricklefs[1], Kerstin Wittbrodt[3], Klaus Schwarzer [3], Nele Markones[1], Anthony D. Fox[4], Stefan Garthe[1]

[1] *Research and Technology Centre (FTZ), Kiel University, Hafentörn 1, 25761 Büsum, Germany*

[2] Swedish University of Agricultural Sciences, Department of Forest Resource Management, Division of Landscape Analysis, 901 83 Umeå, Sweden

[3] Institute for Geoscience, Sedimentology – Coastal and Shelf Research, Kiel University, Otto Hahn Platz 1, 24118 Kiel, Germany

[4] *Department of Bioscience, Aarhus University, Grenåvej 14, 8410 Rønde, Denmark*

* Corresponding author, Email: kottsieper@ftz-west.uni-kiel.de

Abstract

Modelling species abundance patterns in relation to environmental parameters is helpful in understanding factors influencing their distribution. The Common Scoter *Melanitta nigra* (Linneaus, 1758) is an arctic/sub-arctic breeding sea duck, which abundantly occurs in the eastern German Bight during its moulting and wintering season. However, factors driving the distribution of this species remain poorly understood. To determine possible influences, we modelled Common Scoter distribution during the moulting and wintering seasons using count data from Seabirds at Sea (SAS) surveys, benthos and sediment samples collected in the eastern German Bight and selected environmental parameters. These included hydrodynamics, fine sand proportion, distance to coast and ship traffic as a measure of disturbance and bivalve abundance and ash-free-dry mass as measures of available biomass. We applied Zero-inflated Poisson Generalised Additive Models (ZIP GAMs) using Integrated Nested Laplace Approximation (INLA) to model bird densities. The best wintering season model explained 25.12 % of the deviance, whereas the best model for the moulting season explained only 6.53 %. Model results showed that Common Scoters were most likely encountered in shallow waters, at moderate bed shear stress values and in areas with high proportions of fine sand (around 60%), staying closer to shore during moult (distances of 2-3 and 7-8 km) than in winter (distance of 7-11 km). While a previous study conducted on a small spatial scale found strong relationships between predictors and scoter distribution, we could not detect similar strong results. Our study highlights the importance of sufficient data at similar spatial scales across covariates, particularly for abundance and biomass of bivalve species, which were difficult to interpret in most models.

Introduction

Gathering knowledge on species habitat selection is not only important to understand their ecology, it also provides necessary information to support effective conservation measures and develop protection strategies. Modelling a species relative abundance in relation to environmental parameters has proven useful in estimating or predicting spatial occurrence probabilities, although not without its challenges (e.g. Segurado and Araújo 2004, Hernandez et al. 2006, Wisz et al. 2008). While information about several environmental parameters can be sampled using different methods, covering the entirety of ecological information required to model the distribution of a species remains a challenge, especially in relation to seasonal and annual variability (Austin 2002, 2005, Lambert et al. 2017).

The European North and Baltic Sea coasts provide important habitats for a variety of waterbird species, which use these areas for moulting or wintering (Mendel et al. 2008). One such species is the Common Scoter *Melanitta nigra* (Linnaeus, 1758) (e.g. Glutz von Blotzheim and Bauer 1990, Sonntag et al. 2004), a marine diving sea duck feeding predominantly on benthic bivalve prey (Madsen 1954, Fox 2004). The German North and Baltic Sea are of international importance for Common Scoters, as these waters regularly support more than 1% of the estimated flyway population during both the moulting and wintering season (Mendel et al. 2008). Long-term aircraft and ship based Seabirds at Sea surveys confirmed the consistent use of these areas by Common Scoter for more than 20 years (e.g. Hennig and Hälterlein 2000, Hennig and Eskildsen 2001, Markones and Garthe 2011).

Moulting and wintering seasons represent two different stages in the annual cycle of the Common Scoter. During moult, birds annually replace worn flight feathers and are temporarily flightless (Fox et al. 2008). During winter, they need to survive short day length and high thermoregulatory costs, after which they need to restore energy reserves (e.g. by building up fat depots) to migrate back to breeding areas. Consequently, we would assume that habitat selection during both periods is influenced by environmental parameters affecting the feeding profitability of Common Scoters (i.e. the energetic and nutritional profitability of foraging in an area balanced against the costs of being there). Since the German North and Baltic Sea seem to reliably and continuously support high numbers of moulting and wintering Common Scoter, we would assume that these areas provide reliable resources of their prey. As Common Scoters dive to access their benthic prey, water depth is another factor likely influencing habitat selection.

The distribution of bivalve species is influenced by environmental parameters as well, for example by sediment characteristics and hydrodynamics. Therefore, these also likely (indirectly) influence Scoter distribution. *Limecola balthica* (Linnaeus, 1758), *Mya arenaria* (Linnaeus, 1758), *Spisula subtruncata* (da Costa, 1778) and more recently *Ensis leei* (M. Huber, 2015) have been reported as main bivalve prey items amongst others (Fox 2004, Schwemmer et al. 2019, Kottsieper et al. 2019) and all these

species are common in sandy substrates. Moreover, hydrodynamic features such as bed shear stress, which is a measurement of sediment transport (the force per unit area transporting sediment downstream), affect bivalve settlement (Gray and Elliot 2009). Areas with high bed shear stress values represent harsher environments for bivalves as high bed shear forces complicate settlement of larvae or juveniles (Gray and Elliot 2009). However, these areas can be favourable for filter feeding bivalves due to their higher transport rates of food items and nutrients as well as ensuring higher removal rates of excretions (Gray and Elliot 2009).

Previous studies have already shown that Common Scoters prefer shallow waters as this reduces the time and energy needed to dive down through the water column to forage (Madsen 1954, Deppe 2003, Fox 2004) and that their distribution is likely influenced by the distribution of their prey (Kaiser et al. 2006). In a more recent study, Schwemmer et al. (2019) modelled the distribution of Common Scoter in relation to *Ensis leei*, which was shown to be their major prey item, and hydrodynamic features in a small scale approach along the North Frisian Islands in the German Wadden Sea. They could show that the occurrence of *E. leei* best explained the dispersal of Common Scoters in this area alongside negative effects of water depth and positive effects of bed shear stress intensity. The predictors selected for their modelling approach proved to be well suitable. However, this study was conducted at a relatively small spatial scale.

The study of Schwemmer et al. (2019) served as a basis for our own work, which was aiming at extrapolating the previous results to a larger sea area and different seasons enabling more generalised results. We again incorporated abundances and biomass of *E. leei* (and other bivalve prey) as well as hydrodynamic features. Additionally, we added another predictor by incorporating ship traffic as a measure of disturbance into our approach as Common Scoters have been shown to strongly react to ship abundance (Kaiser et al. 2006, Schwemmer et al. 2011, Fliessbach et al. 2019). The shallow waters along the German North (and Baltic) Sea coast are subject to recreational activities especially during summer and fishing activities throughout the entire year, whereas the areas in deeper waters are utilised for ship traffic year round. Evading the potential threats posed by vessels increases energy expenditure through escape behaviour, displaces birds from optimal feeding areas and reduces the time and energy available for foraging, ultimately affecting body condition (e.g. Kight and Swaddle 2007, Riddington et al. 2010, Robinson and Pollitt 2010). Consequently, we would expect that patterns of human maritime activity also influence the distribution of Common Scoters particularly during the moulting season, when birds are flightless. Furthermore, we wanted to include the differences in distribution of Common Scoters between moulting and wintering season and therefore set up separate models for both periods.

In this study, we used Common Scoter count data obtained by ship and aircraft based Seabirds at Sea surveys to model the spatial and temporal distribution of the Common Scoter in response to a number of selected environmental parameters. As we wanted to model the distribution on a large spatial scale, we focused on the areas of the eastern German North Sea coast, from which a detailed count data base of regularly performed surveys was available. Since this count data is characterised by zero-inflation, spatial correlation and large variation in abundance, we used Bayesian computing with Integrated Nested Laplace Approximation (INLA). Previous studies have already shown that this approach is highly suitable for such count data characteristics (e.g. Rue et al. 2016, Sadykova et al. 2017, Bakka et al. 2018). As environmental parameters, we selected water depth (m), distance to coast (km), biomass (g m^{-2}) and abundance (individuals m^{-2}) of benthic bivalve species, proportion of fine sand (%), bed shear stress (N m^{-2}) and ship traffic (number of ships km^{-2}). Based on this approach, we raised the following hypotheses:

- (i) Common Scoter distribution will mainly be influenced by water depth and biomass/abundance of benthic bivalve species.
- (ii) Highest numbers of Common Scoters will be found in areas with lowest ship traffic.
- (iii) Distance to coast, proportion of fine sand and bed shear stress will contribute to explaining Common Scoter distribution, but are expected to have lesser influence.
- (iv) During moult, ship traffic has a greater impact on Common Scoter distribution than prey availability.

Material and Methods

All statistical analyses were performed with R (R Core Team, 2017). All maps were produced with ArcGIS (ESRI, Version 10.2.1, 2013).

2.1 Study area

The study area covered about 4500 km^2 along the eastern German North Sea coast extending from the Elbe river in the south to the northern part of the island Sylt (Fig. 1). It included tidal mud flats close to the coast, as well as intertidal and subtidal areas further offshore. Water depths ranged from 0 to -30 m. The study area is known to provide important habitats for moulting and wintering Common Scoters (e.g. Nehls 1998, Mendel et al. 2008, Markones and Garthe 2011, Spalke et al. 2013). Although Common Scoter are not located on intertidal mudflats, we sampled both intertidal and subtidal areas to set up a valid prediction model of prey abundance throughout the entire area.
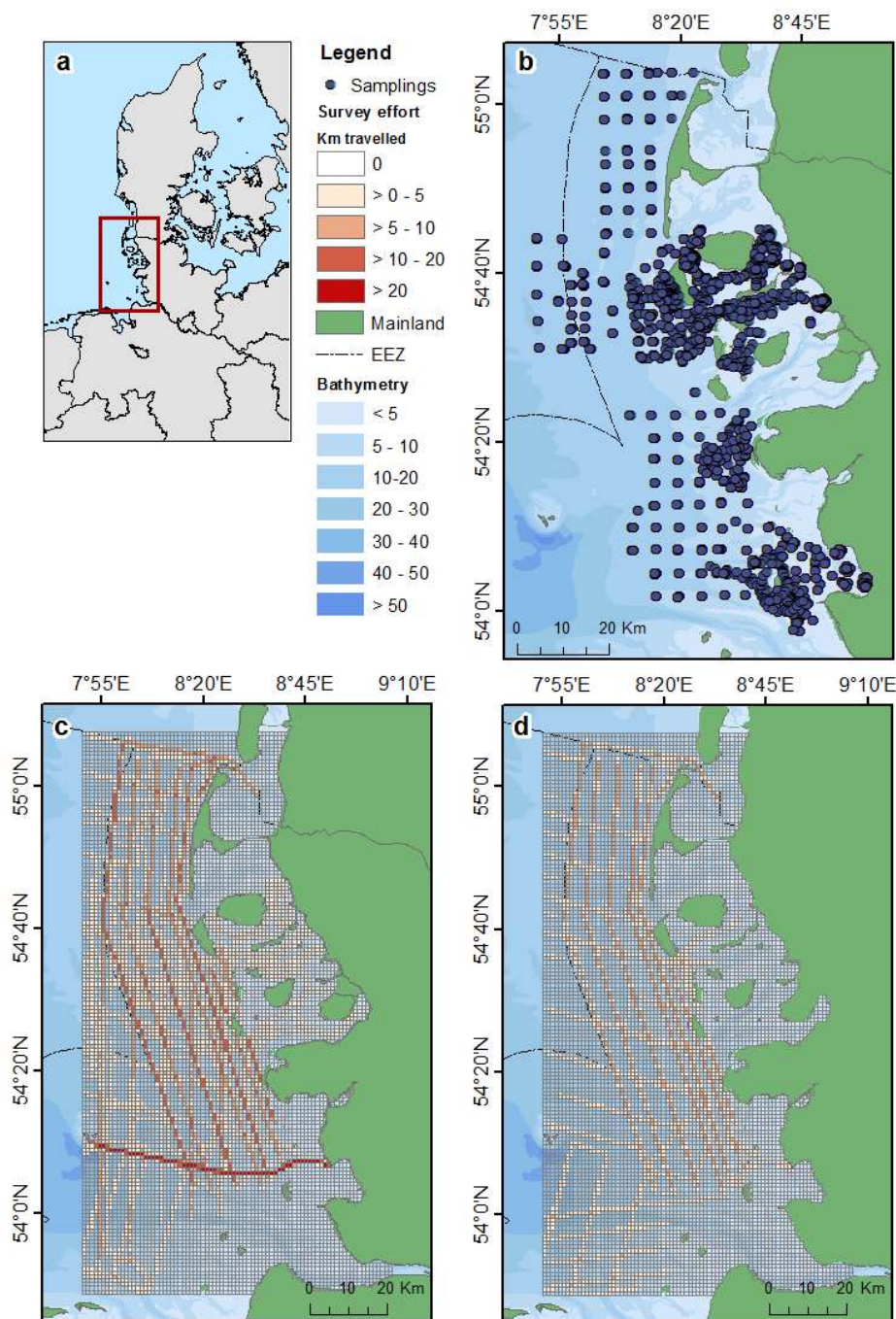
Fig. 1 Study area in the eastern German North Sea with **(a)** overview map and legend, **(b)** all sampling stations, **(c)** survey effort during the moulting season and **(d)** survey effort during the wintering season. Survey effort is shown across the entire prediction grid.

2.2 Seabirds at Sea surveys

Common Scoter distribution data was taken from ship and aerial based Seabird at Sea surveys regularly conducted by the Research and Technology Centre on behalf of the Schleswig-Holstein Agency for Coastal Defence, National Park and Marine Conservation – National Park Authority or parallel to the sampling cruises. In this study, we focused on the moulting and wintering distribution and thus only included survey data from June to September (moult) and December to February (winter). Due to gaps

in the survey data (either caused by bad weather conditions or unavailability of ship/aircraft) data from 2015-2017 was combined. SAS surveys were performed following internationally standardised methods (Camphuysen and Garthe 2004) based on line transects with distance sampling (Buckland et al. 2015). Aerial surveys had either nearly N-S transects parallel to the Schleswig-Holstein coast or nearly E-W transects during flights covering areas offshore across the 12 nautical mile zone (Fig. 1 c, d). Aerial surveys were conducted with a high-winged twin-engine Partenavia P-68 with bubble windows flying at 76 m with a speed of 185 km/h. Birds were counted within 388 m wide transects parallel to the flight track. During ship based surveys, birds were counted within a 300 m wide transect parallel to the keel line of the research vessel. Bird observations were spatially joined in ArcGis with a 1x1 km prediction grid covering the entire study area to calculate the number of individuals per grid cell (see 2.5).

2.3 Biotic environmental variables

1,405 benthos samples were collected in the intertidal and subtidal zone along the coast of Schleswig-Holstein between October 2012 and February 2018 (Fig. 1b). Intertidal samples were collected with a corer (sampling an area of 93.3 cm^{-2} to a depth of 20 cm). Subtidal samples were taken using a Van Veen grab (sampling an area of 1000 cm^2 to a depth of about 20 cm). Three replicates were taken at each sampling station, sieved through a 2 mm mesh and derived specimen were stored in zip lock bags and frozen at -20°C or stored in jars filled with 75% ethanol.

Since Common Scoters are bivalve benthic feeding sea ducks (Madsen 1954, Fox 2004), this study focused on analysing bivalves. All other benthic species were identified as well, but were not included in our analysis. All specimens were identified to species level and counted. Bivalves were measured with callipers to the nearest 0.1 mm (length, width and height). As a measure of biomass, individual ash-free dry weight was determined based on the loss on ignition method (Kramer et al., 1992). All specimens were dried in porcelain crucibles at 50°C for 24 hours and weighed. To determine ash content, dried flesh fractions were combusted in a muffle furnace at 560°C for 12 hours and subsequently weighed. Benthic species abundance data was standardised to m^{-2} and ash free dry weight data was standardised to g/m^{-2}. As three replicates were taken per sampling station, mean bivalve abundances and ash-free dry weights were calculated per sampling station and used for the habitat models. For biomass and abundance data per species, we focused on bivalve species, which are preferred prey items of Common Scoters (Fox 2004, Kottsieper et al. 2019, Schwemmer et al. 2019) and thus selected *Ensis leei* (M. Huber, 2015), *Limecola balthica* (Linneaus, 1758) and *Fabulina fabula* (Gmelin, 1791). For data across species, all other bivalve species collected were included. To visualise distribution and abundances of benthic species, their abundances and biomasses were spatially joined with a 1x1 km grid in ArcGIS and the mean abundance and biomass were calculated per grid cell.

2.4 Abiotic environmental variables

To analyse the influence of abiotic environmental variables on the distribution of Common Scoters, we selected proportion of fine sand (%), water depth (m), distance to coast (km), bed shear stress (N/m^{-2}) and ship traffic. Water depth data based on one metre intervals was taken from an ArcGIS shape file provided by the Federal Maritime and Hydrographic Agency (BSH, Germany, see also Asprion et al. 2013). Distance to coast was computed in the GIS using a map of the coastal zone provided by the national park administration of Schleswig-Holstein (NPV Schleswig-Holsteinisches Wattenmeer). Bed shear stress data was calculated based on a numerical model by Kösters and Winter (2014). Ship traffic data was taken from Seabirds at Sea survey data (FTZ). During aircraft and ship based counts, ships were listed including information on type (cargo, fishery, recreational etc), direction of travel and distance to the observation vessel.

To determine the proportion of fine sand, sediment samples were collected together with benthos samples taken from the first replicate, stored in zip lock bags and frozen at -20°C. Samples were dried at 100°C for 6-8 hours, weighed and treated with a 10% hydrogen peroxide (H_2O_2) solution for 12-24 hours to oxidize all organic constituents. Subsequently, samples were rinsed with freshwater through a 63 µm mesh until the water was clear, dried at 100 °C for another 6-8 hours and weighed. Grain size distribution was analysed by sieving samples in ¼ Phi fractions with mesh sizes ranging from 63 µm to 2 mm and weighing each fraction (modified in accordance with Buchanan, 1984). Based on this sieving cascade, the amount of fine sand (%) was calculated for each sample.

2.5 Prediction grid

To model the distribution of Common Scoter in relation to the selected environmental parameters, a prediction grid with 1 x 1 km cells was created in ArcGIS (Fig. 1 c, d). To cover the entire area along the Schleswig-Holstein coast and thus model the distribution on a larger spatial scale, the prediction grid was expanded beyond the sampling area, covering about 8300 km^{-2}. All environmental parameters as well as the distribution data were spatially joined with the prediction grid subsequently to assign a value of each variable and bird observation to every grid cell. Since the selected environmental variables were available in different spatial resolutions, they needed to be adjusted to the size of the prediction grid. Therefore, the average water depth was calculated for each grid cell. In case of bed shear stress, the value closest to a grid cell was used. Common Scoter observations and ships counted were summed per grid cell. Common Scoter abundances were corrected by survey effort. In the statistical model, the uncorrected bird observations were used, but survey effort was included as an offset.

Benthos and sediment data were either collected based on a 5x5 km grid or random (stratified) sampling. To obtain values for all cells, missing sediment data as well as ash free dry weight and

abundance data were fitted to the grid in R with a generalised additive model (GAM) using the mgcv package (Wood, 2011). Subsequently, missing values were supplemented via the predict function (mgcv package, Wood, 2011). Bed shear stress data had a resolution of 1x1 km close to the coast, but was more fragmentary further offshore. To cover the prediction grid and obtain values for all missing cells, the same procedure of fitting and predicting values was used.

2.6 Common Scoter habitat model

All predictor variables were tested for collinearity visually using the lattice package (Sarkar 2008) and by performing a variance inflation factor analysis (VIF, usdm package, Naimi et al. 2014). If autocorrelation was detected, affected variables were excluded from further analysis. Common Scoter distribution was modelled as a function of the before mentioned selected environmental parameters (from here on referred to as covariates). Due to the structure of the response variable (Common Scoter observations with overdispersion and a large number of zeros), we modelled the distribution with a zero-inflated Poisson generalised additive model (ZIP GAM) using Integrated Nested Laplace Approximation (INLA package, Rue et al. 2009). *Latitude* was included as a random interaction term to account for spatial autocorrelation (Latimer et al. 2006). Since Common Scoter count data included three survey years, *Year* was included as a categorical variable. Abundance and biomass values of the selected bivalve species as well as for the overall benthos were log-transformed to simulate a normal distribution and account for potential outliers. The same applied for the number of counted Common Scoter. All continuous covariates were standardised to avoid numerical estimation problems. The survey effort (distance travelled either by aircraft or ship) was included as an offset. Based on this procedure, the following formulas were defined for *(1)* the moulting and *(2)* the wintering data:

(1) $log(Scoter_i) = Depth_i + Fine\ sand_I + BSS_i + Distance_i + log(Abu_I) + log(Bio_I) + Ships_i + Year_i + f(Latitude) + offset(log(Effort_i))$

(2) $log(Scoter_i) = Depth_i + Fine\ sand_I + BSS_i + Distance_i + log(Abu_I) + log(Bio_I) + Ships_i + Year_i + f(Latitude) + offset(log(Effort_i))$

where *Scoter_i* is the number of Common Scoter, *Fine sand_I* is the proportion of fine sand, *BSS_i* is bed shear stress and *Distance_i* is the distance to the coast. Four separate models with the selected benthic bivalve species were performed for each season with *Abu* and *Bio* representing abundances and biomasses of *E. leei*, *F. fabula*, *L. balthica* and all benthic bivalve species. *Ships_i* is the number of observed ships. *Year_i* is a categorical variable, *f(Latitude)* is the random interaction term and the survey effort was included as *offset(log(Effort_i))*. All values were calculated for every (*i*th) observation. We validated the models by inspecting residual plots and checking for linearity, homogeneity and independence (Zuur et al. 2010). The degrees of freedom (number of knots *k*) for GAM smoothers of

each covariate were set to *k=6* to attain a stronger smooth of model curves and thus allow a better interpretation of potential relationships between covariates and response variable.

Results

3.1 Common Scoter distribution

During the moulting season in 2015-2017, the majority of individuals was located west of Amrum and Norder-/Süderoogsand in the central eastern German Bight (Fig. 2 a). High abundances were also found west of the Eiderstedt peninsula. Most birds stayed close to the coast with water depths of ≤ 5m. Only a small number of Common Scoter was found in deeper waters or further offshore. During winter 2015-2017, the majority of Common Scoter was located west of the Eiderstedt peninsula (Fig. 2b). High numbers of birds were also found west of Norder-/Süderoogsand. These individuals were still located close to the coast. Compared to the moulting season, more birds were observed further offshore within water depths of up to 10 m. Additionally, Common Scoter dispersed more during winter compared to the moulting season when individuals were found mainly aggregated.
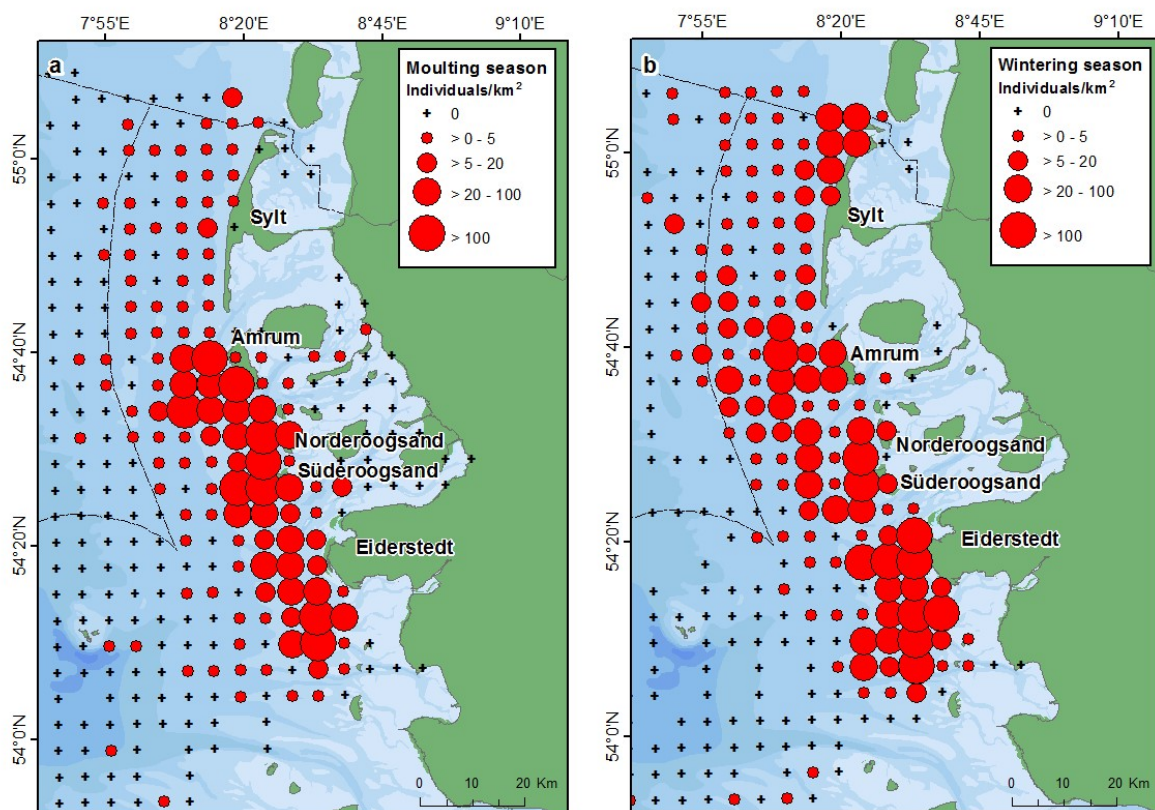

Fig. 2 Distribution of the Common Scoter in the eastern German Bight during (**a**) the moulting and (**b**) the wintering season. For clarity, distribution data was summed in a 5x5 km grid. Abundances of Common Scoters are represented as number of individuals per grid cell.

3.2 Bivalve abundances and ash-free-dry mass

Overall, 9,794.41 bivalve individuals were found in the study area. 63.48 % of these were *E. leei* specimen, 0.69 % *F. fabula* individuals and 6.93 % *L. balthica* specimen (Table 1). The highest abundances across all bivalves were found west of the Eiderstedt peninsula (Fig. 3 a). Additionally, high bivalve abundances across species were observed in the central eastern German Bight around the North Frisian Islands in shallow waters and intertidal areas. The lowest abundances were found west of Sylt. The maximum of *E. leei* individuals was located west of the Eiderstedt peninsula and a few locations with higher abundances were observed further offshore in the south-eastern study area (Fig. 3 b). Lowest abundances were observed west of Sylt. Highest numbers of *F. fabula* individuals found were located west of Sylt and further offshore west of the North Frisian Islands, whereas low abundances were observed in the remaining study area (Fig. 3 c). In case of *L. balthica*, highest numbers were found west of the Eiderstedt peninsula (Fig. 3 d). Additionally, high abundances were located north of the Elbe estuary, as well as among the North Frisian Islands in the central eastern German Bight.

In terms of ash-free-dry mass, a total of 12.79 g/m^{-2} was calculated across all bivalve species. Of this overall ash-free-dry mass, 43.42 % were contributed by *E. leei*, 0.37 % by *F. fabula* and 11.85 % by *L. balthica* (Table 1). The maximum ash-free-dry mass across all bivalves as well as of *E. leei* was found west of the Eiderstedt peninsula. The highest ash-free-dry mass of *F. fabula* was found west of Sylt and the maximum of *L. balthica* west of Norderoogsand in the central eastern German Bight.

Table 1 Abundance (given as individuals/m^{-2}) and ash-free-dry mass (AFDM, given as g/m^{-2}) of the benthic bivalve species collected in the study area. The values of *E. leei*, *F. fabula* and *L. balthica* as well as all other species combined are given.

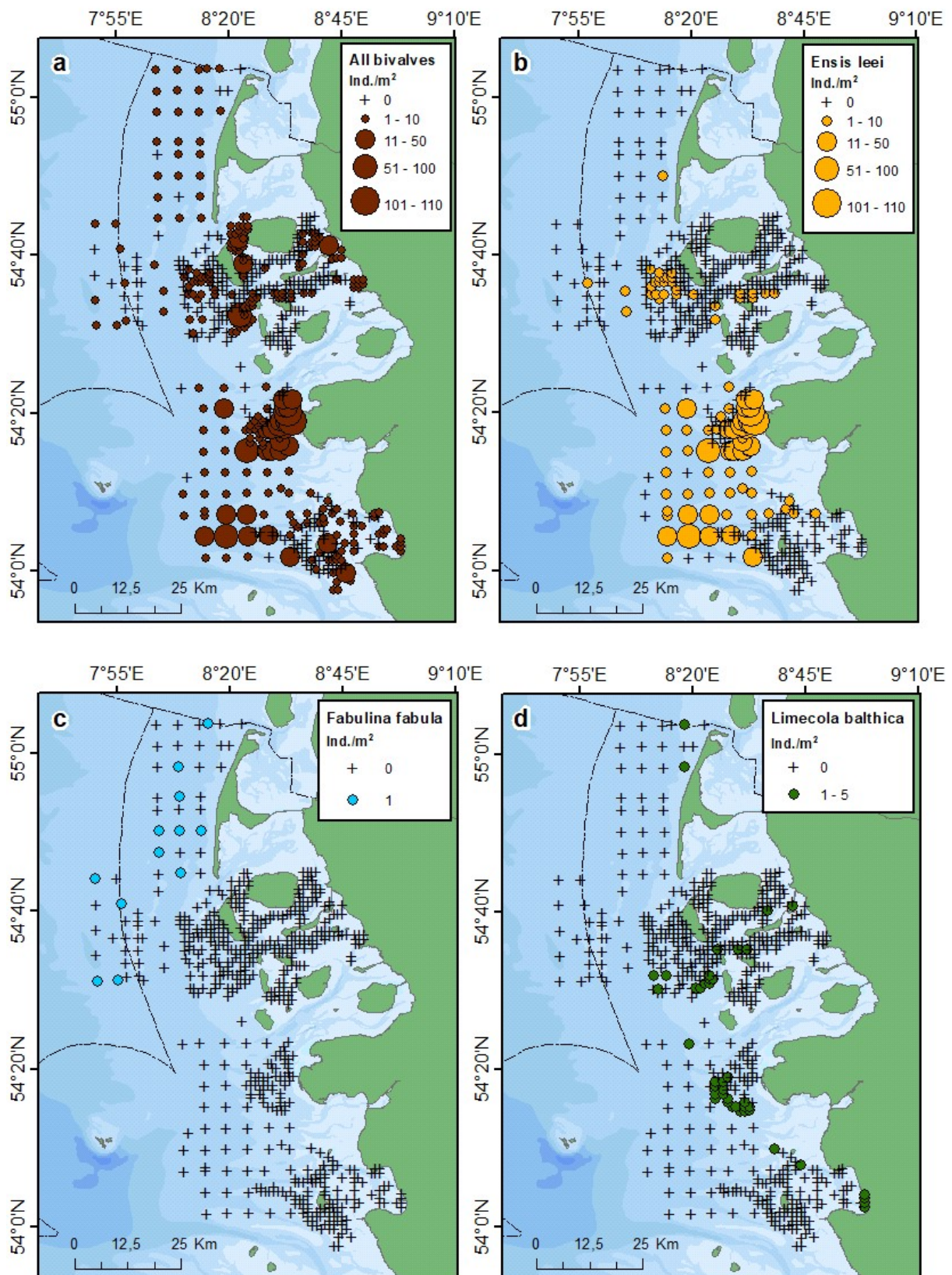|	Abundance (ind./m^2)	Proportion (%)	AFDM (g/m^2)	Proportion (%)
E. leei	6217.56	63.48	75.02	43.42
F. fabula	67.2	0.69	0.64	0.37
L. balthica	678.96	6.93	20.48	11.85
Other species	2830.69	28.90	76.65	44.36

Fig. 3 Abundances of (**a**) all benthic bivalves, (**b**) *Ensis leei*, (**c**) *Fabulina fabula* and (**d**) *Limecola balthica* individuals found in the study area.

3.3 Common Scoter habitat model

Moulting season

Based on the overall deviance explained by each model for the moulting season, the selected covariates were only able to explain a small fraction of Common Scoter distribution (Table 2 a). The model including all benthic bivalve species was the best fitting, explaining 6.53 % of the deviance. In all models performed for the moulting season, water depth, distance to coast, proportion of fine sand and bed shear stress affected Common Scoter distribution significantly (Table 3 a). Bivalve abundance had significant effects on Common Scoter distribution in all four models, whereas biomass showed significant effects in all except for the *E. leei* model. Ship traffic did not have significant impacts on Common Scoter distribution (Table 3 a).

Based on the smoothing functions, the probability to encounter Common Scoters was highest in areas with moderate bed shear stress values and within distances of 2-3 and around 7-8 km to the coast in all four models (see Appendix Fig. 1). The proportion of fine sand showed statistical relationships with scoter distribution in all models with an optimum of ca. 60 %. The models revealed a relationship between scoter distribution and *E. leei* biomass (Fig. 4 II), as well as *F. fabula* abundance (Fig. 4 III). The results for *L. balthica* and the model including all bivalves were difficult to interpret (Fig. 4 I+IV). While the models did not show significant relationships between Scoter distribution and ship traffic, the smoothing functions suggest that they are most likely encountered with either less than 2 (all benthos model) or no ships present in the study area (*E. leei*, *F. fabula* and *L. balthica* model). Smoothing functions for latitude, water depth, fine sand, bed shear stress and distance to coast were similar among all four models, there graphs are shown in the appendix (Appendix Fig. 1-4).

Wintering season

The overall deviance explained was higher for all four wintering season models compared to those of the moulting season (Table 2 b). The model with *L. balthica* data was the best fitting, explaining 25.12 % of the deviance. Water depth, distance to coast, proportion of fine sand and bed shear stress significantly affected the distribution of Common Scoters during the wintering season in all models (Table 3 b). In case of the all benthos and *L. balthica* model, both abundance and biomass had significant impacts. No significant effects of abundance were found for the *E. leei* model. Ship traffic did not have significant impacts on Common Scoter distribution (Table 3 b).

The smoothing functions showed that Common Scoters are most likely encountered in areas with fine sand proportions of ca. 70 %, at moderate bed shear stress values and within distances of 7-11 km to the coast. The model *F. fabula* model revealed a relationship between scoter distribution and biomass (Fig. 5 III). The results for *E. leei*, the *L. balthica* and the model including all bivalves were difficult to interpret (Fig. 5 I+IV). While the models did not show significant relationships between Scoter

distribution and ship traffic, the smoothing functions suggest that they are most likely encountered with a maximum of 10 ships present in all four models. However, this probability increases in all except the *L. balthica* models with more than ca. 11 ships present. Smoothing functions for latitude, water depth, fine sand, bed shear stress and distance to coast were similar among all four models, there graphs are shown in the appendix (Appendix Fig. 5-8).

Table 2 Results of the Zero-inflated Poisson (ZIP) Generalised Additive Model (GAM) with Integrated Nested Laplace Approximation (INLA) for the distribution of Common Scoter during the moulting and wintering season. Modelling results with the overall deviance explained and the deviance information criterion (DIC) of the best fitting model are given for **(a)** the moulting and **(b)** the wintering seasons. The mean ± standard deviation (SD) and the 25 % and 97,5 % quantiles are listed as well. As models were distinguished by the selected benthos variable, they have been named accordingly.

a	Dev. Expl. (%)	DIC	Mean ± SD	0.025 Q	0.975 Q
All benthos	6.53	9976.68	0.76 ± 0.008	0.74	0.77
E. leei	5.89	9472.78	0.76 ± 0.008	0.74	0.77
F. fabula	5.22	9802.67	0.76 ± 0.008	0.74	0.77
L. balthica	5.16	9616.69	0.76 ± 0.008	0.74	0.77

b	Dev. Expl. (%)	DIC	Mean ± SD	0.025 Q	0.975 Q
All benthos	19.75	7348.00	0.62 ± 0.011	0.60	0.64
E. leei	15.40	7280.29	0.62 ± 0.011	0.59	0.64
F. fabula	15.12	7397.69	0.62 ± 0.011	0.60	0.64
L. balthica	25.12	7248.07	0.63 ± 0.011	0.60	0.64

Dev. Expl. Deviance explained · **DIC** Deviance Information Criterion · **SD** Standard deviation · **Q** Quantile

Table 3 Pearson residuals of each parameter in each model for **(a)** the moulting and **(b)** the wintering season. Deviance explained in %, adjusted R^2 and P-value are given for each parameter. As models were distinguished by the selected benthos variable, they have been named accordingly. The parameter with the highest explained deviance is given in bold. Statistical significance codes: <0.001 '***' 0.001 '**' 0.01 '*'

a		MOULT				b		WINTER			
	Parameter	Dev. Expl. (%)	R² adj.	P			Parameter	Dev. Expl. (%)	R² adj.	P	
All benthos	Latitude	0.32	0.00	0.039	*		Latitude	1.55	0.013	<0.001	***
	Depth	1.00	0.008	<0.001	***		Depth	2.76	0.025	<0.001	***
	Fine Sand	0.89	0.007	0.001	**		Fine Sand	3.12	0.027	<0.001	***
	BSS	1.12	0.009	<0.001	***		BSS	2.93	0.025	<0.001	***
	Distance	1.12	0.009	<0.001	***		**Distance**	**4.37**	**0.039**	**<0.001**	***
	Abundance	**1.47**	**0.012**	**<0.001**	***		Abundance	1.79	0.014	<0.001	***
	Biomass	0.59	0.005	0.005	**		Biomass	3.06	0.028	<0.001	***
	Ship traffic	<0.001	<-0.001	0.895			Ship traffic	0.17	<0.001	0.4	
E. leei	Latitude	0.34	0.002	0.038	*		Latitude	1.44	0.012	<0.001	***
	Depth	1.14	0.009	<0.001	***		Depth	2.72	0.025	<0.001	***
	Fine Sand	0.72	0.005	0.01	**		Fine Sand	2.90	0.025	<0.001	***
	BSS	**1.34**	**0.011**	**<0.001**	***		BSS	2.96	0.026	<0.001	***
	Distance	1.24	0.011	<0.001	***		**Distance**	**4.38**	**0.039**	**<0.001**	***
	Abundance	1.09	0.008	<0.001	***		Abundance	0.61	0.004	0.112	
	Biomass	0.01	<-0.001	0.509			Biomass	1.94	0.017	<0.001	***
	Ship traffic	<0.001	<-0.001	0.939			Ship traffic	0.19	<0.001	0.351	
F. fabula	Latitude	0.29	0.002	0.07			Latitude	1.32	0.011	<0.001	***
	Depth	1.01	0.008	<0.001	***		Depth	2.86	0.026	<0.001	***
	Fine Sand	0.17	0.001	0.017	*		Fine Sand	2.69	0.022	<0.001	***
	BSS	**1.15**	**0.009**	**<0.001**	***		BSS	2.57	0.022	<0.001	***
	Distance	1.06	0.009	<0.001	***		**Distance**	**4.13**	**0.037**	**<0.001**	***
	Abundance	0.89	0.007	<0.001	***		*Abundance*	*Excluded due to autocorrelation*			
	Biomass	0.65	0.005	0.001	**		Biomass	1.29	0.011	<0.001	***
	Ship traffic	<0.001	<-0.001	0.965			Ship traffic	0.26	0.001	0.248	
L. balthica	Latitude	0.28	0.002	0.076			Latitude	1.79	0.014	<0.001	***
	Depth	1.05	0.009	<0.001	***		Depth	2.60	0.023	<0.001	***
	Fine Sand	0.42	0.004	0.022	*		Fine Sand	3.12	0.027	<0.001	***
	BSS	1.13	0.009	<0.001	***		BSS	3.86	0.035	<0.001	***
	Distance	**1.19**	**0.010**	**<0.001**	***		Distance	4.6	0.042	<0.001	***
	Abundance	0.47	0.004	0.003	**		Abundance	2.97	0.026	<0.001	***
	Biomass	0.62	0.005	<0.001	***		**Biomass**	**5.99**	**0.056**	**<0.001**	***
	Ship traffic	<0.001	<-0.001	0.957			Ship traffic	0.19	<0.001	0.363	

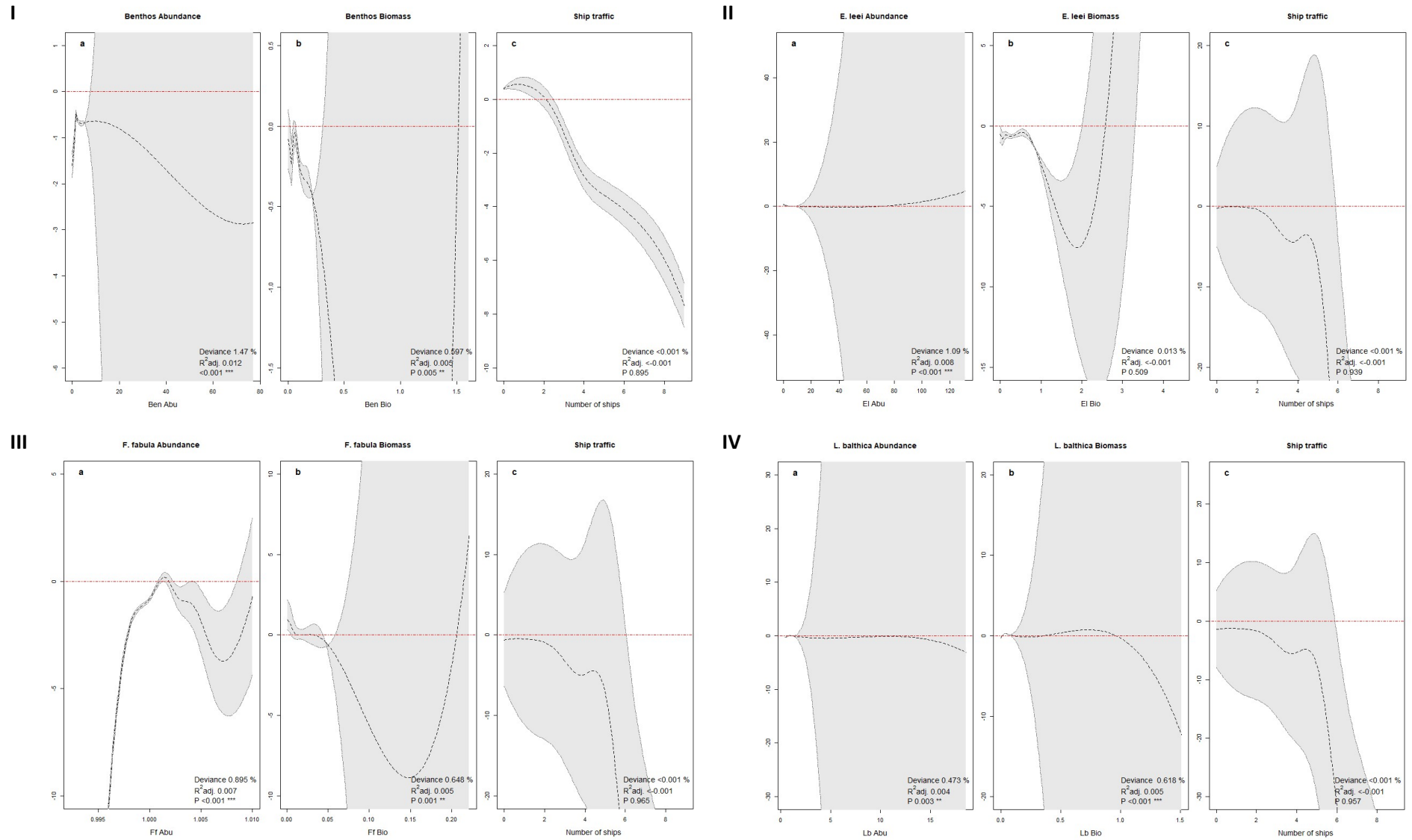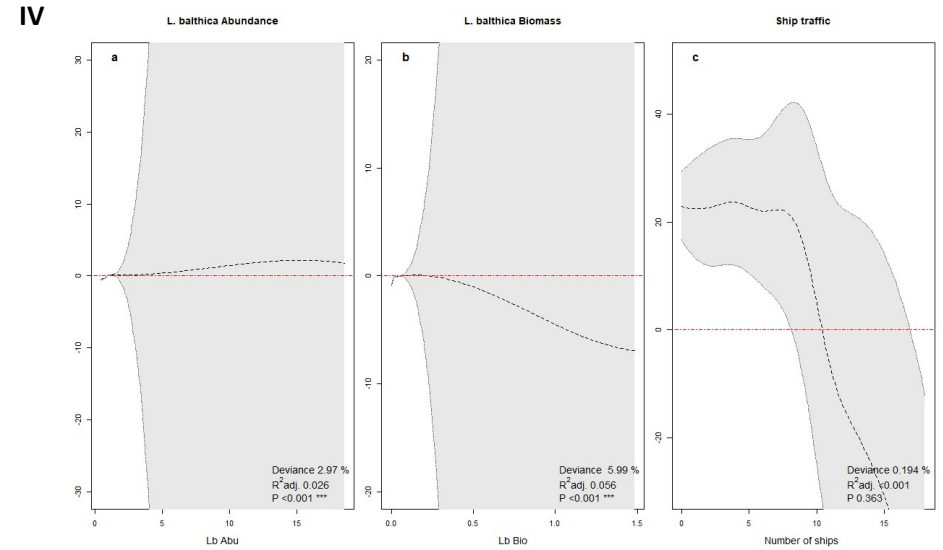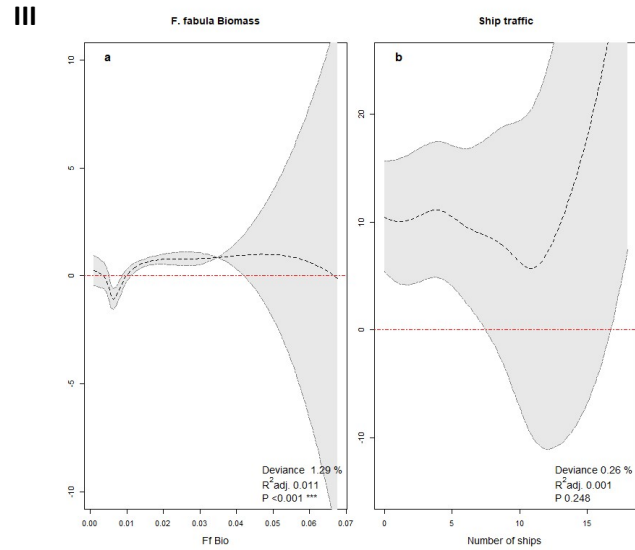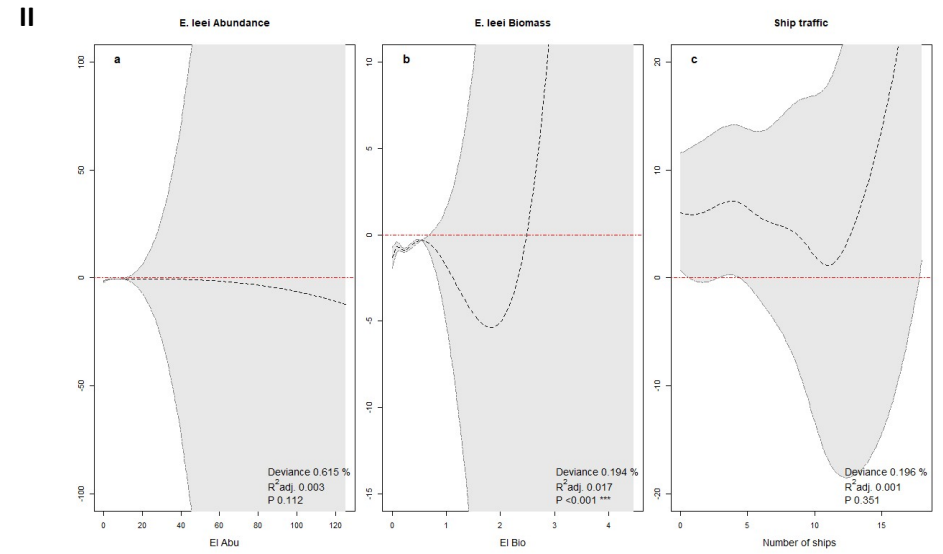**Adj** adjusted · **Dev. Expl.** Deviance explained

Fig. 4 Smoothing functions of the Zero-inflated Poisson (ZIP) Generalised Additive Model (GAM) with Integrated Nested Laplace Approximation (INLA) for the distribution of Common Scoter during the moulting season. Based on the selection of benthos data, smoothing functions are shown for **I** all bivalve benthos species, **II** *E. leei*, **III** *F. fabula* and **IV** *L. balthica* models. Graphs are shown for Common Scoter abundance modelled in relation to **(a)** abundance, **(b)** biomass and **(c)** ship traffic. The deviance explained (%), adjusted R^2 and P-value of the Pearson residuals are given for each covariate. The dashed black middle line represents the smooth function estimate. 95 % confidence intervals are given in grey. Note that the y-axes of abundance and biomass values were log-transformed. **Abu** Abundance · **Ben** Benthos · **Bio** Biomass · **El** *Ensis leei* · **Ff** *Fabulina fabula* · **Lb** *Limecola balthica*.
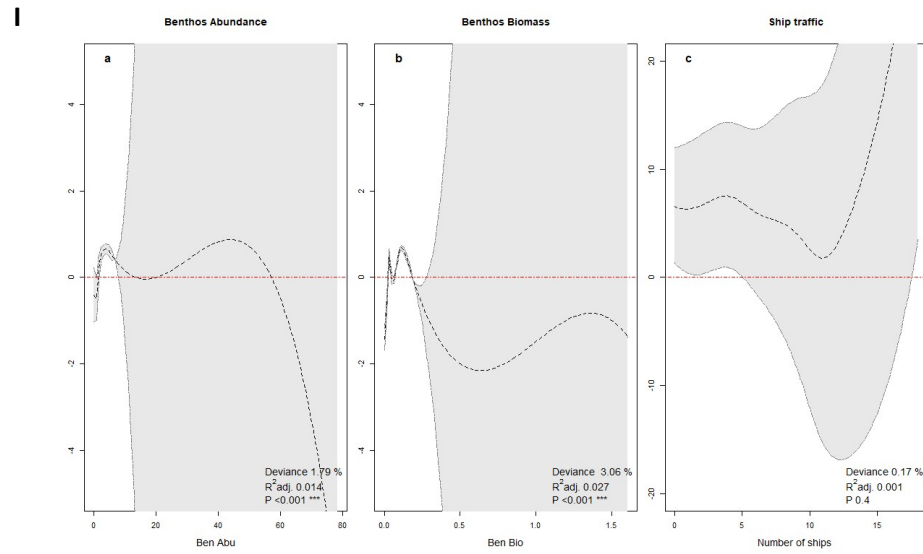
Fig. 5 Smoothing functions of the Zero-inflated Poisson (ZIP) Generalised Additive Model (GAM) with Integrated Nested Laplace Approximation (INLA) for the distribution of Common Scoter during the wintering season. Based on the selection of benthos data, smoothing functions are shown for **I** all bivalve benthos species, **II** *E. leei*, and **IV** *L. balthica* models. Graphs are shown for Common Scoter abundance modelled in relation to **(a)** abundance, **(b)** biomass and **(c)** ship traffic. Graph **III** shows the results for *F. fabula* with **(a)** biomass and **(b)** ship traffic, as abundance had to be excluded from the analysis due to autocorrelation. The deviance explained (%), adjusted R^2 and P-value of the Pearson residuals are given for each covariate. The dashed black middle line represents the smooth function estimate. 95 % confidence intervals are given in grey. Note that the y-axes of abundance and biomass values were log-transformed. **Abu** Abundance · **Ben** Benthos · **Bio** Biomass · **El** *Ensis leei* · **Ff** *Fabulina fabula* · **Lb** *Limecola balthica*.

Discussion

Based on the four hypothesis stated in the introduction, the result of our study confirmed some, but not all of our assumptions.

Water depth, bed shear stress and fine sand

The modelling results showed that the most influential parameters during the moulting and wintering season were water depth, proportion of fine sand and bed shear stress. All three covariates significantly affected Common Scoter distribution in all models during both seasons. Previous studies have stated that water depth is potentially one of the most influential parameters impacting Common Scoter distribution (e.g. Deppe 2003, Schwemmer et al. 2019). During moult, birds replace worn flight feathers, thus being flightless and in particular need of balancing the ratio of energy spent to forage and the energy gained from prey resources. Shallow waters reduce the amount of time spent and energy needed to dive through the water column and obtain prey. During winter, scoters likely have to move to deeper waters as the season progresses since prey resources might have been depleted (Guillemette et al. 1996). Our findings support these assumptions.

The bivalve species Common Scoter prefer as prey items are predominately found in sandy substrates (Fox 2004). This relates to our findings showing that Common Scoter are most likely localised above sediments with high proportions of fine sand as bivalves are easier to detect (by bill-probing) and remove from sandy compared to harder, muddy or consolidated substrates. Areas with moderate bed shear stress are characterised by medium current strength. In general, water currents are responsible for the transport of prey (i.e. phyto- and zooplankton) upon which filtering feeding bivalves rely (Gray and Elliot 2009). Strong currents would complicate bivalve settlement, mobilise substrates and transport organic and inorganic material too quickly, reducing the attractiveness to sedentary bivalve species. If currents were too low on the other hand, supply of sufficient energy resources may jeopardise survival, reducing bivalve abundance (Reise 2012). Consequently, areas with moderate bed shear stress are likely optimal habitats for several bivalve species and thus provide profitable foraging areas for Common Scoter.

Distance to coast

The results of all models for both seasons revealed a significant relationship between the probability of encountering Common Scoter and the distance to the coast. As previously mentioned, Scoters tend to aggregate close to the coast in shallow waters during moult, whereas they spread over larger areas and thus further away from the coastline during winter. Common Scoters are flightless during moult and therefore rely on profitable prey resources in shallower waters. They tend to aggregate in these areas in high densities. As prey resources might therefore be depleted during the season, birds are likely forced to spread over wider areas and into deeper waters as the winter progresses. Thus, they

are located in greater distances to the coast. Consequently, this should be reflected in the results of our habitat models.

Bivalve abundances and ash-free-dry masses

While mapping the distribution patterns of Common Scoter and those of the bivalves collected in the study area showed that highest bird abundances were located in areas with highest bivalve abundances, these results were not distinctively represented in our habitat models. During moult, abundance and ash-free-dry mass showed significant effects on Common Scoter distribution in all except the *E. leei* model, with only abundance having a significant impact. During winter, the distribution was significantly affected by ash-free-dry mass in all four models, as well as the abundance of all benthic species and *L. balthica*. The differences in deviances explained by each selected benthos variable might give us a hint on the importance of certain bivalve species. The model including all benthic bivalves was the best for the moulting season. For the wintering season, the highest explained deviance was found in the *L. balthica* model. These results might indicate that different bivalve species are important as prey resources during different times. If birds prefer to feed on a certain prey item, this could potentially be depleted over time, thus forcing them to rely on other bivalve species.

Despite these findings, the influence of bivalve biomass and abundance on scoter abundance was not as obvious as we expected. Clearly recognizable broad confidence intervals shown in the smoothing functions suggest a lack of insufficient data and the spatial scale of our benthic sampling likely contributed to these indistinct results. Most bivalve species were not evenly distributed across the entire study area. As a result, interpolating values for unsampled areas potentially resulted in the poor power of contribution to the overall models. Matching the scales of these distributions to the scale, which is used to sample the birds and environmental parameters, is challenging. Hernandez et al. (2006) reported that species distribution models are more accurate for species within a limited geographic range and Wisz et al. (2008) highlighted the importance of adequate sample sizes stating that the accuracy of these models decreased with increasing sample sizes. Focusing the study area on the core moulting (west of the Eiderstedt peninsula) and the core wintering area (west of Sylt) and performing the same models on these downsized scales showed a drastic increase in explained deviance. 16.59 % of Common Scoter distribution during moult and 52.01 % of their distribution during winter could be explained (see Appendix Table 1). This supports the assumption that, if we want to model habitats of a species on a large special scale, it is crucial to survey distribution patterns and predictors not only with sufficient samples sizes, but also with adequate matching spatial resolutions to avoid data inaccuracy. Schwemmer et al. (2019), who modelled the distribution of Common Scoter in the central eastern German Bight, found that their selected predictors explained 43.5% of deviance. We used a similar approach and set of predictors in our study, but wanted to expand our model to a

larger spatial scale. As the results of Schwemmer et al. (2019) proved that habitat modelling using GAMs and the choice of predictors were valuable, we assume that our models can still be improved by adding more detailed information to the covariates. We particularly need more emphasis on sampling in relation to seasonal variability. Common Scoter and bivalve distributions underlie seasonal changes. Matching these appropriately for our habitat models will likely improve their quality and explanatory power (Pearman et al. 2008, Lambert et al. 2017, Virgili et al. 2017).

Ship traffic

Our assumption that ship traffic has a negative impact on Scoter distribution was confirmed for the moulting, but not for the wintering season. However, the impact was only significant in the *E. leei* model. During moult, Common Scoter are mainly located close to the coast in shallow areas. These are subject to intensive recreational activities especially during summer and thus overlapping with the moulting period. Previous studies have already shown that Common Scoter are sensitive to disturbance by ship traffic revealing high flush distances compared to other seabird species (Schwemmer et al. 2011, Fliessbach et al. 2019). Escape behaviour during moult, when birds are flightless, demands a high energy expenditure. Moreover, the time used to escape reduces the time available for foraging. Therefore, it is to be expected that Scoters avoid areas with high disturbance potential during moult. The model for the wintering season showed higher probabilities of encountering Scoters in areas with lower ship traffic, but these values were still high compared to the moulting season. Yet the confidence interval of this GAM smooth was quite broad suggesting an insufficient amount of observations. During winter, less recreational activities occur in shallow coastal waters. The majority of ship traffic during this period consists of fishery or cargo vessels potentially reduced in frequency due to harsh weather conditions. Additionally, most of these ships travel in deeper waters further offshore. Thus, Scoters are less likely to encounter them. The reduced amount of SAS surveys (again caused by harsher weather conditions during the winter) likely provided an insufficient data basis and therefore, more data on ship traffic particularly during the winter is needed.

Differences between moulting and wintering season models

In general, the selected covariates were more suitable for the wintering compared to the moulting season models. The main reason for this is likely the difference in spatial scales of the sampled environmental variables and the observed Common Scoter distribution. As discussed before, those disparities may result in inaccuracy in the data, which is for example reflected by broad confidence intervals. The higher values of explained deviances in all four wintering season models seemed to confirm this. As Common Scoters are distributed over wider areas during this time, the spatial scale of observation points was a better match for the spatial scale of environmental parameters. Their high sensitivity against disturbances and long flush distances complicate the recording of their occurrences,

thus making it difficult to relate this highly mobile species to its sessile benthic prey. As Common Scoters aggregate in much smaller areas during moult, the spatial scale of this distribution was quite different compared to the one of the covariates. Consequently, it is not only important to adjust the spatial scales of the species in focus to the predictors. It is also vital to consider seasonal differences in distribution patterns.

Conclusion

Overall, the habitat models had a better fit for the wintering compared to the moulting season. The main cause for this is probably the dispersal of individuals during each season in combination with the spatial scale of sampled predictors, which need to be better matched. However, performing Zero-inflated Poisson Generalised Additive Models using Integrated Nested Laplace Approximation proved to be a useful tool to model the distribution of Common Scoters in the eastern German Bight in relation to their environment. We remain convinced that a more detailed data basis putting more emphasis on considering the seasonal variation in distribution patterns and environmental parameters will give us a more detailed insight into how Common Scoter distribute themselves according to their seasonally varying needs.

Acknowledgments

References

Asprion U, Sbresny J, Griffel G, Elbracht J, 2013. Die Bathymetrie der deutschen Nordsee – Erstellung der projektweiten Bezugsfläche, https://www.gpdn.de/media/1122

Austin MP, 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling 157, 101–118. https://doi.org/10.1016/S0304-3800(02)00205-3

Austin MP, 2005. Chapter 2: Vegetation and environment: discontinuities and continuities. IN VAN DER MAAREL, E.(Ed.) Végétation ecology. Etats-Unis. BLACKWELL PUBLISHING

Bakka H, Rue H, Fuglstad GA, Riebler A, Bolin D, Krainski E, Simpson D, Lindgren F, 2018. Spatial modelling with R-INLA: A review. arXiv:1802.06350 [stat]

Buchanan JB, 1984. *Sediment Analysis* in Methods for the Study of Marine Benthos, 41–63. https://ci.nii.ac.jp/naid/10029032784/

Buckland ST, Rexstad EA, Marques TA, Oedekoven CS, 2015. Distance sampling: methods and applications. Springer.

Camphuysen KC, Garthe S, 2004. Recording foraging seabirds at sea standardised recording and coding of foraging behaviour and multi-species foraging associations. Atlantic Seabirds 6, 1–32

Deppe, L, 2003. 'Die Trauerente (*Melanitta Nigra*) in Der Deutschen Bucht–GIS-Basierte Bewertung Räumlicher Und Zeitlicher Parameter'. Dipl-Arbeit, Universität Hamburg

Environmental Systems Research Institute (ESRI) 2013 ArcGIS Desktop Release Version 10.2.1, https://www.esri.com/de-de/arcgis/about-arcgis/overview

Fliessbach KL, Borkenhagen K, Guse N, Markones N, Schwemmer P, Garthe S (2019) A ship traffic disturbance vulnerability index for Northwest European seabirds as a tool for marine spatial planning. Frontiers in Marine Science 6:192, https://doi.org/10.3389/fmars.2019.00192

Fox AD, 2004. Diet and habitat use of scoters Melanitta in the Western Palearctic - a brief overview. Wildfowl 54, 163–182

Fox AD, Hartmann P, Petersen IbK, 2007. Changes in body mass and organ size during remigial moult in common scoter *Melanitta nigra*. Journal of Avian Biology 0, 071202183307008–0. https://doi.org/10.1111/j.2007.0908-8857.04135.x

Glutz von Blotzheim UN, Bauer KN, 1990. Handbuch der Vögel Mitteleuropas, 2., durchges. Aufl. ed, Handbuch der Vögel Mitteleuropas Anseriformes Teil 1. Aula-Verl, Wiesbaden.

Gray JS, Elliott M, 2009. Ecology of Marine Sediments: From Science to Management. Oxford University Press

Gulllemette M, Himmelman JH, ReedA, 1996. Availability and Consumption of Food by Common Eiders Wintering in the Gulf of St. Lawrence: Evidence of Prey Depletion. *Canadian Journal of Zoology* 74, Nr. 1: 32–38. https://doi.org/10.1139/z96-005

Hennig V, Eskildsen K, 2001. Notwendigkeit Ungestörter Mausergebiete Für Die Trauerente (*Melanitta Nigra*). Landesamt Für Den Nationalpark Schleswig-Holsteinisches Wattenmeer (Eds.): Wattenmeermonitoring, 70–71

Hennig V, Hälterlein B, 2000. Trauerente–Erfassungsschwierigkeiten Einer Offshore-Vogelart. Landesamt Für Den Nationalpark Schleswig-Holsteinisches Wattenmeer (Eds.): Wattenmeermonitoring, 20–23

Hernandez PA. Graham CH, Master LL, Albert DL, 2006. The Effect of Sample Size and Species Characteristics on Performance of Different Species Distribution Modeling Methods. Ecography 29, no. 5:773–85. https://doi.org/10.1111/j.0906-7590.2006.04700.x

Kaiser, MJ, Galanidi M, Showler DA, Elliott AJ, Caldow RWG, Rees EIS, Stillman RA, Sutherland WJ, 2006. Distribution and Behaviour of Common Scoter *Melanitta nigra* Relative to Prey Resources and Environmental Parameters. Ibis 148: 110–28. https://doi.org/10.1111/j.1474-919X.2006.00517.x

Kight CR, Swaddle JP, 2007. Associations of anthropogenic activity and disturbance with fitness metrics of eastern bluebirds (*Sialia sialis*). Biological Conservation 138: 189-197. https://doi.org/10.1016/j.biocon.2007.04.014

Kösters F, Winter C, 2014. Exploring German Bight Coastal Morphodynamics Based on Modelled Bed Shear Stress. Geo-Marine Letters 34, no. 1: 21–36. https://doi.org/10.1007/s00367-013-0346-y

Kottsieper J, Schückel U, Schwemmer P, Fox AD, Garthe S. 2019. Comparison of bivalve communities between moulting and wintering areas used by Common Scoter Melanitta nigra in the German North Sea. Estuarine, Coastal and Shelf Science, 229. https://doi.org/10.1016/j.ecss.2019.106398

Kramer K, Brockmann UH, Warwick RM, 1992. Manual of Sampling and Analytical Procedures for Tidal Estuaries. TNO Institute of Environmental Sciences, Laboratory of Applied Research

Lambert C, Virgili A, Pettex E, Delavenne J, Toison V, Blanck A, Ridoux V, 2017. Habitat Modelling Predictions Highlight Seasonal Relevance of Marine Protected Areas for Marine Megafauna. Deep Sea Research Part II: Topical Studies in Oceanography 141: 262–74. https://doi.org/10.1016/j.dsr2.2017.03.016

Latimer AM, Shanshan W, Gelfand AE, Silander Jr. JA, 2006. Building Statistical Models To Analyze Species Distributions. *Ecological Applications* 16, Nr. 1: 33–50. https://doi.org/10.1890/04-0609

Madsen FJ, 1954. On the Food Habits of the Diving Ducks in Denmark. Danish Review of Game Biology 2

Markones N, Garthe S, 2011.'Monitoring von Seevögeln Im Offshore-Bereich Der Schleswig-Holsteini-Schen Nordsee Im Rahmen von NATURA 2000 in Den Jahren 2004 Bis 2009. Corax 22: 11–50.

Mendel B, Sonntag N, Wahl J, Schwemmer P, Dries H, Guse N, Müller S, Garthe S, 2008. Profiles of Seabirds and Waterbirds of the German North and Baltic Seas: Distribution, Ecology and Sensitivities to Human Activities within the Marine Enviroment. Vol. 61. Naturschutz Und Biologische Vielfalt. Bonn - Bad Godesberg: Bundesamt f. Naturschutz

Naimi B, Hamm NA, Groen TA, Skidmore AK and Toxopeus AG (2014) Where is positional uncertainty a problem for species distribution modelling. Ecography, 37, pp. 191-203. doi: 10.1111/j.1600-0587.2013.00205.x

Pearman PB, Guisan A, Broennimann O, Randin CF, 2008. Niche dynamics in space and time. Trends in Ecology & Evolution 23, 149–158. https://doi.org/10.1016/j.tree.2007.11.005

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statis tical Computing, Vienna, Austria. URL https://www.R-project.org/

Reise, K, 2012. Tidal flat ecology: an experimental approach to species interactions. Bd. 54. Springer Science & Business Media

Riddington R, Hassall M, Lane SJ, Turner PA, Walters R, 1996. The impact of disturbance on the behaviour and energy budgets of Brent Geese Branta b. bernicla. *Bird Study* 43, Nr. 3: 269–79. https://doi.org/10.1080/00063659609461019

Rue H, Riebler A, Sørbye SH, Illian JB, Simpson DP, Lindgren FK, 2016. 'Bayesian Computing with INLA: A Review'. ArXiv:1604.00860 [Stat], 4 April 2016. http://arxiv.org/abs/1604.00860

Sadykova, D, Scott BE, De Dominicis M, Wakelin SL, Sadykov A, Wolf J, 2017. Bayesian Joint Models with INLA Exploring Marine Mobile Predator–Prey and Competitor Species Habitat Overlap. Ecology and Evolution 7, no. 14: 5212–26. https://doi.org/10.1002/ece3.3081

Sarkar D, 2008. Lattice: Multivariate Data Visualization with R, Springer. ISBN: 978-0-387-75968-5. http://lmdvr.r-forge.r-project.org/

Schwemmer P, Mendel B, Sonntag N, Dierschke V, Garthe S, 2011. Effects of ship traffic on seabirds in offshore waters: implications for marine conservation and spatial planning. Ecological Applications 21:1851–1860

Schwemmer P, Volmer H, Enners L, Riemers HC, Binder K, Horn S, Eskildsen K, Adler S, Fox AD, Garthe S (2019) Modelling summer distribution patterns of common scoters (*Melanitta nigra*) by its most important prey species, the razor clam (*Ensis directus*), and hydrodynamic parameters. Estuar Coast Shelf Sci 225

Segurado P, Araújo MB, 2004. An Evaluation of Methods for Modelling Species Distributions: Methods for Modelling Species Distributions. Journal of Biogeography 31, no. 10: 1555–68. https://doi.org/10.1111/j.1365-2699.2004.01076.x

Sonntag N, Engelhard O, Garthe S, 2004. Sommer- und Mauservorkommen von Trauerenten *Melanitta nigra* und Samtenten *M. fusca* auf der Oderbank (südliche Ostsee). Vogelwelt 125: 77–82

Spalke J, Diederichs A, Grünkorn T, Rassmus J, Nehls G, 2013. Trauerenten (*Melanitta nigra*) an der schleswig-holsteinischen Nordseeküste. Corax 22, no. Sonderheft 1 (2014): 12

Virgili A, Lambert C, Pettex E, Dorémus G, Van Canneyt O, Ridoux V, 2017. Predicting seasonal variations in coastal seabird habitats in the English Channel and the Bay of Biscay. Deep Sea Research Part II: Topical Studies in Oceanography 141, 212–223. https://doi.org/10.1016/j.dsr2.2017.03.017

Wisz MS, Hijmans RJ, Peterson JLAT, Graham CH, Guisan A, 2008. Effects of Sample Size on the Performance of Species Distribution Models. Diversity and Distributions 14, no. 5: 763–73. https://doi.org/10.1111/j.1472-4642.2008.00482.x

Wood, SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73(1):3-36

Zuur, AF, Elena N, Elphick, CS, 2010 A Protocol for Data Exploration to Avoid Common Statistical Problems. Methods in Ecology and Evolution 1: 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Modelling the distribution of the Common Scoter Melanitta nigra in relation to environmental parameters in the eastern German North Sea
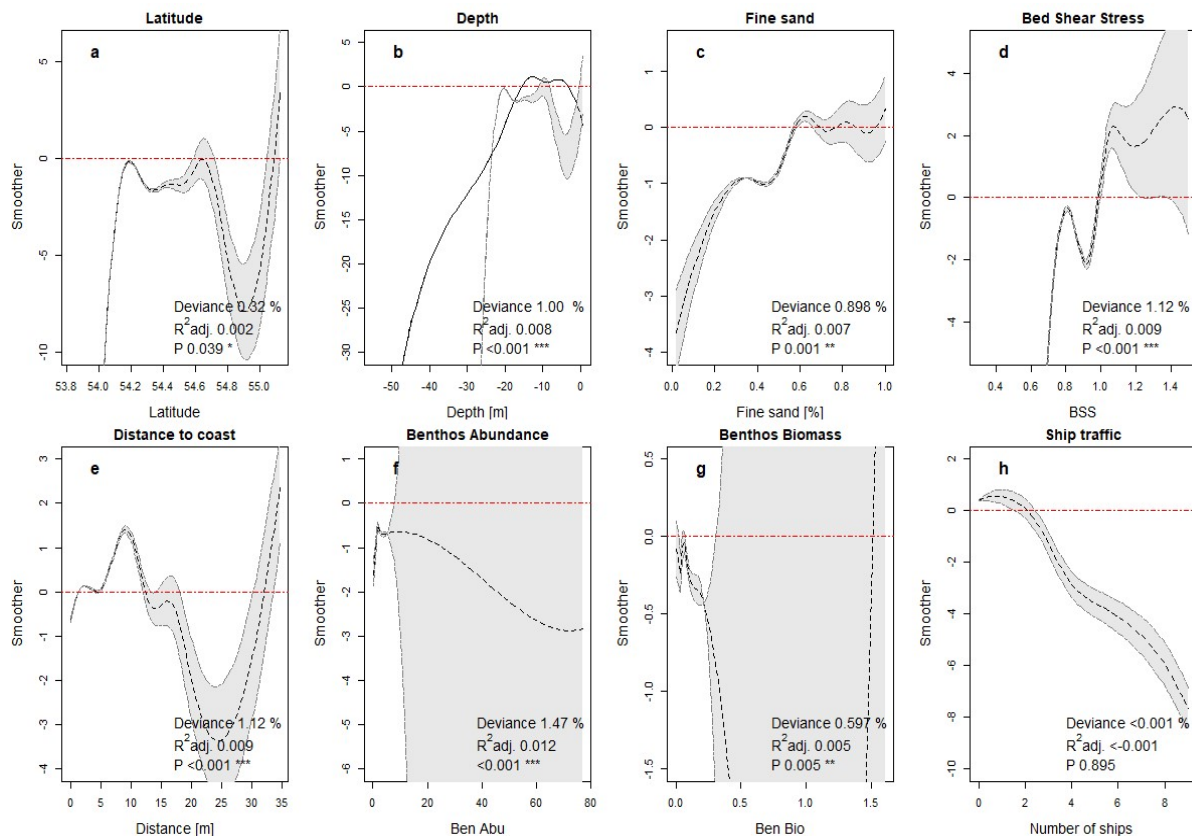
124

Appendix

Fig. 1 Smoothing functions of the Zero-inflated Poisson (ZIP) Generalised Additive Model (GAM) with Integrated Nested Laplace Approximation (INLA) for the distribution of Common Scoter during the moulting season including all benthic bivalve species. Common Scoter abundance was modelled in relation to **(a)** Latitude, **(b)** Depth, **(c)** Fine sand, **(d)** Bed shear stress, **(e)** Distance to coast, **(f)** Abundance, **(g)** Biomass and **(h)** ship traffic. The deviance explained (%), adjusted R^2 and P-value of the Pearson residuals are given for each covariate. The dashed black middle line represents the smooth function estimate. 95 % confidence intervals are given in grey. Note that the y-axes of abundance and biomass values were log-transformed and that fine sand is given as a proportion, not as percentage.
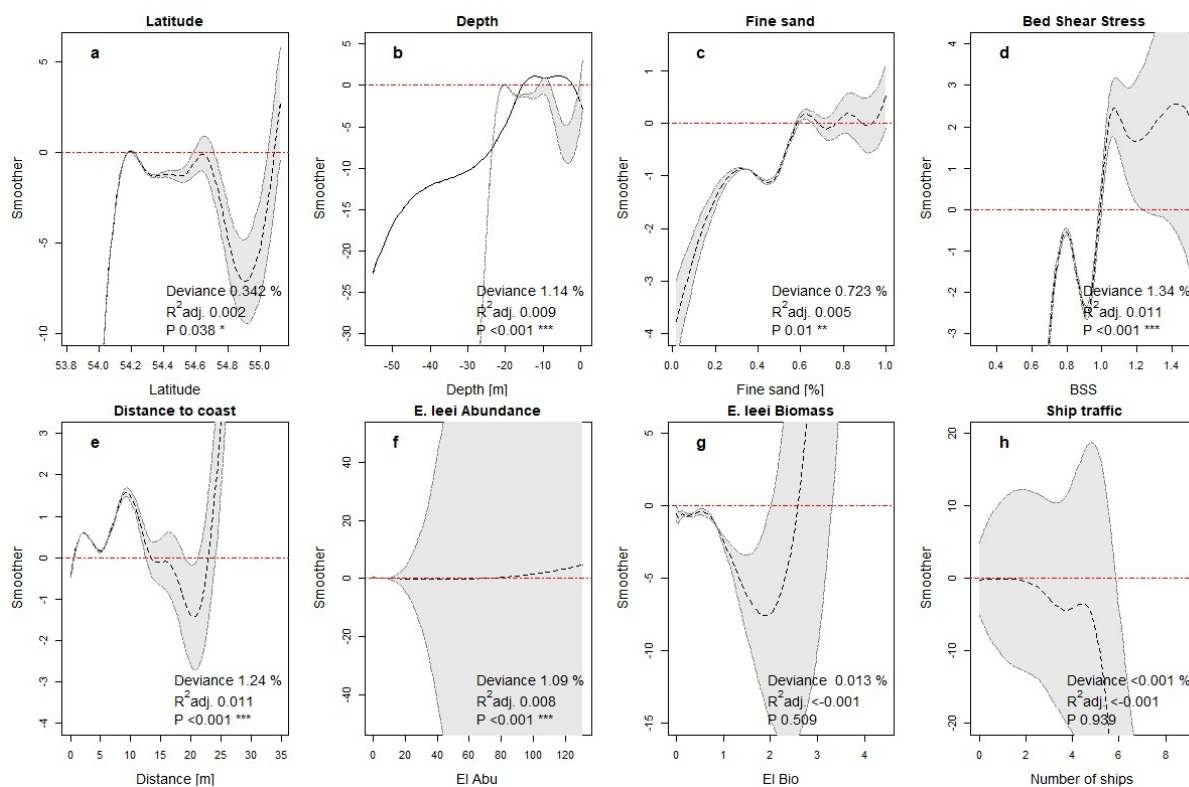**Abu** Abundance · **Ben** Benthos · **Bio** Biomass · **BSS** Bed shear stress

Fig. 2 Smoothing functions of the Zero-inflated Poisson (ZIP) Generalised Additive Model (GAM) with Integrated Nested Laplace Approximation (INLA) for the distribution of Common Scoter during the moulting season including *E. leei* individuals. Common Scoter abundance was modelled in relation to **(a)** Latitude, **(b)** Depth, **(c)** Fine sand, **(d)** Bed shear stress, **(e)** Distance to coast, **(f)** Abundance, **(g)** Biomass and **(h)** ship traffic. The deviance explained (%), adjusted R^2 and P-value of the Pearson residuals are given for each covariate. The dashed black middle line represents the smooth function estimate. 95 % confidence intervals are given in grey. Note that the y-axes of abundance and biomass values were log-transformed and that fine sand is given as a proportion, not as percentage. **Abu** Abundance · **Bio** Biomass · **BSS** Bed shear stress
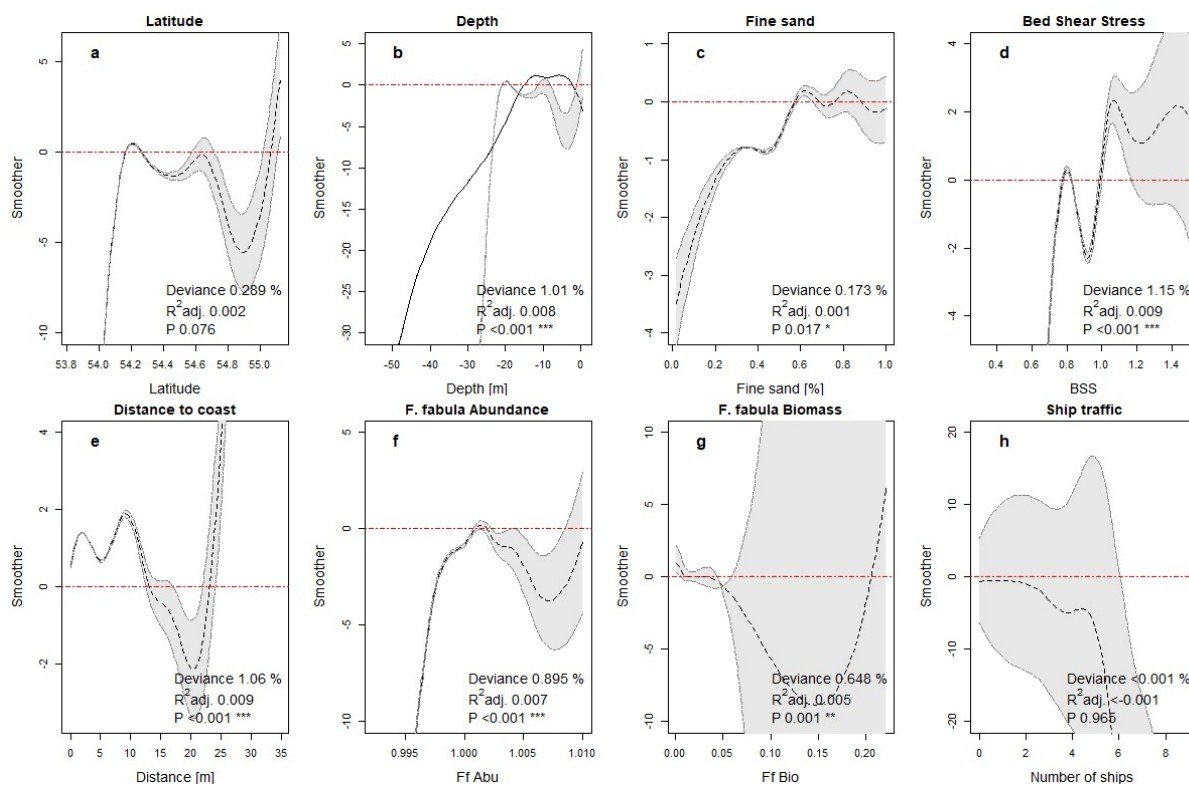
Fig. 3 Smoothing functions of the Zero-inflated Poisson (ZIP) Generalised Additive Model (GAM) with Integrated Nested Laplace Approximation (INLA) for the distribution of Common Scoter during the moulting season including *F. fabula* individuals. Common Scoter abundance was modelled in relation to **(a)** Latitude, **(b)** Depth, **(c)** Fine sand, **(d)** Bed shear stress, **(e)** Distance to coast, **(f)** Abundance, **(g)** Biomass and **(h)** ship traffic. The deviance explained (%), adjusted R^2 and P-value of the Pearson residuals are given for each covariate. The dashed black middle line represents the smooth function estimate. 95 % confidence intervals are given in grey. Note that the y-axes of abundance and biomass values were log-transformed and that fine sand is given as a proportion, not as percentage. **Abu** Abundance · **Bio** Biomass · **BSS** Bed shear stress
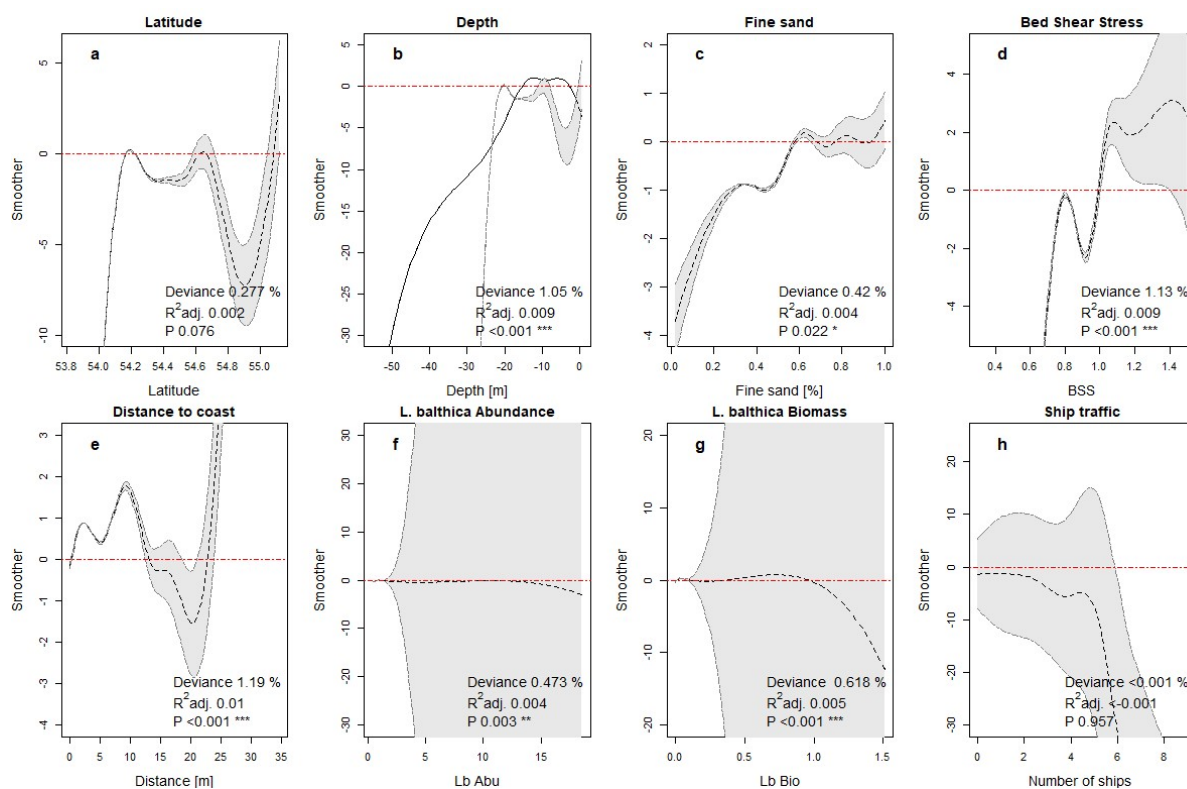
Fig. 4 Smoothing functions of the Zero-inflated Poisson (ZIP) Generalised Additive Model (GAM) with Integrated Nested Laplace Approximation (INLA) for the distribution of Common Scoter during the moulting season including *L. balthica* individuals. Common Scoter abundance was modelled in relation to **(a)** Latitude, **(b)** Depth, **(c)** Fine sand, **(d)** Bed shear stress, **(e)** Distance to coast, **(f)** Abundance, **(g)** Biomass and **(h)** ship traffic. The deviance explained (%), adjusted R^2 and P-value of the Pearson residuals are given for each covariate. The dashed black middle line represents the smooth function estimate. 95 % confidence intervals are given in grey. Note that the y-axes of abundance and biomass values were log-transformed and that fine sand is given as a proportion, not as percentage. **Abu** Abundance · **Bio** Biomass · **BSS** Bed shear stress
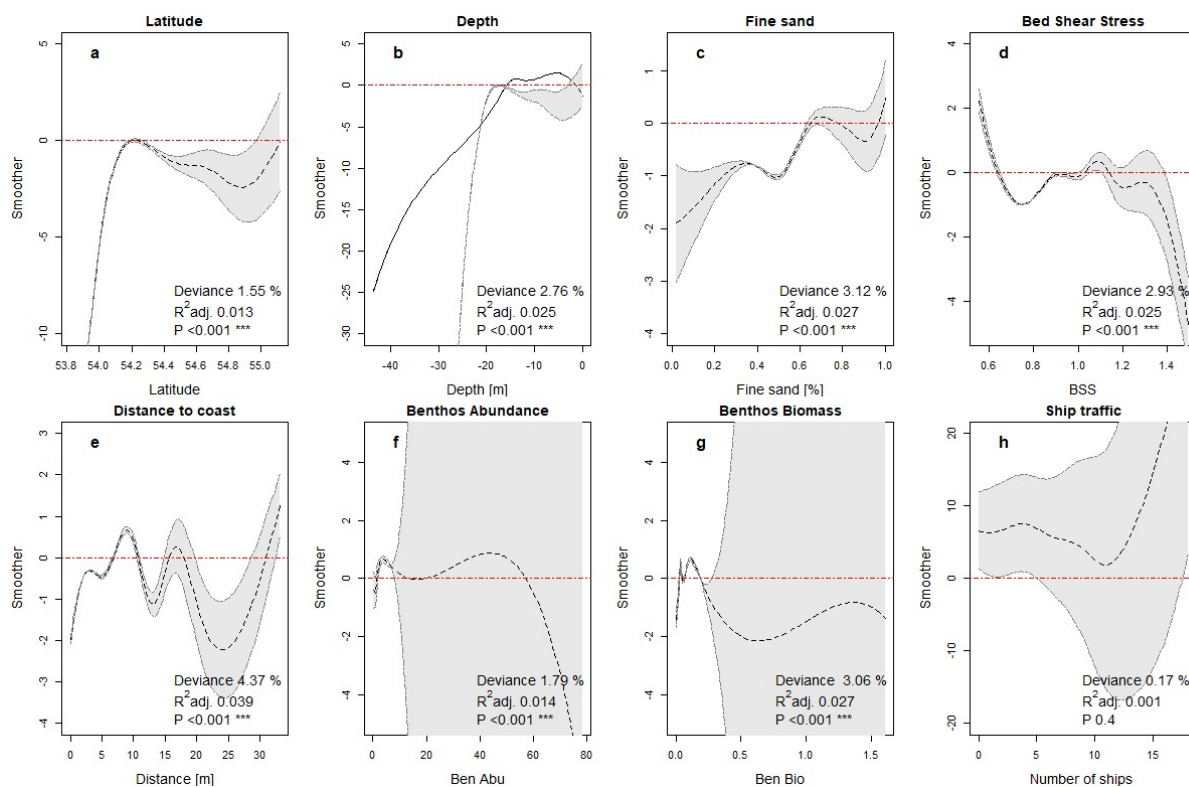
Fig. 5 Smoothing functions of the Zero-inflated Poisson (ZIP) Generalised Additive Model (GAM) with Integrated Nested Laplace Approximation (INLA) for the distribution of Common Scoter during the wintering season including all benthic bivalve species. Common Scoter abundance was modelled in relation to **(a)** Latitude, **(b)** Depth, **(c)** Fine sand, **(d)** Bed shear stress, **(e)** Distance to coast, **(f)** Abundance, **(g)** Biomass and **(h)** ship traffic. The deviance explained (%), adjusted R^2 and P-value of the Pearson residuals are given for each covariate. The dashed black middle line represents the smooth function estimate. 95 % confidence intervals are given in grey. Note that the y-axes of abundance and biomass values were log-transformed and that fine sand is given as a proportion, not as percentage. **Abu** Abundance · **Bio** Biomass · **BSS** Bed shear stress
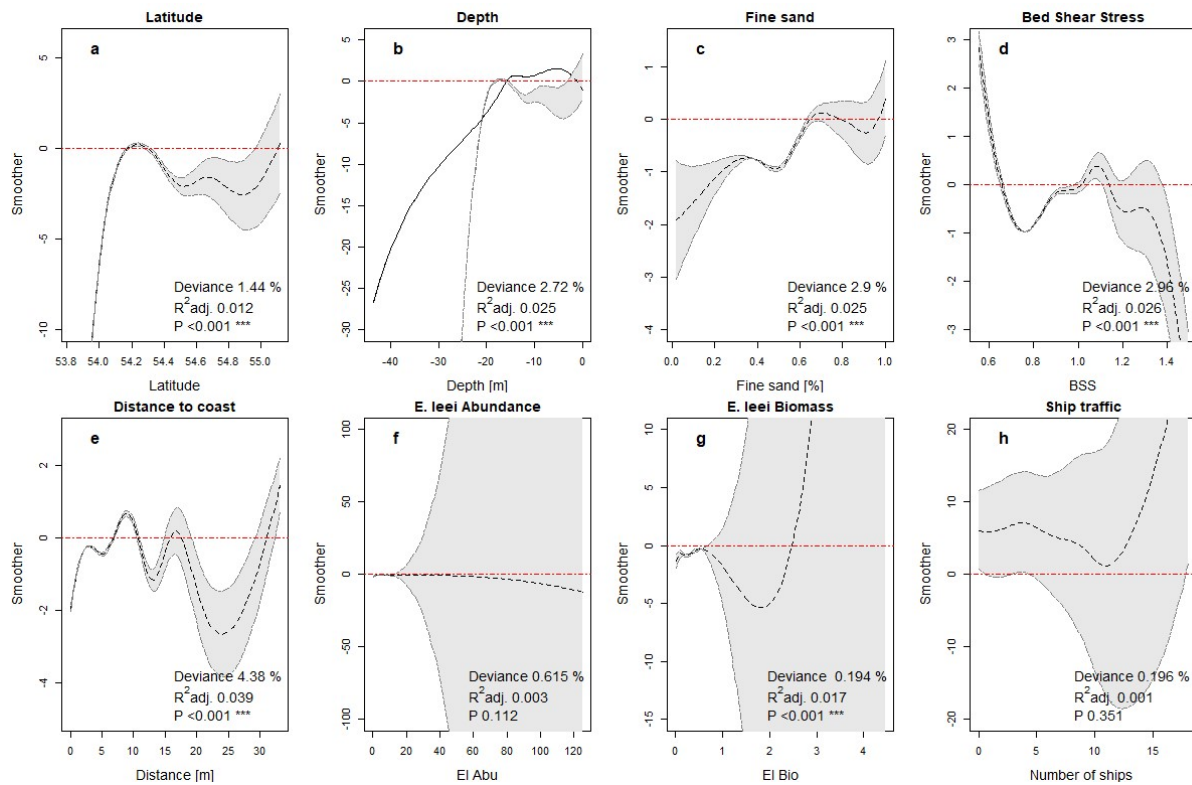
Fig. 6 Smoothing functions of the Zero-inflated Poisson (ZIP) Generalised Additive Model (GAM) with Integrated Nested Laplace Approximation (INLA) for the distribution of Common Scoter during the wintering season including *E. leei* individuals. Common Scoter abundance was modelled in relation to **(a)** Latitude, **(b)** Depth, **(c)** Fine sand, **(d)** Bed shear stress, **(e)** Distance to coast, **(f)** Abundance, **(g)** Biomass and **(h)** ship traffic. The deviance explained (%), adjusted R^2 and P-value of the Pearson residuals are given for each covariate. The dashed black middle line represents the smooth function estimate. 95 % confidence intervals are given in grey. Note that the y-axes of abundance and biomass values were log-transformed and that fine sand is given as a proportion, not as percentage. **Abu** Abundance · **Bio** Biomass · **BSS** Bed shear stress

Fig. 7 Smoothing functions of the Zero-inflated Poisson (ZIP) Generalised Additive Model (GAM) with Integrated Nested Laplace Approximation (INLA) for the distribution of Common Scoter during the wintering season including *F. fabula* individuals. Common Scoter abundance was modelled in relation to **(a)** Latitude, **(b)** Depth, **(c)** Fine sand, **(d)** Bed shear stress, **(e)** Distance to coast, **(f)** Biomass and **(g)** ship traffic. The deviance explained (%), adjusted R^2 and P-value of the Pearson residuals are given for each covariate. The dashed black middle line represents the smooth function estimate. 95 % confidence intervals are given in grey. Note that the y-axes of abundance and biomass values were log-transformed and that fine sand is given as a proportion, not as percentage. **Abu** Abundance · **Bio** Biomass · **BSS** Bed shear stress
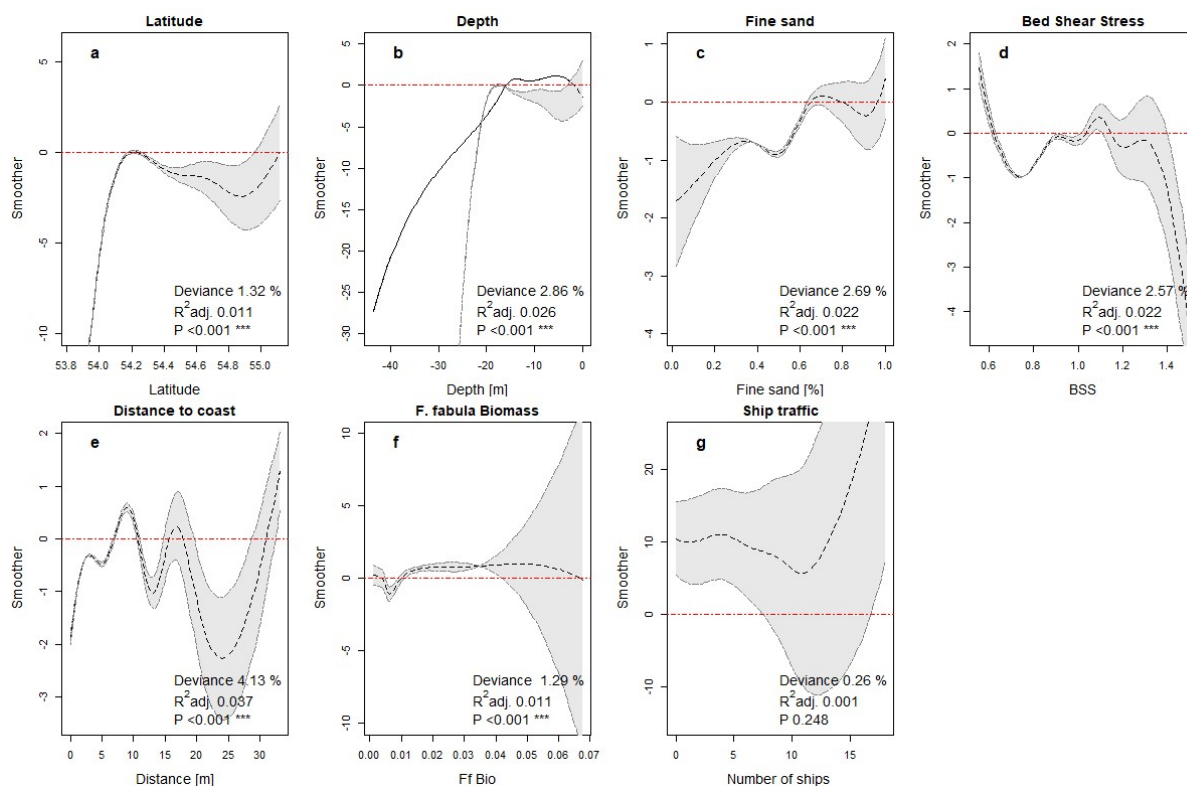
Fig. 8 Smoothing functions of the Zero-inflated Poisson (ZIP) Generalised Additive Model (GAM) with Integrated Nested Laplace Approximation (INLA) for the distribution of Common Scoter during the wintering season including *L. balthica* individuals. Common Scoter abundance was modelled in relation to **(a)** Latitude, **(b)** Depth, **(c)** Fine sand, **(d)** Bed shear stress, **(e)** Distance to coast, **(f)** Abundance, **(g)** Biomass and **(h)** ship traffic. The deviance explained (%), adjusted R^2 and P-value of the Pearson residuals are given for each covariate. The dashed black middle line represents the smooth function estimate. 95 % confidence intervals are given in grey. Note that the y-axes of abundance and biomass values were log-transformed and that fine sand is given as a proportion, not as percentage. **Abu** Abundance · **Bio** Biomass · **BSS** Bed shear stress
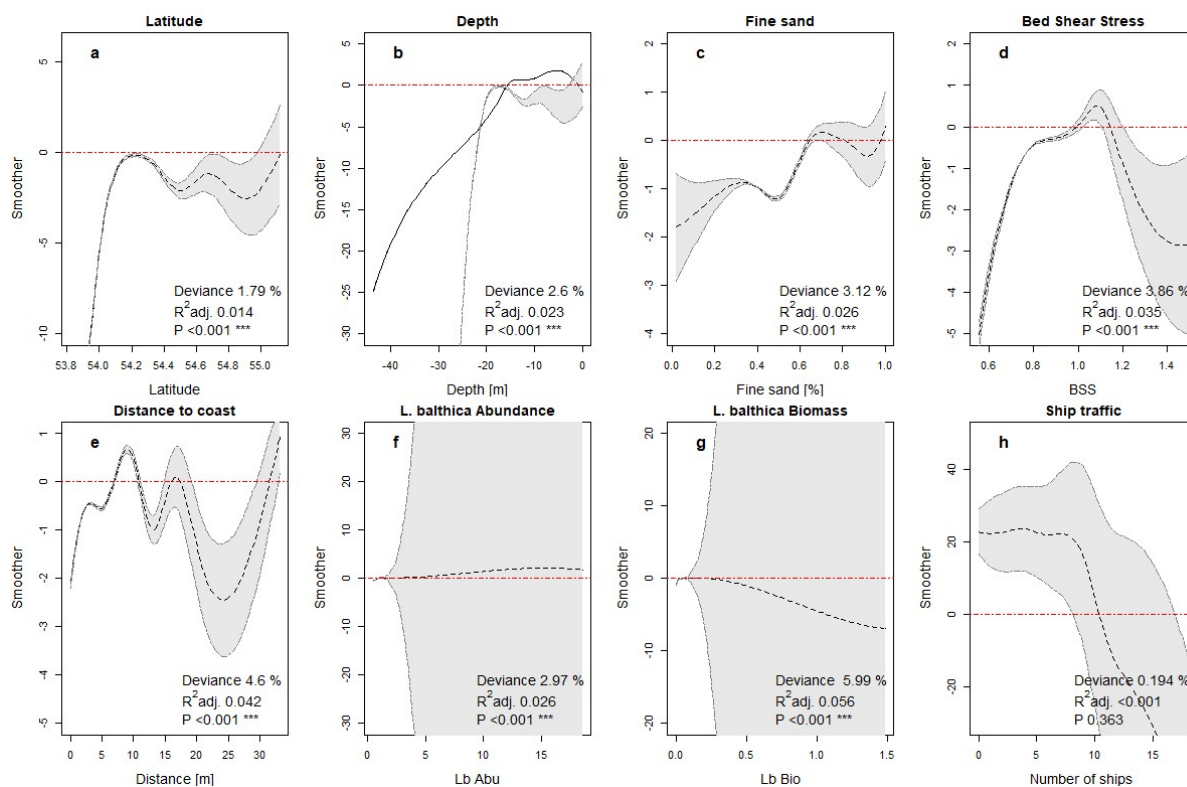
Table 1 Results of the Zero-inflated Poisson (ZIP) Generalised Additive Model (GAM) with Integrated Nested Laplace Approximation (INLA) for the distribution of Common Scoter during the moulting and wintering season. Modelling results with the overall deviance explained and the deviance information criterion (DIC) of the best fitting model are given for **(a)** the moulting and **(b)** the wintering seasons. The mean ± standard deviation (SD) and the 25 % and 97,5 % quantiles are listed as well. As models were distinguished by the selected benthos variable, they have been named accordingly.

a	Dev. Expl. (%)	DIC	Mean ± SD	0.025 Q	0.975 Q
All benthos	11.72	174212.38	0.67 ± 0.001	0.66	0.67
E. leei	8.96	2264.86	0.93 ± 0.002	0.93	0.93
F. fabula	10.42	179341.47	0.52 ± 0.00	0.52	0.53
L. balthica	16.59	174932.87	0.29 ± 0.0002	0.29	0.29

b	Dev. Expl. (%)	DIC	Mean ± SD	0.025 Q	0.975 Q
All benthos	44.17	1691.40	0.90 ± 0.0008	0.90	0.90
E. leei	35.13	1641.14	0.90 ± 0.0001	0.90	0.90
F. fabula	28.17	1692.01	0.90 ± 0.0004	0.90	0.90
L. balthica	52.01	1410.14	0.45 ± 0.001	0.45	0.45

Dev. Expl. Deviance explained · **DIC** Deviance Information Criterion · **SD** Standard deviation · **Q** Quantile

GENERAL DISCUSSION

This thesis aimed at investigating the distribution and habitat selection of the Common Scoter in the eastern German North Sea. Based on previous studies, we already had some insight into their moulting and wintering season distributions in the German North and Baltic Sea, including knowledge regarding potentially preferred locations (Berndt & Busche 1993, Bräger et al. 1995, Garthe et al. 2003, Sonntag et al. 2004/2006, Garthe et al. 2007, Mendel et al. 2008, Markones & Garthe 2011). Moreover, a number of studies had investigated Common Scoter dietary composition and prey items (Madsen 1954, Durinck et al. 1993, Degraer et al. 1999, Fox 2004, Wolf & Meininger 2004, Baptist & Leopold 2009). Two studies had attempted to relate Common Scoter and prey distribution (Kaiser et al. 2006, Schwemmer et al. 2019). Recently, a few studies have investigated scoter dispersal in the eastern German North Sea in connection to environmental parameters (Deppe 2003, Heinänen et al. 2017, Schwemmer et al. 2019). Despite these previous studies illustrating dispersal patterns in German Waters throughout the year, we still lack more detailed knowledge on small scale seasonal and diurnal movement patterns. Since we assume that a species distributes in response to energetic demands and that these vary through the course of the year (both for predators and their prey), spatial and temporal scales need to be matched appropriately (Jones 2001). Therefore, the focus of this thesis was set on closing this gap by studying Common Scoter dispersal patterns and the influence of environmental parameters in relation to seasonal variation on a larger spatial scale.

The results of the current thesis showed that Common Scoters consistently used the eastern German North Sea during their moulting and wintering season (**Chapter I**), thus confirming previous studies (e.g. Berndt & Busche 1993, Garthe et al. 2003/2007, Mendel et al. 2008). They also revealed a recent southbound shift in distribution during both seasons, which to my knowledge has not been reported before (**Chapter I**). Investigating prey characteristics and environmental parameters in a selected moulting and wintering area highlighted that those share some similarities, but they also display distinct differences (**Chapters II, III and V**). These distinctions could be the determining factors when it comes to differences in moulting and wintering distribution. Particularly prominent was the high abundance of a single bivalve species, the invasive alien *E. leei* (**Chapter III**). While it is known from previous studies that this species had successfully settled along the coasts of Schleswig-Holstein (e.g. Dannheim & Rumohr 2012), an abundance as high as it was found during the study period has to my knowledge not been reported before. Compared to other bivalve species found in the same areas, *E. leei* seems to be more profitable due to a higher flesh/shell ratio (**Chapter II**). Combined with its high abundance, this bivalve species thus offers a rich and reliable food resource for Common Scoter. Highest abundances of *E. leei* were detected in the southern part of the study area (one of the core

moulting areas), which might be a potential explanation for the increasing abundances of scoters in this region and thus suggests the importance of this alien bivalve species as a food resource. Examining seasonal distribution patterns of Common Scoter in two contrasting marine systems (the German North and the Danish Baltic Sea) revealed that despite environmental differences, scoters displayed the same dispersal patterns (**Chapter IV**). To my knowledge, this is a new result, which has not been reported so far. While the influence of environmental parameters on Common Scoter distribution has been studied before (Deppe 2003, Kaiser et al. 2006, Schwemmer et al 2019), no attempt has been made to model their distribution on a large spatial scale including seasonal differences. While this thesis demonstrated that a distribution model can be successfully applied, it also highlighted the importance of a matching spatial and temporal scale with data of sufficient spatial and temporal resolution (**Chapter V**).

Each thesis chapter contains a detailed discussion regarding the specific questions they targeted. In the following, key findings and their conclusions, which have not been discussed within the chapters, will be considered in a broader context and in terms of their general application. Particularly the subsequent questions, which have already been established in the introduction, will be addressed:

- Are there spatial and temporal differences in distribution patterns between the moulting and wintering season?
- Can we identify between and within year variations in moulting and wintering dispersal patterns?
- What influence do environmental parameters such as sediment, benthic communities, water depth and water current or anthropogenic activities (e.g. ship traffic) have on the distribution of Common Scoters in the German Bight?
- Do moulting and wintering areas display distinct differences regarding these habitat parameters?

Spatial and temporal variations in distribution patterns

Analysing the long term distribution patterns of Common Scoters in the eastern German North Sea showed that this species consistently utilised the same areas as moulting and wintering grounds. Moreover, they revealed a consistency in dispersal patterns regarding each period. During moult, birds first aggregated in shallowest areas close to the coast and subsequently spread into deeper waters as the winter progressed. These differences in dispersal already give us a hint on preferred habitat characteristics for each season. During moult, Common Scoter apparently select for areas fulfilling their energetic demands while minimising the costs of obtaining prey. As they regrow flight feathers

and are thus flightless during this time, maximising energetic intake rates while simultaneously minimising the costs of acquiring these resources is of particular importance. Moreover, due to their extreme vulnerability, moulting scoters need to minimise disturbance levels as time and energy needed to escape from predators or anthropogenic activities reduce the time and energy available for foraging. During winter, scoters can afford to spent more time and energy on foraging and thus are able to exploit potentially and relatively less profitable resources in deeper waters. Based on the distinct differences in dispersal patterns between moulting and wintering seasons, we can conclude that the choice and utilisation of habitats in the eastern German North Sea are made in response to the specific life-history demands Common Scoters have during each season. As a consequence, since they choose different areas for each period, the provided resources in these regions likely underlie seasonal changes as well.

Investigating the distribution of Common Scoter in the Danish Baltic Sea revealed that this species shows the same dispersal patterns despite distinct differences in both environments. In the German North Sea, scoters reside in tidal, more exposed waters whereas they are located in relatively sheltered regions with restricted tidal influence in the Danish Baltic Sea. Nevertheless, they distribute in similar ways: aggregating in shallow waters close to the coast during moult and spreading to deeper waters further offshore through the course of winter. Based on this result, we can conclude that, independent of the environmental variations between these two contrasting systems, they distribute themselves in order to maximise energy intake rates while minimising the costs of gaining resources. On the basis of these findings, the question arises why Common Scoter spread to deeper waters as the season progresses, if the environmental conditions are favourable to their energetic demands especially during moult. As described in **Chapter IV**, scoters aggregate in dense flocks during the moulting season. Consequently, a large cluster of birds is exploiting food resources in a limited space. Thus, these food resources are potentially depleted with more moulting birds arriving during the summer forcing them to move into deeper waters to feed in other, more profitable areas. Guillemette et al. (1996) have concluded that Common Eiders deplete mussel beds when wintering in the Gulf of Lawrence, which in turn affected their distribution. The findings of the current study highlight that Common Scoters not only disperse in relation to their specific demands. Their distribution is also shaped by the impacts of their choice of habitat.

Despite the long term stable distribution patterns in the eastern German North Sea, slight fluctuations within as well as between areas are not uncommon. They have been reported in previous studies assuming an exchange of individuals between German Waters (movements between North and Baltic Sea) as well as between different North and Baltic Sea regions (fluctuations between Dutch, German or Scandinavian Waters) (Berndt & Busche 1993, Henning & Eskildsen 2001, Sonntag et al. 2004).

Movement shifts can also be assessed on a smaller spatial scale. The data analysed within this thesis suggests a recent shift in dispersal with more birds aggregating in the southern parts of the study area. This apparently is not only true for the moulting, but also for the wintering season. Up until now, it has been stated that moulting and wintering distribution are decisively different (e.g. Mendel et al. 2008, Markones et al. 2011). The findings of this thesis suggest however, that this segregation seems to be subject to fluctuations as well. When analysing the distribution of a species, we should therefore always keep in mind that dispersal patterns are not permanent. Several factors influence habitat selection and thus also the dispersal of a species (i. e. predation risk, type and quality of resources, interactions with or behaviour of conspecifics, Morris 2003). Hence, changes in one of these factors will ultimately result in an adjustment of the distribution pattern (Davoren et al. 2003, Morris 2003). If we want to be able to define appropriate conservation measures and protection strategies for a species, we should therefore pay attention to seasonal variations and their causes (Austin 2002, Hernandez et al. 2006). Most management plans are fixed. Borders of Special Protection Areas for example cannot be changed easily. Moreover, habitat changes are difficult to predict. Nevertheless, the results of this thesis highlight the importance of investigating habitat selection and use in relation to seasonality (preferably using long term data sets). To improve the quality of conservation measures and site-safeguard networks, we need to incorporate seasonal variability in habitat demands, as these will be reflected in seasonally varying distribution patterns (Lambert et al 2017).

Habitat selection – effects of environmental parameters

The comparison of moulting and wintering area characteristics revealed distinct differences particularly in their benthos community structures. Not all bivalve species collected were found at both sites. Moreover, abundances of those species shared between areas were different while their ash-free-dry masses and flesh-to-shell ratios were similar. Relating the findings of the distribution pattern analysis to those results revealed that the most influential factor is likely prey abundance, hence confirming Davoren et al. (2003). This assumption is once again validated, when we look at the potential cause of the recently occurred southbound distribution shifts of Common Scoters. In the southern parts of the eastern German North Sea, the abundance of the American Razor Clam *Ensis leei* has been increasing at least since 2015/2016. Previous studies have already shown that this bivalve species is a profitable prey resource commonly foraged on by Common Scoters (and other seabird species) (Wolf & Meininger 2004, Schwemmer et al. 2019). Apparently, this change in prey condition has been stable enough to support moulting as well as wintering scoters for a longer time. Thus, they continuously aggregated in the south-eastern German North Sea during both periods.

When it comes to analysing distribution patterns in relation to habitat parameters, the current thesis has shown how important it is to match temporal and spatial scales appropriately (Seguardo & Araújo 2004, Hernandez et al. 2006, Wisz et al. 2008). We expect Common Scoters to have different demands during their moulting and wintering phases and these demands should be reflected in their habitat choice. Incorporating this assumption into a habitat model is challenging, especially if some of the selected parameters are rather distinct, while others are quite similar. Identifying the most influential factors is thus not an easy task. However, the first attempt of modelling Common Scoter distribution on a large spatial scale has been partly successful. Base on the results of the habitat models the most decisive environmental parameters for the moulting and the wintering season could be identified. Moreover, including ship traffic as a factor into the analysis showed that the presence of ships has a strong negative impact on scoter distribution particularly during moult. Once again, this emphasizes the importance of low disturbance levels during the moulting season when scoters are most vulnerable.

Recent studies have demonstrated that modelling the distribution of a species and predicting suitable habitats are useful tools for conservation decision making (e.g. Austin 2002, Johnson & Gillingham 2005, Guisan et al. 2013, Lambert et al. 2017, Virgili et al. 2017). Using Species Distribution Models does not only enable us to better understand the ecology of a species in terms of the relation between the distribution and the suitability or quality of a habitat (Johnson &Gillingham 2005). It can also be beneficial for a better connection between scientists and conservation professionals (Guisan et al 2013).

OUTLOOK

The results of this thesis gave us a more detailed insight into the distribution and habitat selection of the Common Scoter in the eastern German North Sea and how these are influenced by seasonality. Nevertheless, several questions remain unanswered.

The biggest challenge of investigating seasonal variation is probably the adequate incorporation of similar (if not identical) temporal and spatial scales. Relating the distribution of Common Scoters to the abundances and distribution patterns of their prey is one example. Scoters disperse across an area of several 1000s of km^2, whereas differences in benthic species distributions can occur on a scale of <1m. While we can visually map the dispersal patterns of both and investigate the contents of stomachs and guts (e.g. Stempniewicz 1986, Durinck et al 1993, Leopold et al. 2007, Schwemmer et al. 2019), this does not provide us with the final evidence that Scoters have actively been feeding in places where they were observed. Long flush distances (Schwemmer et al. 2011, Fliessbach et al 2019) and the fact that Common Scoter occur in areas further offshore (Hennig & Hälterlein 2000) complicate this specie's observation. A possible way of closing this gap in knowledge is the utilisation of gps data loggers recording diving depth. They have successfully been used in Common Eiders (*Somateria mollissima*, Linneaus, 1758) among other species (e.g. Guillemette et al. 2007, Pelletier et al. 2007). Recording time and location of dives would enable us to identify locations where Common Scoters are foraging. As this information could potentially be obtained during the course of the year, more detailed insight into the exploitation of food resources during different seasons could be gathered as well. This would improve our understanding of habitat selection in response to seasonal variations.

We know from previous studies that Common Scoters migrate to German Waters to moult and winter (e.g. Berndt & Busche 1993, Sonntag et al. 2004, Garthe et al. 2007, Mendel et al. 2008). Additionally, we have an overview of the extent of their breeding grounds (e.g. Glutz von Blotzheim & Bauer 1990, Cramp 1994). In case of the German Waters, migration sites with a high number of individuals passing by have been described for several locations (e.g. Berndt & Busche 1993, Nehls & Zöllick 1990, Garthe et al. 2003). However, the origin of these migrating individuals still needs to be verified. Hence, the migration routes taken and thus the interconnectivity between these areas have yet to be investigated. Movements and migrations of sea ducks have already been studied by American researchers to a greater extent mainly by using satellite transmitters (e.g. De La Cruz et al. 2009, Loring et al. 2014), although the effect of these devices are subject to controversial discussions (e.g. Barron et al. 2010, White et al. 2013, Weiser et al. 2016, Geen et al. 2019). The constant advancement of this technology and its concepts opens up new possibilities and can help us further our understanding of how moulting and wintering areas in German Waters are connected to breeding grounds of Common Scoters

(Robinson et al. 2010). Moreover, this would provide us with the possibility to study influences they are subject to during their migration. Combining knowledge on migration routes and habitat selection reflected in distribution patterns will enhance our understanding of Common Scoter ecology and enable us to define and implement suitable future conservation measures.

REFERENCES

Armonies W, Reise K. On the population development of the introduced razor clam Ensis americanus near the island of Sylt (North Sea). Helgoländer Meeresuntersuchungen. 1999; 52(3):291.

Armonies W, Herre E, Sturm M. Effects of the severe winter 1995/96 on the benthic macrofauna of the Wadden Sea and the coastal North Sea near the island of Sylt. Helgoland Marine Research. 1. August 2001; 55(3):170–5.

Asprion U, Sbresny J, Griffel G, Elbracht J. Die Bathymetrie der deutschen Nordsee - Erstellung der projektweiten Bezugsfläche [Internet]. 2013. Verfügbar unter: https://www.gpdn.de/media/1122

Austin MP. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling. November 2002; 157(2–3):101–18.

Austin MP. Chapter 2: Vegetation and environment: discontinuities and continuities. IN VAN DER MAAREL, E.(Ed.) Végétation ecology. Etats-Unis. Blackwell Publishing; 2005.

Austin M. Species distribution models and ecological theory: A critical assessment and some possible new approaches. Ecological Modelling. Januar 2007; 200(1–2):1–19.

AquaNIS Editorial Board (2015) Information system on Aquatic Non-Indigenous and Cryptogenic Species. World Wide Web electronic publication. www.corpi.ku.lt/databases/aquanis. Version 2.36+. Accessed 2018-07-30.

Bakka H, Rue H, Fuglstad G-A, Riebler A, Bolin D, Krainski E, u. a. Spatial modelling with R-INLA: A review. arXiv:180206350 [stat] [Internet]. 18. Februar 2018 [zitiert 5. Juni 2019]; http://arxiv.org/abs/1802.06350

Banks AN, Sanderson WG, Hughes B, Cranswick PA, Smith LE, Whitehead S, u. a. The Sea Empress oil spill (Wales, UK): Effects on Common Scoter Melanitta nigra in Carmarthen Bay and status ten years later. Marine Pollution Bulletin. Mai 2008; 56(5):895–902.

Baptist MJ, Leopold MF. The effects of shoreface nourishments on Spisula and scoters in The Netherlands. Marine Environmental Research. Juli 2009; 68(1):1–11.

Barron DG, Brawn JD, Weatherhead PJ. Meta-analysis of transmitter effects on avian behaviour and ecology: Meta-analysis of avian transmitter effects. Methods in Ecology and Evolution. 15. Februar 2010; 1(2):180–7.

Bautista LM, Alonso JC, Alonso JA (1995) A Field Test of Ideal Free Distribution in Flock-Feeding Common Cranes. J Anim Ecol 64:747–757. https://www.jstor.org/stable/5853.pdf

Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W. Marine invasive alien species: a threat to global biodiversity. Marine Policy. Juli 2003;27(4):313–23.

Berndt RK, Busche G. Vogelwelt Schleswig-Holsteins. Bd. 4: Entenvögel II. Bd. 4. Neumünster: Karl Wachholtz Verlag; 1993.

Bernstein C, Kacelnik A, Krebs Individual Decisions and the Distribution of Predators in a Patchy Environment. II. The Influence of Travel Costs and Structure of the Environment. J Anim Ecol 1991; 60:205–225. https://www.jstor.org/stable/pdf/5455.pdf

Beukema JJ, Knol E, Cadbe GC. Effects of temperature on the length of the growing season in the tellenid bivalve *Macoma balthica* (L.) living on tidal flats in the Dutch Wadden Sea. J. Exp. Mar. Bio. Ecol. 1985; 90, 129-144.

Beukema JJ, Cadée GC, Dekker R, Philippart CJM. Annual and spatial variability in gains of body weight in Macoma balthica (L.): Relationships with food supply and water temperature. Journal of Experimental Marine Biology and Ecology. August 2014; 457:105–12.

Beukema J, Dekker R, Jansen J. Some like it cold: populations of the tellinid bivalve Macoma balthica (L.) suffer in various ways from a warming climate. Marine Ecology Progress Series. 29. Mai 2009; 384:135–45.

Beukema J, Drent J, Honkoop P. Maximizing lifetime egg production in a Wadden Sea population of the tellinid bivalve Macoma balthica: a trade-off between immediate and future reproductive outputs. Marine Ecology Progress Series. 2001; 209:119–29.

BirdLife International (2015) Species factsheet: *Melanitta nigra*. Downloaded from http://www.birdlife.org on 15/06/2015.

BirdLife International (2019) Species factsheet: *Melanitta nigra*. Downloaded from http://www.birdlife.org on 04/02/2019.

Blott SJ, Pye K. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surface Processes and Landforms. Oktober 2001; 26(11):1237–48.

Bräger S, Meißner J, Thie M. Temporal and spatial abundance of wintering Common Eider Somateria mollissima, Long-tailed Duck Clangula hyemalis, and Common Scoter Melanitta nigra in shallow water areas of the southwestern Baltic Sea. Ornis Fennica. 1995; 72:11.

Buchanan JB. Sediment analysis. In: Methods for the Study of Marine Benthos [Internet]. 1984 [zitiert 24. Juli 2018]. S. 41–63. Verfügbar unter: https://ci.nii.ac.jp/naid/10029032784/

Buckland ST, Rexstad EA, Marques TA, Oedekoven CS. Distance sampling: methods and applications. Springer; 2015. 277 S.

Cadee GC (2001) Herring gulls learn to feed on a recent invader in the Dutch Wadden Sea, the Pacific Oyster Crassostrea gigas. Basteria 65(1-3):33-42. http://natuurtijdschriften.nl/download?type=document&docid=643840

Camphuysen CJ, Fox AD, Leopold MF, Petersen IK. Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the U.K. COWRIE-Report BAM-02-2002. 2004. Royal Netherlands Institute for Sea Research, Texel

Camphuysen KC, Garthe S. Recording foraging seabirds at sea standardised recording and coding of foraging behaviour and multi-species foraging associations. Atlantic Seabirds. 2004; 6(1):1–32.

Cosel R, Dörjes J, Mühlenhardt-Siegel U. Die amerikanische Schwertmuschel Ensis directus (Conrad) in der Deutschen Bucht: I. Zoogeographie und Taxonomie im Vergleich mit den einheimischen Schwertmuschel-Arten = The american jackknife clam Ensis directus (Conrad) in the German Bight: I. Zoogeography and taxonomy in comparison with the native jackknife and razor clams. Senckenbergiana Maritima: wissenschaftliche Mitteilungen der Senckenbergischen naturforschenden Gesellschaft [Internet]. 1982 [zitiert 30. Juli 2018]; (3–4). Verfügbar unter: http://www.vliz.be/en/imis?refid=115578

Cramp S, Herausgeber. Ostrich to ducks. Reprinted. Oxford: Oxford Univ. Press; 1994. 722 S. (Handbook of the birds of Europe, the Middle East and North Africa).

Croy MI, Hughes RN. The role of learning and memory in the feeding behaviour of the fifteen-spined stickleback, Spinachia spinachia L. Animal Behaviour. 1991; 41(1):149–159.

Dannheim J. Zur Biologie von Ensis directus und Spisula solida (Mollusca: Bivalvia) in den Küstengewässern der östlichen Nordsee [Internet] [diplom]. Institut für Meereskunde, Universität Kiel; 2002 [zitiert 20. Juli 2018]. Verfügbar unter: http://epic.awi.de/14508/

Dannheim J, Rumohr H. The fate of an immigrant: Ensis directus in the eastern German Bight. Helgoland Marine Research. September 2012; 66(3):307–17.

Davoren G, Montevecchi W, Anderson J. Scale-dependent associations of predators and prey: constraints imposed by flightlessness of common murres. Marine Ecology Progress Series. 2002; 245:259–72.

Davoren G, Montevecchi W, Anderson J. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. Marine Ecology Progress Series. 2003; 256:229–42.

De Caceres M, Legendre P. Associations between species and groups of sites: indices and statistical inference. Ecology, 2009; URL http://sites.google.com/site/miqueldecaceres/

Degraer S, Vincx M, Meire P, Offringa H. The macrozoobenthos of an important wintering area of the common scoter (Melanitta nigra). Journal of the Marine Biological Association of the UK. April 1999; 79(2):243–51.

Dekker R, Beukema JJ. Long-term dynamics and productivity of a successful invader: The first three decades of the bivalve Ensis directus in the western Wadden Sea. Journal of Sea Research. Juli 2012; 71:31–40.

Deppe L. Die Trauerente (Melanitta nigra) in der deutschen Bucht–GIS-basierte Bewertung räumlicher und zeitlicher Parameter. Dipl-Arbeit, Universität Hamburg. 2003

De La Cruz SEW, Takekawa JY, Wilson MT, Nysewander DR, Evenson JR, Esler D, u. a. Spring migration routes and chronology of surf scoters (Melanitta perspicillata): a synthesis of Pacific coast studies. Canadian Journal of Zoology. November 2009; 87(11):1069–86.

Durinck J, Christensen KD, Skov H, Danielsen F. Diet of the Common Scoter Melanitta nigra and Velvet Scoter Melanitta fusca wintering in the North Sea. 1993; 70:4.

Ellingsen K. Soft-sediment benthic biodiversity on the continental shelf in relation to environmental variability. Marine Ecology Progress Series. 2002; 232:15–27.

Environmental Systems Research Institute (ESRI), 2013. ArcGIS Desktop Release Version 10.2.1, https://www.esri.com/de-de/arcgis/about-arcgis/overview

Fijn RC, Leopold MF, Dirksen S, Arts F, Asch M van, Baptist MJ, u. a. Een onverwachte concentratie van Zwarte Zee-eenden in de Hollandse kustzone in een gebied met hoge dichtheden van geschikte schelpdieren. Limosa. 2017; 90(3):97–117.

Fliessbach KL, Borkenhagen K, Guse N, Markones N, Schwemmer P, Garthe S. A Ship Traffic Disturbance Vulnerability Index for Northwest European Seabirds as a Tool for Marine Spatial Planning. Front Mar Sci. 11. April 2019; 6:192. https://www.frontiersin.org/article/10.3389/fmars.2019.00192/full

Fox AD. Diet and habitat use of scoters Melanitta in the Western Palearctic - a brief overview. Wildfowl. 2004; 54:163–82.

Fox AD, Hartmann P, Petersen IbK. Changes in body mass and organ size during remigial moult in common scoter Melanitta nigra. Journal of Avian Biology. 2008; 39:35-40.

Fox AD, Kottsieper J, Petersen IK, Markones N, Schwemmer P, Garthe S Large-scale depth-related sesonal dispersal patterns of a benthic-feeding sea duck in two contrasting marine systems. Submitted to: Marine Ecological Progress Series *under review*

Fretwell SD. On territorial behavior and other factors influencing habitat distribution in birds. Acta biotheoretica. 1969; 19(1):45–52.

Freudendahl AS, Jensen KT. Population dynamics of the American razor clam (Ensis americanus) at Horns Rev. Report by University of Aarhus, Department of Marine Ecology for Energi2. 2006;

Freudendahl ASL, Nielsen MM, Jensen T, Jensen KT. The introduced clam Ensis americanus in the Wadden Sea: field experiment on impact of bird predation and tidal level on survival and growth. Helgoland Marine Research. Juni 2010; 64(2):93–100.

Garthe S. Verteilungsmuster und Bestände von Seevögeln in der Ausschließlichen Wirtschaftszone (AWZ) der deutschen Nord- und Ostsee und Fachvorschläge für EU-Vogelschutzgebiete. 2003; 43.

Garthe S, Hüppop O, Weichler T. Anleitung zur Erfassung von Seevögeln auf See von Schiffen. Seevögel.

2002; 23(2):47–55.

Garthe S, Sonntag N, Schwemmer P, Dierschke V. Estimation of seabird numbers in the German North Sea throughout the annual cycle and their biogeographic importance. 2007; 16.

Geen GR, Robinson RA, Baillie SR. Effects of tracking devices on individual birds–a review of the evidence. Journal of Avian Biology. 2019; 50(2).

Glutz von Blotzheim UN, Bauer KN. Handbuch der Vögel Mitteleuropas. 2., durchges. Aufl. Wiesbaden: Aula-Verl; 1990. 534 S. (Handbuch der Vögel Mitteleuropas Anseriformes Teil 1; Bd. 2).

Gollasch S. Overview on introduced aquatic species in European navigational and adjacent waters. Helgoland Marine Research. Mai 2006; 60(2):84–9.

Gollasch S, Kerckhof F, Craeymeersch J, Goulletquer P, Jensen K, Jelmert A, u. a. Alien Species Alert: Ensis directus. Current statuts of invasions by the marine bivalve Ensis directus. ICES Cooperative Research Report. 1. Januar 2015; (323):1–36.

Gosling EM (2015) Marine bivalve molluscs, Second edition. Wiley Blackwell, Chichester, West Sussex, UK ; Hoboken, NJ, USA

Goss-Custard JD (1980) Competition for food and interference amongst waders. Ardea 68:31–52. https://doi.org/10.5253/arde.v68.p31

Gray JS, Elliott M. Ecology of Marine Sediments: From Science to Management. Oxford University Press; 2009. 249 S.

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG. The impacts of a nonindigenous marine predator in aCalifornia Bay. Ecology. Mai 2000; 81(5):1206–24.

Guillemette M, Himmelman JH, Reed A. Availability and consumption of food by common eiders wintering in the Gulf of St. Lawrence: evidence of prey depletion. Can J Zool. Januar 1996; 74(1):32–8.

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, u. a. Predicting species distributions for conservation decisions. Ecology Letters. 2013; 16(12):1424–35.

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, u. a. A Global Map of Human Impact on Marine Ecosystems. Science. 15. Februar 2008; 319(5865):948–52.

Harper DGC. Competitive foraging in mallards: "Ideal free' ducks. Animal Behaviour. 1. Mai 1982; 30(2):575–84.

Havard R, Martino S, Chopin N. Approximate Bayesian Inference for Latent Gaussian Models Using Integrated Nested Laplace Approximations (with discussion). Journal of the Royal Statistical Society B, 2009; 71, 319-392

Heinänen S, Žydelis R, Dorsch M, Nehls G, Skov H. High-resolution sea duck distribution modeling: Relating aerial and ship survey data to food resources, anthropogenic pressures, and topographic variables. The Condor. Mai 2017; 119(2):175–90.

Hennig V, Eskildsen K. Notwendigkeit ungestörter Mausergebiete für die Trauerente (Melanitta nigra). Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer (Eds): Wattenmeermonitoring. 2001; 70–71.

Hennig V, Hälterlein B. Trauerente–Erfassungsschwierigkeiten einer Offshore-Vogelart. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer (Eds): Wattenmeermonitoring. 2000;20–23.

Hernandez PA, Graham CH, Master LL, Albert DL. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography. 2006; 29(5):773–85.

Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can Entomol 91:293–320.

Holm TE, Clausen P, Nielsen RD, Bregnballe T, Petersen IK, Mikkelsen P, Bladt J (2018) *Fugle 2018 NOVANA.* Research report from Aarhus University/Danish Centre for the Environment and Energy, Aarhus, Denmark. (In Danish). Accessible at: http://dce2.au.dk/pub/SR261.pdf

Honkoop PJC, Beukema JJ. Loss of body mass in winter in three intertidal bivalve species: an experimental and observational study of the interacting effects between water temperature, feeding time and feeding behaviour. Journal of Experimental Marine Biology and Ecology. Mai 1997; 212(2):277–97.

Horne JK, Schneider DC. Lack of spatial coherence of predators with prey: a bioenergetic explanation for Atlantic cod feeding on capelin. Journal of Fish Biology. 1994; 45:191–207.

Houziaux JS, Craeymeersch JAM, Merckx B, Kerckhof F, Van Lancker V, Courtens W, u. a. EnSIS-Ecosystem Sensivity to Invasive Species. Belgian Science Policy; 2011.

Johnson CJ, Gillingham MP. An evaluation of mapped species distribution models used for conservation planning. Environmental Conservation. Juni 2005; 32(2):117–28.

Johnson DH. The comparison of usage and availability measurements for evaluating resource preference. Ecology. 1980; 61(1):65–71.

Jones J. Habitat Selection Studies in Avian Ecology: A Critical Review. The Auk. 2001; 118(2):557.

Kaiser MJ, Galanidi M, Showler DA, Elliott AJ, Caldow RWG, Rees EIS, u. a. Distribution and behaviour of Common Scoter Melanitta nigra relative to prey resources and environmental parameters. Ibis. 148(s1):110–28.

Karsten Reise, Stephan Gollasch, Wolff WJ. Introduced marine species of the North Sea coasts. Helgoländer Meeresuntersuchungen. 1978; 52:219–34.

Kear J, Herausgeber. Ducks, geese and swans. Vol. 2: Species accounts (Cairina to Mergus). Oxford: Oxford Univ. Pr; 2005. 447 S. (Bird families of the world).

Kenchington E, Duggan R, Riddell T. Early Life History Characteristics of the Razor Clam, Ensis Directus, and the Moonsnails, Euspira Spp., with Applications to Fisheries and Aquaculture. Department of Fisheries & Oceans, Science Branch, Maritimes Region, Invertebrate Fisheries Division, Bedford Institute of Oceanography; 1998.

Kight CR, Swaddle JP. Associations of anthropogenic activity and disturbance with fitness metrics of eastern bluebirds (Sialia sialis). Biological Conservation. 2007; 138(1–2):189–97.

Kösters F, Winter C. Exploring German Bight coastal morphodynamics based on modelled bed shear stress. Geo-Marine Letters. Februar 2014; 34(1):21–36.

Kottsieper J, Schückel U, Schwemmer P, Fox AD, Garthe S. 2019. Comparison of bivalve communities between moulting and wintering areas used by Common Scoter Melanitta nigra in the German North Sea. Estuarine, Coastal and Shelf Science, 229. https://doi.org/10.1016/j.ecss.2019.106398

Kottsieper J, Schwemmer P, Markones N, Fox AD, Garthe S (2019) An invasive alien bivalve apparently provides a novel food source for moulting and wintering benthic feeding sea ducks. Helgoland Marine Research 73 (1)

Kramer KJ, Brockmann UH, Warwick RM. Manual of sampling and analytical procedures for tidal estuaries. TNO Institute of Environmental Sciences, Laboratory of Applied Research; 1992.

Krause J, Wollny-Goerke K, Boller F, Hauswirth M, Heinicke K, Herrmann C, u. a. The German marine protected areas in the North Sea and Baltic Sea. Natur und Landschaft. 2011; 86(9):397.

Kröncke I, Reiss H, Eggleton JD, Aldridge J, Bergman MJN, Cochrane S, Craeymeersch JA, Degraer S, Desroy N, Dewarumez JM, Duineveld GCA, Essink K, Hillewaert H, Lavaleye MSS, Moll A, Nehring S, Newell R, Oug E, Pohlmann T, Rachor E, Robertson M, Rumohr H, Schratzberger M, Smith R, Berghe EV, van Dalfsen J, van Hoey G, Vincx M, Willems W, Rees HL. Changes in North Sea macrofauna communities and species distribution between 1986 and 2000. Estuarine, Coastal and Shelf Science. Juli 2011;

94(1):1–15.

Kunitzer A, Basford D, Craeymeersch JA, Dewarumez JM, Dorjes J, Duineveld GCA, Eleftheriou A, Heip C, Herman P, Kingston P, Niermann U, Rachor E, Rumohr H, de Wilde PAJ. The benthic infauna of the North Sea: species distribution and assemblages. ICES Journal of Marine Science. 1. Mai 1992;49(2):127–43.

Lambert C, Virgili A, Pettex E, Delavenne J, Toison V, Blanck A, Ridoux V. Habitat modelling predictions highlight seasonal relevance of Marine Protected Areas for marine megafauna. Deep Sea Research Part II: Topical Studies in Oceanography. Juli 2017; 141:262–74.

Latimer AM, Wu S, Gelfand AE, Silander Jr. JA. Building Statistical Models To Analyze Species Distributions. Ecological Applications. Februar 2006; 16(1):33–50.

Leopold MF, Wolf P. Zee-eenden eten ook Ensis. Nieuwsbrief Nederlandse Zeevogelgroep. 2003; 4(3):5.

Leopold MF, Spannenburg PC, Verdaat HJP, Kats RKH. Identification and size estimation of Spisula subtruncata and Ensis americanus from shell fragments in stomachs and faeces of Common Eiders Somateria mollissima and Common Scoters Melanitta nigra. Atlantic Seabirds. 2007;24.

Loring PH, Paton PWC, Osenkowski JE, Gilliland SG, Savard J-PL, Mcwilliams SR. Habitat use and selection of black scoters in southern New England and siting of offshore wind energy facilities: Black Scoters and Offshore Wind. The Journal of Wildlife Management. Mai 2014; 78(4):645–56.

Lovvorn JR. Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks. Hydrobiologia 1994; 278/279:223–233. https://link.springer.com/content/pdf/10.1007/BF00027856.pdf

Lovvorn JR, Gillingham MP. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. Ecology 1996; 77:435–451. https://www.jstor.org/stable/pdf/2265620.pdf

Lovvorn JR, Jones DR. Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.). Can J Zool 1991; 69:2879–2887. https://www.nrcresearchpress.com/doi/pdfplus/10.1139/z91-406

Lovvorn JR, Jones DR, Blake WR. Mechanics of underwater locomotion in diving ducks: drag, buoyancy and acceleration in a size gradient of species. J Exp Biol 1991; 159:89–108. http://jeb.biologists.org/content/jexbio/159/1/89.full.pdf

MacArthur RH, Pianka ER. On Optimal Use of a Patchy Environment. The American Naturalist. 1. November 1966; 100(916):603–9.

Madsen FJ. On the food habits of the diving ducks in Denmark. 1954; 157–266 S. (Danish Review of Game Biology).

Margaritis D, Schückel U, Kottsieper J, Eskildsen K, Scheu S. 2019. Comparison of trophic structure and function of different food webs in the subtidal of the Wadden Sea by using Ecological Network Analysis. Estuar. Coast. Shelf Sci. *Under review*

Markones N, Garthe S. Monitoring von Seevögeln im Offshore-Bereich der schleswig-holsteini-schen Nordsee im Rahmen von NATURA 2000 in den Jahren 2004 bis 2009. Corax. 1. Januar 2011; 22:11–50.

Martinez Arbizu, P., 2017. pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.0.1. https://github.com/pmartinezarbizu/pairwiseAdonis

Meissner J, Bräger S. The feeding ecology of wintering eiders Somateria mollissima and common scoters Melanitta nigra on the Baltic Sea coast of Schleswig-Holstein, FRG. Wader study group bulletin. 1990; 58:10–12.

Mendel B, Sonntag N, Wahl J, Schwemmer P, Dries H, Guse N, u. a. Artensteckbriefe von See-und

Wasservögeln der deutschen Nord-und Ostsee: Verbreitung, Ökologie und Empflindlichkeiten gegenüber Eingriffen in ihren marinen Lebensraum. Bonn - Bad Godesberg: Bundesamt f. Naturschutz; 2008. (Naturschutz und Biologische Vielfalt; Bd. 59).

Mendel B, Sonntag N, Wahl J, Schwemmer P, Dries H, Guse N, u. a. Profiles of seabirds and waterbirds of the German North and Baltic Seas: Distribution, ecology and sensitivities to human activities within the marine enviroment. Bonn - Bad Godesberg: Bundesamt f. Naturschutz; 2008. (Naturschutz und Biologische Vielfalt; Bd. 61).

Molnar JL, Gamboa RL, Revenga C, Spalding MD. Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment. November 2008; 6(9):485–92.

Morris DW. Toward an ecological synthesis: a case for habitat selection. Oecologia. 1. Juni 2003; 136(1):1–13.

Naimi B, Hamm NAS, Groen TA, Skidmore AK, Toxopeus AG. Where is positional uncertainty a problem for species distribution modelling? Ecography. Februar 2014; 37(2):191–203.

Nehls G. Bestand und Verbreitung der Trauerente Melanitta nigra im Bereich des Schleswig-Holsteinischen Wattenmeeres. Seevögel. 1998; 19:19–22.

Nehls HW, Zöllick H. The moult migration of the Common Scoter (Melanitta nigra) off the coast of the GDR. Baltic Birds. 1990; 5(2):36–46.

Nehring S. Biological Invasions into German Waters: An Evaluation of the Importance of Different Human-Mediated Vectors for Nonindigenous Macrozoobenthic Species. In: Invasive Aquatic Species of Europe Distribution, Impacts and Management [Internet]. Springer, Dordrecht; 2002 [zitiert 30. Juli 2018]. S. 373–83. Verfügbar unter: https://link.springer.com/chapter/10.1007/978-94-015-9956-6_38

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2018. vegan: Community Ecology Package. R package version 2.5-2. https://CRAN.R-project.org/package=vegan

Orians GH, Wittenberger JF. Spatial and temporal scales in habitat selection. The American Naturalist. 1991; 137: S29–S49.

Pearman PB, Guisan A, Broennimann O, Randin CF. Niche dynamics in space and time. Trends in Ecology & Evolution. März 2008; 23(3):149–58.

Pelletier D, Guillemette M, Grandbois JM, Butler PJ. It is time to move: linking flight and foraging behaviour in a diving bird. Biology Letters. 22. August 2007; 3(4):357–9.

Peters, G., 2018. userfriendlyscience: Quantitative analysis made accessible, R package version 0.7.1, <URL: https://userfriendlyscience.com>, URL: http://doi.org/10.17605/osf.io/txequ.

Petersen IK, Fox AD, Clausager I (2003) Distribution and numbers of birds in Kattegat in relation to the proposed offshore wind farm south of Læsø - Ornithological impact assessment. Report to Elsam Engineering A/S. National Environmental Research Institute, Kalø, Denmark.

Piersma T, van Gils J, De Goeij P, van der Meer J (1995) Holling's Functional Response Model as a Tool to Link the Food-Finding Mechanism of a Probing Shorebird with its Spatial Distribution. J Anim Ecol 64:493–504. https://www.jstor.org/stable/pdf/5652.pdf

Pihl S, Holm TE, Clausen P, Petersen IK, Nielsen RD, Laursen K, Bregnballe T, Søgaard B (2015) Fugle 2012-2013 NOVANA. Videnskabelig Rapport 125 fra DCE-Nationalt Center for Mijø og Energi. Aarhus Universitet, Denmark.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rachor E, Nehmer P. Erfassung und Bewertung ökologisch wertvoller Lebensräume in der Nordsee. BfN;

2003 S. 175.

Reise K. Tidal flat ecology: an experimental approach to species interactions. Bd. 54. Springer Science & Business Media; 2012.

Reiss H, Greenstreet S, Sieben K, Ehrich S, Piet G, Quirijns F, u. a. Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. Marine Ecology Progress Series. 18. November 2009; 394:201–13.

Reiss H, Kröncke I. Seasonal variability of infaunal community structures in three areas of the North Sea under different environmental conditions. Estuarine, Coastal and Shelf Science. Oktober 2005; 65(1–2):253–74.

Riddington R, Hassall M, Lane SJ, Turner PA, Walters R. The impact of disturbance on the behaviour and energy budgets of Brent Geese Branta b. bernicla. Bird Study. 1. November 1996;43(3):269–79.

Robinson JA, Pollitt MS. Sources and extent of human disturbance to waterbirds in the UK: an analysis of Wetland Bird Survey data, 1995/96 to 1998/99. Bird Study. November 2002; 49(3):205–11.

Robinson WD, Bowlin MS, Bisson I, Shamoun-Baranes J, Thorup K, Diehl RH, u. a. Integrating concepts and technologies to advance the study of bird migration. Frontiers in Ecology and the Environment. September 2010; 8(7):354–61.

Rodriguez LF. Can Invasive Species Facilitate Native Species? Evidence of How, When, and Why These Impacts Occur. Biol Invasions. Juni 2006; 8(4):927–39.

Rue H, Martino S, Chopin N. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society: Series B (Statistical Methodology). 2009; 71(2):319–92.

Rue H, Riebler A, Sørbye SH, Illian JB, Simpson DP, Lindgren FK. Bayesian Computing with INLA: A Review. arXiv:160400860 [stat] [Internet]. 4. April 2016 [zitiert 5. Juni 2019]; Verfügbar unter: http://arxiv.org/abs/1604.00860

Sadykova D, Scott BE, De Dominicis M, Wakelin SL, Sadykov A, Wolf J. Bayesian joint models with INLA exploring marine mobile predator–prey and competitor species habitat overlap. Ecology and Evolution. Juli 2017; 7(14):5212–26.

Sarkar D. Lattice: Multivariate Data Visualization with R, Springer, 2008. ISBN: 978-0-387-75968-5. http://lmdvr.r-forge.r-project.org/

Salewski V, Bruderer B. The evolution of bird migration—a synthesis. Naturwissenschaften. 20. März 2007; 94(4):268–79.

Schwemmer P, Mendel B, Sonntag N, Dierschke V, Garthe S. Effects of ship traffic on seabirds in offshore waters: implications for marine conservation and spatial planning. Ecological Applications. 2011; 21(5):1851–60.

Schwemmer P, Volmer H, Enners L, Reimers H-C, Binder K, Horn S, u. a. Modelling distribution of common scoter (Melanitta nigra) by its predominant prey, the American razor clam (Ensis leei) and hydrodynamic parameters. Estuarine, Coastal and Shelf Science. 30. September 2019(a); 225

Schwemmer P, Adler S, Enners L, Volmer H, Kottsieper J, Ricklefs K, Stage M, Schwarzer K, Wittbrodt K, Reimers HC, Binder K, Asmus R, Asmus H, Horn S, Schückel U, Kohlus J, Eskildsen K, Klingbeil K, Gräwe U, Garthe S. Modelling and predicting habitats for the neobiotic American Razor Clam Ensis leii in the Wadden Sea. Estuarine, Coastal and Shelf Science 2019 (b); 231:

Segurado P, Araújo MB. An evaluation of methods for modelling species distributions: Methods for modelling species distributions. Journal of Biogeography. 13. September 2004; 31(10):1555–68.

Shannon C, Weaver W (1964) The Mathematical Theory of Communication. University of Illinois, Urbana, USA.

Skov H, Durinck J, Erichsen A, Kloster RM, Møhlenberg F, Leonhard SB. Horns Rev II Offshore Wind Farm Food Basis for Common Scoter: Baseline Studies 2007-08. Final Report by Orbicon/DHI/Marine Observers to DONG Energy A/S, Copenhagen; 2008.

Sonntag N, Engelhard O, Garthe S. Sommer- und Mauservorkommen von Trauerenten Melanitta nigra und Samtenten M. fusca auf der Oderbank (südliche Ostsee). Vogelwelt. 2004; 125:77–82.

Sonntag N, Mendel B, Garthe S. Die Verbreitung von See-und Wasservogeln in der deutschen Ostsee im Jahresverlauf. Vogelwarte. 2006; 44(2):81.

Spalke J, Diederichs A, Rassmus J, Dorsch M, Brandt MJ, Pieper V, Nehls G. Fachliche Vorschläge für ein Management der Trauerente an der schleswig-holsteinischen Nordseeküste. Im Auftrag des Landesbetriebs für Küstenschutz, Nationalpark und Meeresschutz. Created by BioConsult SH, Husum & GFN, Kiel 2013

Spalke J, Diederichs A, Grünkorn T, Rassmus J, Nehls G. Trauerenten (Melanitta nigra) an der schleswig-holsteinischen Nordseeküste. Corax. 2014; 22(Sonderheft 1):12.

Stempniewicz L. The food intake of two Scoters Melanitta fusca and M. nigra wintering in the Gulf of Gdańsk, Polish Baltic coast. V\a ar F\a agelv, Suppl. 1986; 11:211–214.

Stephens DW, Krebs JR. *Foraging theory*. University Press, Princeton, USA 1986

Troost K, Perdon KJ, Zwol J van, Jol J, Asch M van. Schelpdierbestanden in de Nederlandse kustzone in 2017 [Internet]. IJmuiden: Stichting Wageningen Research, Centrum voor Visserijonderzoek (CVO); 2017 [zitiert 20. Juli 2018] S. Report No.: 17.014. https://library.wur.nl/WebQuery/wurpubs/526296

Tulp I, Craeymeersch J, Leopold M, van Damme C, Fey F, Verdaat H. The role of the invasive bivalve Ensis directus as food source for fish and birds in the Dutch coastal zone. Estuarine, Coastal and Shelf Science. Dezember 2010; 90(3):116–28.

Virgili A, Lambert C, Pettex E, Dorémus G, Van Canneyt O, Ridoux V. Predicting seasonal variations in coastal seabird habitats in the English Channel and the Bay of Biscay. Deep Sea Research Part II: Topical Studies in Oceanography. Juli 2017; 141:212–23.

Warton DI, Wright TW, Wang Y. Distance-based multivariate analyses confound location and dispersion effects. *Methods Ecol. Evol* 2012; 3, 89–101.

Weiser EL, Lanctot RB, Brown SC, Alves JA, Battley PF, Bentzen R, u. a. Effects of geolocators on hatching success, return rates, breeding movements, and change in body mass in 16 species of Arctic-breeding shorebirds. Movement Ecology [Internet]. Dezember 2016 [zitiert 20. Juli 2018]; 4(1). http://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-016-0077-6

Werner S, Mortl M, Bauer H-G, Rothhaupt K-O. Strong impact of wintering waterbirds on zebra mussel (Dreissena polymorpha) populations at Lake Constance, Germany. Freshwater Biol. August 2005; 50(8):1412–26.

White CR, Cassey P, Schimpf NG, Halsey LG, Green JA, Portugal SJ. Implantation reduces the negative effects of bio-logging devices on birds. Journal of Experimental Biology. 15. Februar 2013; 216(4):537–42.

Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A. Effects of sample size on the performance of species distribution models. Diversity and Distributions. 2008; 14(5):763–73.

Wood, SN. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 2011; 73(1):3-36

Wolf P, Meininger PL. Meer zeevogels met kleurafwijkingen. 2004; http://natuurtijdschriften.nl/download?type=document;docid=557430

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. Mixed effects models and extensions in ecology with R. New York, NY: Spring Science and Business Media. 2009

Zuur AF, Ieno EN, Elphick CS. A protocol for data exploration to avoid common statistical problems. Methods

in Ecology and Evolution. 2010; 1(1):3–14.

ERKLÄRUNG

Hiermit erkläre ich, dass die vorliegende Abhandlung – abgesehen von der Beratung durch meine Betreuer – nach Inhalt und Form meine eigene Arbeit ist. Die vorliegende Arbeit hat weder ganz noch zum Teil einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegen. Sie wurde ebenfalls weder veröffentlicht, noch zur Veröffentlichung eingereicht.

Die vorliegende Arbeit ist unter Einhaltung der Regeln guter wissenschaftlicher Praxis der Deutschen Forschungsgemeinschaft entstanden.

Mir wurde kein akademischer Grad entzogen.

Büsum, den 22.12.2020

Johanna Kottsieper

とうだいもとくらし。