Schlussbericht

DIVER

Deutsche Telemetriestudie an Seevögeln im Bereich geplanter Offshore Windparks am Beispiel der Seetaucher

German tracking study of seabirds in areas of planned Offshore Wind Farms at the example of divers

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Authors:

BioConsult SH:	Monika Dorsch, Claudia Burger, Alexander Schubert, Georg Nehls
JLU:	Birgit Kleinschmidt, Petra Quillfeldt
DHI:	Stefan Heinänen
Ornitela:	Ramūnas Žydelis
Klaipèda University:	Julius Morkūnas

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The project DIVER ‚Deutsche Telemetriestudie an Seevögeln im Bereich geplanter Offshore Windparks am Beispiel der Seetaucher‘ (German tracking study of seabirds in areas of planned Offshore Wind Farms at the example of divers) is a joint research project between BioConsult SH GmbH & Co. KG and Justus Liebig University of Gießen (JLU, Department Animal Ecology and Systematics, Research Group Behavioural Ecology and Ecophysiology) and DHI, Ornitela and DVM Julius Morkūnas as subcontracting partners.

Project partners:

BioConsult SH GmbH & Co. KG
Dr. Georg Nehls (project manager)
Schobüller Straße 36
D-25813 Husum
Germany

Tel: +49 4841 6632911
Fax: +49 4841 6632919
Email: g.nehls@bioconsult-sh.de

Justus Liebig University of Gießen (JLU)
Department Animal Ecology and
Systematics, Research Group Behavioural
Ecology and Ecophysiology
Prof. Dr. Petra Quillfeldt
Heinrich-Buff-Ring 38
D-35392 Gießen
Germany

Tel: +49 641 9935770
Email: Petra.Quillfeldt@bio.uni-giessen.de

Project subcontractors:

DHI
Dr. Stefan Heinänen
Agern Allé 5
DK-2970 Hørsholm
Denmark

Tel: +45 4516 9200
Email: she@dhigroup.com
Current email: stefan.heinanen@novia.fi

Ornitela, UAB
Dr. Ramūnas Žydelis
Švitrigailos g. 11K–109
LT-03228 Vilnius
Lithuania

Tel: +370 685 62327
Email: zydelis@ornitela.eu

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Co-authors are listed in alphabetical order. The order does not reflect the author‘s contribution to the study.

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Specific contributions are further acknowledged in the report chapters.

CONTENTS

List of figures

List of tables

1 ENGLISH SUMMARY

Red-throated divers are among the most sensitive waterbird species with regard to disturbances from anthropogenic activities. Preferred wintering and staging areas of the species in the relatively shallow coastal waters of the eastern German Bight are also used for anthropogenic activities, such as shipping, fishing and recently also offshore wind farms (OWFs). Investigations at existing OWFs have shown that there is a high potential for conflicts between wind farms and divers. The DIVER project was initiated to fill relevant knowledge gaps and to evaluate the impacts of OWFs on red-throated divers by studying the seasonal movements and habitat use of birds tagged with implantable satellite transmitters in the main diver distribution area in the German North Sea. The analysis of tracking data in the core study area was supplemented by analyses of digital aerial survey data and studying diver winter diet from faecal samples by using state of the art genetic methods.

Red-throated diver tracking data revealed that birds using the eastern German Bight in late winter and spring originate from a large range of breeding areas, including West-Greenland, East-Greenland, Norway, Svalbard and (the majority of the birds) Northern Russia (European and Siberian part). Temporal and spatial movement patterns of tagged divers showed a high variability among individuals, but individual divers used the same routes and general staging, moulting and wintering areas in consecutive years with some flexibility regarding routes and the use of areas at small scale. Red-throated divers were very mobile in their wintering area, which is reflected in large winter home ranges. Movements during winter varied among individuals, ranging from birds staying within a relatively small area for the entire wintering period, to others almost continuously moving between different wintering sites. Individual winter home ranges included different areas in the eastern German Bight, but also areas in the Baltic Sea (Kiel Bight), the Kattegat, the southern German Bight (east Frisian coast), the Southern Bight including the English Channel (Dutch, Belgium and French coast, the British east coast with the Thames Estuary and the greater Wash area), and Liverpool Bay in the Irish Sea.

Divers were found in strongly reduced numbers around OWFs and were almost absent within OWF areas and 5 km around. The displacement effect gradually decreased with distance from OWFs, but a significant effect could be detected up to 10–15 km away. Telemetry and aerial surveys provided similar results. Red-throated divers moved longer distances in the proximity of OWFs as compared to further away. During weather conditions indicating poor visibility (e.g. high wind speeds and high precipitation) red-throated divers were located closer to OWFs than during good visibility. Divers kept longer distances to OWFs at night, when wind turbines are illuminated with bright red aviation lights and white navigation lights.

Analyses on the effect of ship traffic on red-throated diver distribution and movements suggested that large relocation distances of red-throated divers are related to disturbance by ships, which often trigger birds to take flight. In addition, ship speed was identified to have a strong effect on divers: after disturbance from high-speed vessels resettlement of the disturbed area took longer than after disturbance from slow- or medium speed vessels.

Genetic analysis of red-throated diver diet in the eastern German Bight revealed the species being a generalist opportunistic fish-eating species, but pelagic schooling fish which aggregate at frontal zones and have a high energetic value seem to be favoured.

Results of the DIVER study suggest some flexibility of red-throated divers in using different areas and switching between different available prey species. There is indication that red-throated divers have some capacity to cope with being displaced from OWF areas. However, information on red-throated diver energy budgets and large-scale international monitoring data are required to analyse the cumulative impacts of OWFs and whether this affects the species at population level.

A number of recommendations were made with regard to improving marine spatial planning in order to avoid or reduce the adverse effects of OWFs and shipping in red-throated diver wintering areas.

2 DEUTSCHE ZUSAMMENFASSUNG

Sterntaucher gehören zu den empfindlichsten Wasservogelarten in Bezug auf Störungen durch anthropogene Aktivitäten. Die bevorzugten Überwinterungs- und Aufenthaltsgebiete der Art in den relativ flachen Küstengewässern der östlichen Deutschen Bucht unterliegen auch verschiedenen anthropogenen Nutzungen wie Schifffahrt, Fischerei und seit jüngerer Vergangenheit auch die Offshore-Windenergienutzung. Untersuchungen an bestehenden Offshore-Windparks (OWPs) haben gezeigt, dass ein hohes Konfliktpotenzial zwischen dem geplanten Ausbau der Offshore-Windenergienutzung und dem Schutz der Seetaucher-Arten besteht. Das Projekt DIVER wurde initiiert, um relevante Wissenslücken zu schließen und die Auswirkungen von OWPs auf Sterntaucher zu beurteilen. Hierzu wurden Sterntaucher im Seetaucher-Hauptverbreitungsgebiet der deutschen Nordsee mit implantierbaren Satellitensendern ausgestattet und mittels dieser Daten die saisonalen Bewegungsmuster und die Habitatnutzung der besenderten Vögel untersucht. Die Analysen basierend auf den Satellitentelemetrie-Daten wurden ergänzt durch Analysen von digitalen Flugerfassungsdaten im Seetaucher-Hauptverbreitungsgebiet in der deutschen Nordsee und durch nahrungsökologische Untersuchungen an den besenderten Sterntauchern mittels modernster genetischer Analysemethoden anhand von Kotproben.

Basierend auf den Telemetrie-Daten konnte gezeigt werden, dass Sterntaucher, die die östliche Deutsche Bucht im späten Winter und Frühjahr nutzen, aus vielen verschiedenen Brutgebieten stammen. Hierbei konnten Brutgebiete in Westgrönland, Ostgrönland, Norwegen, Spitzbergen und (für die Mehrheit der Vögel zutreffend) Nordrussland (europäischer und sibirischer Teil) als Herkunftsgebiete nachgewiesen werden. Die zeitlichen und räumlichen Bewegungsmuster der besenderten Sterntaucher zeigten eine hohe individuelle Variabilität, einzelne Individuen zeigten sich jedoch treu in Bezug auf die Nutzung ihrer generellen Zugrouten sowie großräumigen Rast-, Mauser- und Überwinterungsgebiete. Bei kleinskaliger Betrachtung von Zugrouten und Gebietsnutzung in aufeinanderfolgenden Jahren wurde hier jedoch eine gewisse Flexibilität in der Wahl von Gebieten festgestellt. Sterntaucher waren in ihrem Wintergebiet sehr mobil, was sich in großen Winter-Home Ranges widerspiegelt. Die Winter-Bewegungsmuster variierten individuell und reichten von Individuen, die sich während der gesamten Winter-Saison in einem relativ kleinen Gebiet aufhielten, bis hin zu anderen, die sich fast kontinuierlich zwischen verschiedenen Überwinterungsgebieten bewegten. Zu den einzelnen Winter- Home Ranges gehörten verschiedene Gebiete in der östlichen Deutschen Bucht, aber auch in der Ostsee (Kieler Bucht), dem Kattegat, der ostfriesischen Küste, der Südlichen Bucht mit Ärmelkanal (niederländische, belgische und französische Küste, britische Ostküste mit der Themse-Mündung und dem Gebiet The Wash) sowie der Liverpool Bay in der Irischen See.

Die Ergebnisse aus dem DIVER-Vorhaben beschreiben einen starken Vertreibungseffekt von OWPs auf Sterntaucher. Innerhalb und bis in eine Entfernung von 5 km um OWPs wurden fast keine Sterntaucher festgestellt. Der Vertreibungseffekt nahm mit zunehmender Entfernung zu den OWPs allmählich ab, ein signifikanter Effekt wurde bis zu einer Entfernung von 10–15 km festgestellt. Telemetrie- und Flugerfassungsdaten kamen hierbei zu vergleichbaren Ergebnissen. Die Entfernung zwischen aufeinanderfolgenden Positionen (Verlagerungsdistanzen) von besenderten Sterntauchern war in der Nähe von OWPs signifikant größer als weiter entfernt. Bei Wetterbedingungen, die auf schlechte Sicht hinweisen (z.B. hohe Windgeschwindigkeiten und starke Niederschläge), hielten Sterntaucher geringere Abstände zu OWPs ein als bei guter Sicht. Nachts waren die Abstände der Sterntaucher zu den OWPs größer als bei Tag, was auf eine hohe Scheuchwirkung der Nachtbefeuerung der Anlagen hindeutet.

Analysen zu den Auswirkungen des Schiffsverkehrs auf die Verteilung der Sterntaucher und deren Bewegungsmuster deuten darauf hin, dass große Verlagerungsdistanzen der Sterntaucher mit Störungen durch Schiffe zusammenhängen. Darüber hinaus wurde festgestellt, dass die Schiffsgeschwindigkeit einen starken Effekt auf die Sterntaucher-Reaktion hat: Nach einer Störung durch schnelle Schiffe dauerte die Wiederbesiedlung des gestörten Bereichs länger als nach einer Störung durch Schiffe mit langsamer oder mittlerer Geschwindigkeit.

Die Ergebnisse der genetischen Nahrungsanalysen ergab, dass es sich beim Sterntaucher um eine generalistisch-opportunistische, fischfressende Art handelt, die jedoch offensichtlich pelagische Schwarmfische, die v.a. in marinen Frontensystemen zu finden sind und eine energiereiche Nahrung darstellen, bevorzugt.

Die Ergebnisse der DIVER-Studie deuten auf eine gewisse Flexibilität der Sterntaucher bei der Nutzung verschiedener Gebiete und verschiedener verfügbaren Nahrungsfischarten hin. Hieraus lässt sich ableiten, dass Sterntaucher zu einem gewissen Grad in der Lage sein sollten, nach großräumiger Vertreibung aus den OWP-Bereichen in alternative Gebiete auszuweichen. Für eine kumulative Auswirkungsprognose sowie die Bewertung, inwiefern die festgestellten Effekte der OWPs auf Sterntaucher einen Populationseffekt bewirken sind jedoch Informationen über den Energiehaushalt von Sterntauchern im Wintergebiet sowie großräumige internationale Monitoring-Daten erforderlich.

Auf Basis der Forschungsergebnisse des DIVER-Vorhabens wurde eine Reihe von Empfehlungen hinsichtlich der marinen Raumordnung formuliert, um die negativen Effekte von OWPs und Schifffahrt in wichtigen Wintergebieten von Sterntauchern zu vermeiden bzw. zu verringern.

3 INTRODUCTION TO THE PROJECT

3.1 Background

The development of offshore wind farms is an important element towards expanding the share of renewable energy in Germany and many other countries with marine territories. Germany has defined the target to establish offshore wind farms with a total capacity of 15 GW by 2030 (Offshore Wind Energy Act), resulting in the construction of more than 2,000 turbines. The development of offshore wind farms aims to provide clean energy and aims to become an important measure in protecting the environment and the climate. The large-scale expansion of offshore wind farms will inevitably be accompanied by additional anthropogenic impacts in marine waters which are already subject to various activities such as shipping and fisheries and often show impaired environmental conditions. It has thus been defined from the start of this new development that the establishment of offshore wind farms in German waters shall follow a stepwise process in order to make use of experience made during the process[1]. The development of offshore wind farms has thus been subject to extensive monitoring programs commissioned by the wind industry and accompanying research projects commissioned by the German government which both aim to identify the impacts on the marine environment and inform the process of further developments.

Wintering seabirds are an important part of the marine ecosystem. Some species react sensitively to anthropogenic structures and activities and may thus be vulnerable to the expansion of offshore wind farms (e.g. FURNESS et al. 2013). As many seabirds have rather wide distributions and utilise different habitats they are likely to come in contact with offshore wind farms. In this respect, special attention has been paid to the red-throated diver, which occurs in coastal shallow waters often overlapping with areas suitable for offshore wind farms.

Divers belong to the family Gaviidae, divided in five species, great northern diver (*Gavia immer*), white-billed diver (*Gavia adamsii*), Pacific diver (*Gavia pacifica*), black-throated diver (*Gavia arctica*) and red-throated diver (*Gavia stellata*). Only the latter two species occur in relevant numbers in the German Bight and the red-throated diver being by far the most abundant diver species in this area. Red-throated diver wintering distribution in Europe extends along the coasts of the North Sea, the Baltic Sea and the northern Mediterranean. The breeding distribution of the European population covers a large area including Russia, Fennoscandia, Great Britain, Iceland and Greenland. However, before the start of this project, not much was proven about locations of origin because recoveries of ringed birds are very rare. In the offshore areas of the North Sea divers occur in internationally important numbers during wintering period and spring, using a wide range of areas and being highly mobile within them. As red-throated divers are highly sensitive to disturbance from ship traffic (BELLEBAUM et al. 2006) the species has been much in focus when considering possible impacts from offshore wind farms. Germany, Denmark and the UK have established offshore wind farms in important diver areas which has led to a very

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[1] Strategie der Bundesregierung zur Windenergienutzung auf See (2002). http://www.loy-energie.de/download/Bundesregierung,%20windenergie_strategie_br,%2001-2002.pdf

controversial debate where to establish marine protected areas and where to license offshore wind farm sites.

Investigations at existing offshore wind farms have shown that there is a high potential for conflicts between wind farms and divers. Divers are known to be very sensitive to disturbance and as a consequence show a significant avoidance reaction (e.g. PETERSEN et al. 2006, 2014; DEWAR 2011; DIERSCHKE et al. 2012; MENDEL et al. 2019a). They use areas with a wide range of water depths and occur in the North Sea in areas with water depths up to 40 meters (MENDEL et al. 2008; PETERSEN & NIELSEN 2011). Due to their mobility during the wintering season divers can be affected cumulatively by several offshore wind farm projects (MENDEL et al. 2008; IMARES 2011). To evaluate the interactions and impacts between offshore wind farms and divers, information about the following aspects are essential:

- Habitat use during wintering season in areas with and without offshore wind farms
- Characterisation of winter movements with focus on home ranges, timing and identification of core wintering areas
- Exchange between different resting areas/ stop-over sites
- Site fidelity to different areas used during the annual cycle
- Identification of breeding areas to establish which breeding populations are affected

Systematic investigations concerning these species are essential to fill the knowledge gaps and to improve and facilitate the process of decision making regarding current and future action of offshore wind farm planning in proximity to important diver habitats.

The research project DIVER has been initiated aiming to provide novel knowledge on red-throated diver ecology with emphasis to the species reactions towards anthropogenic pressures such as offshore wind farms and shipping. State of the art telemetry methods were used to collect data about red-throated diver habitat use and movement patterns during the wintering season in the North Sea as well as localisation of their potential breeding, moulting and staging areas and identification of migration routes. Animal tracking has become a highly recognised tool to gather data on individual movements to analyse habitat utilisation of marine species over full annual cycles and to inform policy and management (e.g. HAYS et al. 2019). While in the US tracking of red-throated divers and other diver species has been established for a while this is the first large-scale study on divers in Europe. Further, bird faecal samples were taken for the non-invasive study of the diet of red-throated divers wintering in the German Bight. Additionally, blood samples allowed for gender determination of tagged divers and analysis of blood parasites. Neck feather samples were used in combination with results of tracking data to study interannual fidelity of tagged divers to autumn moulting areas.

3.2 Project objectives

The project followed the overall objective to fill important knowledge gaps regarding the ecology of red-throated divers, such as habitat use and movement patterns within critical areas aiming to support conservation plans for this species as well as to improve conditions for developing conservation tools and actions for this species. Considering offshore wind farm developments, spatial distribution and temporal characteristics of habitat use of red-throated divers were analysed to set a sound basis for the relation of habitat loss due to offshore wind farms and habitat requirements of divers. Prior to the project start, the following knowledge gaps were identified:

Little was known about habitat use and movements of divers within and between different wintering areas. It has been suggested that diver habitat choice varies in relation to tidal currents, other hydrological changes and weather.

Migration patterns and general movement schedules throughout the annual cycle of red-throated divers were largely unknown. Diver numbers fluctuate substantially in different wintering areas and intensive movements have been recorded along the coasts of the Baltic and North Sea (e.g. BERNDT & DRENCKHAHN 1990; DIERSCHKE 2002). This indicates a high mobility during the non-breeding period. However, it has been unclear how different staging and wintering areas are linked to each other and how wintering home ranges of individual divers are characterised. Knowledge on this is essential information for evaluation of cumulative impacts on divers.

Site fidelity to wintering areas and other areas visited along the annual migration routes was unknown. Whether birds are highly site faithful and return to the same places year after year or are flexible in using different geographic areas has important implications in evaluating potential impacts on red-throated diver populations.

Locations of origin were rather unknown. During the non-breeding period red-throated divers are widely dispersed along the coasts and offshore areas in the Baltic and North Seas and northern Atlantic. Breeding populations are widely distributed across high latitudes of Russia, Scandinavian Peninsula, Great Britain, Iceland and Greenland. Recoveries of ringed birds are scarce and therefore it was unknown which breeding populations are being affected on specific wintering and staging grounds.

Diet composition of seabirds outside the breeding season, when they remain at sea, is notoriously difficult to study. Only little was known about red-throated diver diet composition in its main wintering area in the North Sea. Knowledge on diet composition and feeding strategies is essential for understanding habitat selection and assessment of consequences of habitat changes.

3.3 Planning and realisation of the project

The project is a Joint Venture between BioConsult SH, Justus Liebig University of Gießen (Department Animal Ecology and Systematics, Research Group Behavioural Ecology and Ecophysiology), DHI and Ornitela within a four year period between 1 November 2014 and 30 October 2018. With the project HELBIRD, lead and carried out by FTZ Büsum, cooperation and share of digital aerial survey data was agreed. For reaching the project goals different working packages (Arbeitspakete AP 1–5) were defined and tasks completed.

3.3.1 AP 1: Coordination

This working package includes the coordination of all activities between project partners and Funding Agency Project Management Jülich PtJ respectively Federal Ministry for Economic Affairs and Energy (BMWi), project-related communication, coordination of meetings and a project workshop with external experts and compiling of technical project reports. Main contribution to this working package was made by Bioconsult SH.

3.3.2 AP 2: Data sampling (captures and transmitter deployment)

This working package includes all field work in context of red-throated diver captures and transmitter deployment in the three consecutive winter/spring seasons of the years 2015–2017. Equal contributions to this working package were made by Bioconsult SH, JLU Gießen, DHI and Ornitela.

3.3.3 AP 3: Data analyses

This working package includes all tasks in context of telemetry and digital aerial survey data analyses. It comprises four different sub-working packages and additional analyses which were developed in the course of the project time. Equal contributions to this working package were made by Bioconsult SH, JLU Gießen, DHI and Ornitela.

- T-AP 1: Data processing of telemetry data: see chapter 4.3.3
- T-AP 2: Home Range analyses: see chapter 5.3.6.1
- T-AP 3: Origin and site fidelity of the tagged divers: see chapters 5.2.1 and 5.2.3
- T-AP 4: Habitat models: see chapter 6

3.3.4 AP 4: Genetic diet analyses and gender determination

This working package includes all tasks in context of genetic analyses of red-throated diver fecal and blood samples. Main contribution to this working package was made by JLU Gießen.

- T-AP 1: Genetic analyses of red-throated diver diet to species level by applying a state of the art method of DNA metabarcoding by using fecal samples collected of captured red-throated divers
- T-AP 2: Genetic gender determination of captured red-throated divers from blood samples.

3.3.5 AP 5: Online interface and project homepage

This working package includes all works in context of continuous data backup using the online database for telemetry data Movebank (movebank.org) (T-AP 1) and the setup and update of the project website www.divertracking.com (T-AP 2). Equal contributions to this working package were made by Bioconsult SH and JLU Gießen.

3.3.6 Expanded analyses within the DIVER project not defined in working packages

Additionally to the tasks defined in the working package expanded analyses were carried out (for contributions see 3.3.3 and 3.3.4):

- Habitat modelling at different spatial scales using telemetry and digital survey datasets with the focus on bird displacement from existing offshore wind farms (add AP 3, T-AP 4)
- Habitat modelling of telemetry data when accounting for daytime and meteorological factors (add AP 3, T-AP 4)
- Analysis of diver movement decisions during the annual cycle (add AP 3, T-AP 3)
- Analyses on the effect of shipping traffic on red-throated diver distribution and movements based on telemetry and aerial survey data: see chapter 6.6 (add AP 3)
- Additional laboratory work – stable isotope analysis: see chapter 5.3.5 (add AP 3, T-AP 3)
- Additional laboratory work – blood parasite analysis: see chapter 9 (add AP 4)

3.3.7 Project milestones

For the total project period seven milestones were defined, which all were reached in time (Table 3.1).

Table 3.1 Milestones of the DIVER project.

Milestone	Description	Due date
MS1	Successful capture and transmitter deployment of 10-20 divers in the first project winter/spring season; sampling for genetic gender determination and diet analysis for the first field season.	30.04.2015
MS2	Setup of the project homepage with visualisation of the tracks of already tagged individuals. Continuous updates also after the milestone due date. Setup of a database structure for continuous telemetry data backup (e.g. Movebank)	30.06.2015
MS3	Successful capture and transmitter deployment of 10-20 divers in the second project winter/spring season; sampling for genetic gender determination and diet analysis for the second field season.	30.04.2016
MS4	Processing of environmental data for the habitat modelling and establishing of the model setup and model fitting, first results of data analyses.	31.09.2016
MS5	Organisation of a workshop with members of the project working group (Projektarbeitsgemeinschaft PAG) and experts: Presentation of the interim project results from data of the first two study years and discussion of results.	30.11.2016
MS6	Successful capture and transmitter deployment of the remaining of the in total 45 divers in the third project winter/spring season; sampling for genetic gender determination for the third field season.	30.04.2017
MS7	Finalisation of data analyses for all three study years and preparatory works for the final report.	30.10.2018

4 STUDY APPROACH AND METHODS

4.1 Study species red-throated diver (*Gavia stellata*)

The red-throated diver (*Gavia stellata*) has a circumpolar distribution and breeds on lakes in coastal tundra habitats of North America, Europe and Asia. During the non-breeding season, the species is found broadly in coastal waters in the Northern Hemisphere (CRAMP & SIMMONS 1977). Red-throated diver is a strictly protected species, which is listed in Annex I of the EU Birds Directive, in Annex II of the Bern Convention, in the African Eurasian Waterbird Agreement (AEWA) and is further listed by the HELCOM Convention as a critically endangered species, though as of least concern by IUCN (BIRDLIFE INTERNATIONAL 2016). The European breeding population is estimated to 84,200–186,000 red-throated divers (BIRDLIFE INTERNATIONAL 2019). Red-throated divers have a wide distribution range during the wintering season which extends along Atlantic shores from Iceland to Spain and the wintering areas include the Mediterranean Sea and the Black Sea (CRAMP & SIMMONS 1977).

Birds spending their non-breeding period in the Baltic Sea, the North Sea and the NE-Atlantic belong to the NW-European wintering population (BIRDLIFE INTERNATIONAL 2019). This wintering population is currently estimated at 216,000 to 429,000 divers (WETLANDS INTERNATIONAL 2018), which originate from breeding areas ranging from Greenland to Siberia. Red-throated divers use the North Sea as wintering area with first birds arriving in autumn and last birds leaving the area in May for the breeding grounds. The total number of red-throated divers wintering (December – March) in the North Sea has been estimated at 48,000 individuals, with the main part occurring at the eastern shores from the Rhine and Schelde delta up to mid of the Danish west coast (SKOV et al. 1995). The distribution within the North Sea changes seasonally and in spring (April-May) most divers concentrate in the eastern part north from Helgoland up to Hanstholm in Denmark. Total spring numbers were estimated at 30,000 divers with about 80% concentrating in the above mentioned area along the German–Danish west coast.

The figures provided by SKOV et al. (1995) were at that time mainly based on opportunistic ship-based surveys and likely underestimated total diver numbers in the North Sea. For example, in the Outer Thames Estuary SPA recent systematic aerial digital video surveys revealed a total number of 22,000 red-throated divers (IRWIN et al. 2019) while the first estimate from SKOV et al. (1995) only came to 230 individuals. For the eastern part of the North Sea no recent population estimates have been compiled on an international level. The available data indicate that some 15 to 25% of the NW-European wintering populations occur at a time in the North Sea.

Our study area in the eastern German Bight, presents an internationally important resting site for red-throated divers during the non-breeding season (GARTHE et al. 2012, 2015) with a recent estimate of 22,000 red-throated divers using the German North Sea in spring (SCHWEMMER et al. 2019).

4.2 Study area

The DIVER study focused on the north-eastern part of the German North Sea, where high densities of red-throated divers occur in winter and especially in spring. The area therefore has been defined as a main diver distribution area by German authorities (BUNDESMINISTERIUM FÜR UMWELT, NATURSCHUTZ UND REAKTORSICHERHEIT 2009). The study area in the German Bight is a shallow shelf sea, strongly influenced by tidal motion (OTTO et al. 1990). The area consists mainly of sandy sediments and gravel. The 40 m depth contour extends up to 200 km from the coast confining a large shallow water area. There are two main water masses, the North Sea water mass and the continental coastal water mass (BECKER et al. 1992). The coastal water mass has lower salinity influenced by river outflows and the frontal zone between the two water masses is dynamic (BECKER et al. 1992). In the eastern German Bight a dynamic frontal systems exists in the mixing zone of coastal and riverine waters. This is especially pronounced to the north of the river Elbe mouth. From March to end of September, when the open North Sea water is thermally stratified, this mixing zone starts at the 30 m depth contour, where it turns towards the coastal shallow waters mixed by wind and tides. Pronounced frontal systems usually appear for a few days and their persistence is subject to weather conditions (BSH 2019). Frontal zones are usually associated with increased ecological activity through local enhancement of nutrients and red-throated divers have previously been shown to prefer the frontal zones between these two water masses in the German Bight (SKOV & PRINS 2001).

The area is subject to various human activities with several offshore wind farms operating in the area and adjacent Danish waters[2]. There are no larger ports north of the river Elbe and shipping in this part of the German Bight is dominated by fisheries with some other commercial vessels commuting through this area and more recently vessels used for construction and service of offshore wind farms. In order to protect red-throated divers and other seabirds, several large marine protected areas have been established within the Natura 2000 network in German as well as in adjacent Danish waters (Figure 4.1).

Red-throated divers were captured and equipped with satellite transmitters in this diver hotspot in the German Exclusive Economic Zone (EEZ, Figure 4.1). Also large-scale digital aerial surveys were conducted within that area (data provided by the project HELBIRD, FTZ, Büsum). For analyses regarding habitat use of red-throated divers and the effect of shipping traffic on divers (see chapters 6 and 6.6) specific study areas were defined. For other analyses no clear study areas were predefined, bird localisations determined the areas for which analyses were undertaken for answering specific questions.

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[2] https://www.bsh.de/DE/THEMEN/Offshore/Nutzungskarten/_Anlagen/Downloads/Nordsee-Nutzungen_Schutzgebiete.pdf?__blob=publicationFile&v=1

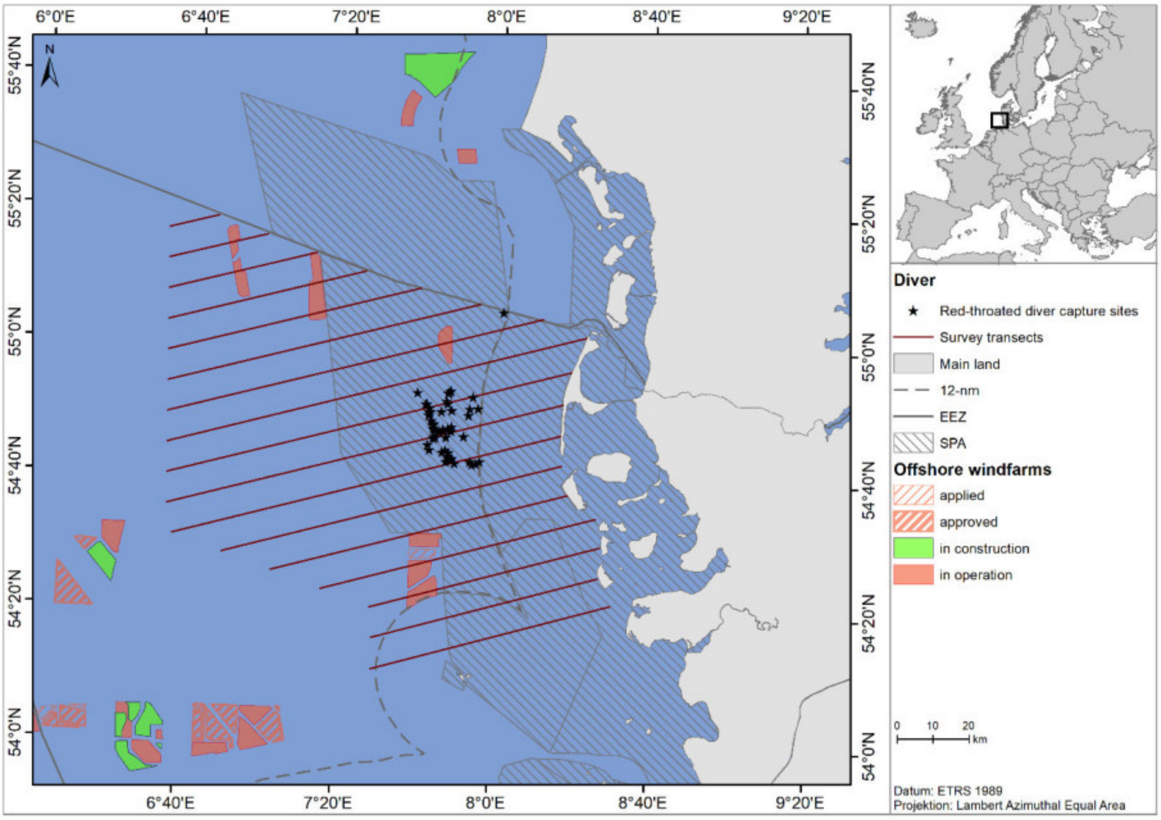


Figure 4.1 *Main study area, red-throated diver capture locations for fitting birds with transmitters and digital aerial survey transects. Wind farms present during the study period are shown.*

4.3 Satellite telemetry

4.3.1 Diver captures and transmitter deployment

Between 2015 and 2017 in total 45 red-throated divers were captured in their wintering area in the German North Sea and equipped with implantable satellite transmitters. Bird captures took place during three consecutive spring seasons: March – April 2015, February – March 2016 and March 2017. Birds were captured in the German North Sea in an area between 54°30’N and 55°00’N, 20–30 km offshore in the German EEZ (Figure 4.1).

Birds were captured from a boat at sea using the “night lighting technique" (WHITWORTH et al. 1997). On dark and calm nights birds were searched from a small boat using a bright light. We used two different types of lamps: a Hella hand held search lamp with a short range 55 W bulb and a long range 100 W bulb with an opening of 154 mm and an Acebeam X60M with three LED bulbs of 10,000 lm and an opening of 108 mm. Both types of lamps worked well. Once found, divers were disoriented by using the bright light which allowed the capture team to approach the diver close enough to catch it with a hand net attached to a pole (Figure 4.2).

Figure 4.2 Dinghy with capture crew as it was used for diver captures.

The captured birds were placed into well ventilated and specially adapted kennels. The kennel floor was made from elevated mesh in order to keep birds dry and clean; inner wall were padded with soft material or cardboard making sure that there were no holes in the crate that are big enough for birds' bill to go through. Only one bird was placed per kennel when transporting, and the kennels were stored outside to prevent birds from overheating. Within minutes after capturing the birds were injected sedative Midazolam by administering approximately 2 mg/kg. Sedation is necessary for this species as red-throated divers have a tendency of getting stressed.

The captured birds were delivered from the small capture boat to a larger ship. During the first tagging period in 2015 transmitter implanting was conducted in a temporary land-based surgery room with all required equipment. To reduce handling time the surgeries during the following two tagging periods were conducted in a similar temporary surgery room on board the ship instead if conditions allowed. Transmitters were abdominally implanted with external percutaneous antenna following standard surgical technique used for diving birds (KORSCHGEN et al. 1996; MULCAHY & ESLER 1999). Birds were released 2–4 hours after completed surgery. Captivity time from the moment of capture to release was reduced in the course of the project from a mean of 18.2 h in 2015 (range 6.5–27.4 h) and a mean of 9.3 h in 2016 (range 6.8–12.9 h) to a mean of 7.5 h in 2017 (range 4.9–10.8 h). Surgeries (done by an experienced veterinarian) and all fieldwork (animal capture, sampling and tagging) were conducted under appropriate ethics and approvals; approved by BfN (Federal Agency for Nature Conservation), Germany, 05.08.2014; and Ministry of Environment and Food Denmark, Danish Veterinary and Food Administration, permit no. 2014-15-0201-00239, issued 18.12.2014).

We used implantable Argos satellite platform terminal transmitters (PTTs) manufactured by Telonics, Inc. (IMPTAV-2635 (5 units), IMPTAV-2640 (20 units), IMPTAV-2645 (15 units)) and Sirtrack, Ltd (K3I 171A, 5 units). PTTs weighing between 35 and 45 grams were implanted in birds weighing on average 1,729 grams (SD ± 174) and comprised on average 2.65% (SD ± 0.36) of body weight.

Transmitters were programmed using varying duty cycles with 3 or 4 transmission hours and 12–24 hour intervals between them in the period when birds were expected to be on wintering grounds or on migration and longer 60–68 hour intervals during the breeding season (Table 4.1).

Table 4.1 Transmitter characteristics and duty cycles used in the different deployment years of the project.

Year of transmitter deployment	Transmitter manufacturer	Transmitter specification	Transmitter weight	Season	Argos schedule		Number of transmitters deployed
					Loop length	ON period	
2015	Sirtrack	K3I 171A	37g	START – START+120 days	24h	4h	5
				START+120 days – END	72h		
2015	Telonics	IMPTAV-2640	45g	START – 15.06.15	28h	4h	11
				15.06.15 – END	64h		
2016	Telonics	IMPTAV-2645	45g	START – 16.06.16	27h	3h	10
				16.06.16 – 01.09.16	63h		
				01.09.16 – END	27h		
2016	Telonics	IMPTAV-2645	45g	START – 16.06.16	15h	3h	5
				16.06.16 – 01.11.16	63h		
				01.11.16 – END	27h		
2016	Telonics	IMPTAV-2635	35g	START – 01.05.16	27h	3h	5
				01.05.16 – 01.11.16	63h		
				01.11.16 – END	27h		
2017	Telonics	IMPTAV-2640	45g	START – 16.06.17	27h	3h	9
				16.06.17 – 01.09.17	63h		
				01.09.17 – END	27h		

4.3.2 Transmitter performance and telemetry data

Collected ARGOS data was delivered by CLS France (CLS 2013). Data were downloaded automatically to the online tracking database Movebank (www.movebank.org) and additionally manually from ARGOS website (www.argos-system.cls.fr) for backup. Transmitter performance and data received varied between different transmitters and birds (Table 4.2). Telemetry data were collected from 36 birds in total, which later could be used for analyses. Nine of 45 transmitters delivered no useable data due to early transmitter shut down for unknown reasons (transmitter failure) or early mortality. The death of a bird was assumed when with tracking data showed that body temperature of the tracked bird dropped below 39 °C. Total length of data sampling period ranged from a few weeks of tracking data to almost 23 months (Table 4.2). In most cases the end of data sampling was due to transmitter battery drain, but also due to transmitter failure for unknown reasons and mortality. Surgery or transmitter related mortality cannot be excluded in five cases, when tagged birds died within the first two weeks after transmitter deployment.

Table 4.2 Technical information on birds, capture date and transmitter performance for all red-throated divers tagged within the DIVER project between 2015 and 2017. Grey cells indicate birds for which data were not used for any analyses.

No	Argos ID	Ring No.	Sex	Body weight (g)	Transmitter deployment date	Period of data sampling (days)	Reason for end of sampling
1	146437	E081-51	f	1720	20.03.2015	10	Body temp. < 39°C
2	146438	E081-52	m	2020	20.03.2015	577	
3	146439	E081-53	f	1690	20.03.2015	89	Body temp. < 39°C
4	146440	E081-54	f	1550	20.03.2015	519	
5	146441	E081-55	f	1690	20.03.2015	9	Body temp. < 39°C
6	146442	E081-56	m	1850	21.03.2015	688	
7	146443	E081-57	f	1690	21.03.2015	600	
8	146444	3409888	f	1670	25.03.2015	599	
9	146445	E081-58	m	2000	25.03.2015	72	Body temp. < 39°C
10	146446	3409889	f	1440	25.03.2015	7	Body temp. < 39°C
11	146449	E08160	f	1950	20.04.2015	58	
12	146450	E08159	f	1820	20.04.2015	10	Transmitter failure
13	146451	E08160	f	1710	20.04.2015	100	
14	146452	E08161	f	1660	20.04.2015	137	
15	146453	E08162	f	1820	20.04.2015	155	
16	146437(2)	E08163	f	1770	20.04.2015	229	
17	158316	E08174	f	1810	11.03.2016	154	
18	158317	E08173	f	1640	11.03.2016	222	
19	158318	E08176	f	1770	11.03.2016	205	
20	158319	E08178	f	1850	12.03.2016	9	Body temp. < 39°C
21	158320	E08179	f	1760	12.03.2016	240	
22	158321	E08180	f	1720	12.03.2016	223	
23	158322	E08401	f	1650	12.03.2016	183	
24	158323	E08402	f	1700	12.03.2016	246	
25	158324	E08403	m	2030	13.03.2016	391	

No	Argos ID	Ring No.	Sex	Body weight (g)	Transmitter deployment date	Period of data sampling (days)	Reason for end of sampling
26	158325	E08404	f	1570	13.03.2016	222	
27	158326	E08165	m	1680	28.02.2016	216	Body temp. < 39°C
28	158327	E08168	f	1460	28.02.2016	366	
29	158328	E08169	f	1520	29.02.2016	509	
30	158329	E08171	m	2050	29.02.2016	173	
31	158330	E08172	f	1550	29.02.2016	186	
32	158331	E08166	f	1430	28.02.2016	84	
33	158332	E08167	f	1480	28.02.2016	194	
34	158333	E08170	f	1450	29.02.2016	31	Transmitter failure
35	158334	E08175	f	1570	11.03.2016	277	
36	158335	E08177	f	1620	11.03.2016	7	Body temp. < 39°C
37	52062	290151	f	1680	25.03.2017	101	Body temp. < 39°C
38	52063	290156	m	1950	26.03.2017	65	Body temp. < 39°C
39	56572	290152	m	2060	25.03.2017	4	Transmitter failure
40	57331	290158	f	1660	26.03.2017	502	
41	57332	290153	f	1700	25.03.2017	199	
42	57335	290165	f	1800	26.03.2017	110	Body temp. < 39°C
43	57339	290159	m	1750	26.03.2017	390	
44	57345	290163	m	2040	25.03.2017	443	
45	57346	290164	f	1840	25.03.2017	319	

4.3.3 Filtering of telemetry data

The location quality of received positions was classified into one of six Argos quality classes as provided by CLS (2013) with the accuracy ranging from < 250 m to > 1,500 m, and there were also locations with unavailable accuracy information (Table 4.3). Error distances of different quality classes, however, have been shown to be actually larger (DOUGLAS et al. 2012; see Table 5.1). Therefore, satellite telemetry data requires filtering to reduce noise by location fixes with low or unknown accuracy. Prior to all data analyses we applied Freitas filter to the entire telemetry dataset to eliminate unlikely locations on the basis of location quality class, calculated bird moving speed, distance between successive locations, and turning angles (FREITAS et al. 2008). When applying Freitas algorithm, we set a maximum moving speed of divers at 20 m/s and kept other parameters on default settings. Package ‘argosfilter’ (FREITAS et al. 2008) in R statistical environment (R CORE TEAM 2018) was used to apply the filtering algorithm.

Table 4.3 Defined ARGOS position quality classes (CLS 2013) and distribution of received data to the different classes before and after data filtering.

Class	Estimated error [m]	Number of positions in the unfiltered dataset	Number of positions in the filtered dataset	%
3	< 250	4,970	4,210	18.5
2	250–500	3,353	2,806	12.3
1	500–1,500	2,451	1,946	8.6
0	> 1,500	1,698	1,118	4.9
A	No accuracy information	4,878	3,746	16.5
B	No accuracy information	11,629	8,918	39.2
Z	Invalid location	74	0	0.0
TOTAL		29,053	22,744	100

Filtering successfully eliminated the majority of unlikely locations outside of animal presence areas and removed ‘spikes’ along bird tracks. The filtered dataset was further inspected visually and several obvious outlier positions were flagged and eliminated from the dataset. Finally, positions recorded during the first two weeks after the release were excluded from any analyses due to possible unnatural behaviour during that period. Further filtering or subsampling of the dataset for different analyses is described in the respective method descriptions of the different chapters in this report.

4.4 Digital aerial surveys

Digital aerial surveys were conducted within the project HELBIRD (FTZ, Büsum) running in parallel and in close cooperation with the DIVER project. Diver data of four large-scale digital aerial surveys, which were dedicated for surveying diver abundance and distribution in the study area of the DIVER project, were analysed. The surveys were conducted during 10 April 2016, 1 May 2016, 25 March 2017 and 11 May 2017, using a transect design consisting of 17 transects with a total length of roughly 1,300 km and with a transect spacing of about 8 km. The total area surveyed, as defined by a convex hull around the survey transects, was approximately 11,500 km^2 (Figure 4.1) and of these approximately 720 km^2 per survey were covered by the survey transect. The duration of a survey was 9–11 hours, of which approximately 7 hours were spent on transect. Surveys started in the morning around 1.5–2 hours after sunrise to ensure having enough daylight hours for completing the survey within one day, including a 2–4 hours break during midday.

The surveys were conducted using the HiDef video camera system at 549 m flight altitude (Weiß et al. 2016; Žydelis et al. 2019). The camera system consists of a rig with four cameras with a ground resolution of 2 cm per pixel. The two outermost cameras in the row cover a strip of 143 m each while the innermost two cameras a strip of 129 m each and each strip is separated by 20 m (i.e. in total a video strip width of 544 m). The flight track was recorded in intervals (segments) of one second using a Garmin GPSMap GPS receiver 296 with a precision of 1 m. Image frames from the video footage were georeferenced to the corresponding survey segment.

Bird identification was done by trained observers in the lab and divers were identified to species level in most cases. Only red-throated divers identified to the species level were retained for the analyses, i.e. black-throated divers (0.1%) and unidentified divers (3% of all divers) were discarded. The detection and identification of objects on the video footage was done in two steps. In the first step observers marked all birds and marine mammals occurring in the video footage. For quality assurance 20% of the video footage (for each camera strip) were randomly selected and analysed by an independent observer. If < 90% agreement was obtained the video footage was reanalysed. In the second step the marked objects (birds and marine mammals) were identified to the lowest possible taxonomic level by experienced ornithologists. Additionally behaviour, age, sex and other potentially useful information was noted. Similarly to the first step, a quality assurance of 20% of all identified objects was conducted. If < 90% agreement was obtained bird identification was redone. The valid bird observations identified in the videos were spatially and temporarily combined with the flight effort. The red-throated diver observations were summed per segment of approximately 500 m (the length of the original survey segments were summed until 500 m was reached). Bird densities (birds/km^2) were calculated by dividing the number of observed birds by the area covered in each segment. The environmental data (described below) was finally extracted to the survey data based on position and time.

5 MOVEMENT PATTERNS OF SATELLITE TRACKED RED-THROATED DIVERS DURING THEIR ANNUAL CYCLE

This chapter contains different analyses regarding red-throated diver annual movements covering origin, migration routes, timing, site fidelity to different areas of birds captured in the eastern German Bight in late winter, dedicated analyses regarding the autumn staging and wintering areas (home range analysis, relocation distances in relation to OWFs, site fidelity) and an additional analysis regarding the effects of meteorological factors in red-throated diver migration (chapter 5.5).

5.1 Introduction

This part of the project focuses on annual movements, breeding origin, migration patterns, wintering movements and area use of red-throated divers captured in the eastern part of the German Bight during the non-breeding season. The chapter analyses how red-throated divers originating from different breeding areas utilise the focal area of this study and how the eastern German Bight is connected with other areas during their annual cycle.

Monitoring data from red-throated divers prior to construction of offshore wind farms revealed that the highest numbers of wintering divers occur in spring in the north-eastern part of the German Bight, west of the North Frisian Islands (GARTHE et al. 2015). Red-throated divers arrive to the German North Sea in October, their abundance increases until December and a distribution is centred along the East Frisian Islands. In December and January most birds are found along the East Frisian Islands, close to the offshore island Helgoland and within the area of the North Frisian Islands. In March and April the divers concentrate west of the North-Frisian Islands and close to the Danish border (GARTHE et al. 2015).

Migration presents one of the most challenging time periods for birds and information about species ecology and all the different aspects of migratory behaviour is crucial for species conservation. Data from satellite tracked red-throated divers from Alaska (SCHMUTZ 2014) pointed at higher risk of adult mortality during the non-breeding season (migration and winter) linked with marine conditions. Migratory species depend on different habitats and resources in different locations during their annual cycle (COX 2010). Determining breeding origin of individuals and their respective migration route is essential to link possible consequences of environmental changes in one staging site to other sites along the migration route and to assign which population or sub-population could be affected. Thus, Information about the migratory connectivity between individuals from one breeding origin of a species population, its utilised sites during the non-breeding season and along the migration route presents a basic requirement to understand the effects of environmental changes, also in a cumulative perspective. A lot of data exists from seawatching stations and observations presenting important information about utilisation of the corresponding sites in space and time but these present only specific parts of the red-throated divers annual cycle and no clear overview can be obtained about where these birds migrate to or where they come from. Most ringing recoveries of red-throated divers were documented in Great Britain and revealed ringing origin of these recovered birds from Shetlands, Greenland, Sweden and Finland (OKILL 1994); but ringed bird recoveries in the eastern German

Bight area are rare. Consequently, little is published about origin (breeding areas), migration routes and migration patterns of red-throated divers wintering in the eastern German Bight. Tracking studies in the United States have shown that red-throated divers stayed on their wintering areas from November until May (GRAY et al. 2017). Local and large scale movements in wintering areas were observed and large bays along the coastline with an offshore use up to 25 miles were utilised but habitat use was most commonly concentrated within 5 miles from the shore (GRAY et al. 2017). Only few studies analysed migration of red-throated divers but recently MCCLOSKEY et al. (2018) examined migration patterns of satellite-tagged red-throated divers from four breeding populations in Alaska. Red-throated divers underwent long autumn and spring migrations of approx. 6,300 km predominantly along coastlines. Migration routes observed in this study demonstrated that some geographically distinct breeding populations overlap in wintering distribution while others differed (MCCLOSKEY et al. 2018).

For assessing the impact of displacement from offshore wind farms it is important to understand the movement patterns of red-throated divers within their wintering and staging areas. Due to the absence of tracking studies in the German Bight there was no information on size and variation of individual wintering home ranges and whether individual birds use one or several distinct wintering areas. Home range analysis is a tool for identifying the utilisation distribution (UD) of individuals at different scales. The 50% UD contour in the wintering area for example allows for identifying core wintering areas. Individual home ranges provide important information on the habitat use of animals and help to understand the possible consequences of habitat displacement from anthropogenic activities.

Red-throated divers are highly faithful with regard to their breeding sites (OKILL 1992, Petersen pers. comm.). However, before this study little information was available on site fidelity of red-throated divers towards their wintering and staging areas. If findings about site fidelity show that a species uses several sites or habitats between years, it is likely to be flexible and capable to adapt to a changed environment or to explore new habitats. And *vice-versa*, if a species shows high philopatry to the same areas every year, it is likely conservative when it comes to site or habitat choice and is probably not adaptable to a changing environment. For another diver species, the common loon (*Gavia immer*), a strong winter site fidelity was reported by PARUK (2015).

As changing environmental conditions on the wintering grounds, along migration routes or on staging areas may affect survival and reproduction on breeding grounds (TRIERWEILER et al. 2014), it is important to investigate the migratory connectivity and thus the degree to which individuals from a breeding population use the same areas during the non-breeding season.

Aiming to fill some of the major knowledge gaps mentioned above about the movement ecology of red-throated divers wintering in the eastern German Bight, we used the tracking data of red-throated divers tagged in their wintering area. This knowledge will be helpful for species conservation and management of human developments in the marine environment. Furthermore we aimed to characterise the function of the German Bight for red-throated divers in their annual cycle. Beside the utilisation of the eastern German Bight during winter and spring, particular attention was payed to localise and define potential moulting sites in autumn. The annual moult includes a flightless period of about three weeks when red-throated divers moult their primary feathers and birds are then bound to a particular location due to being flightless. Thus this period, which usually occurs between September and December (Cramp & Simmons 1977; Berndt & Drenckhahn 1990; Mendel et al. 2008), presents a critical time when divers – as other waterbirds - might be particularly sensitive to disturbance (Mendel et al. 2008).

Specifically we aim a) to identify the origin (breeding regions) of birds tagged in the eastern German Bight; b) to characterise movement patterns and timing of tagged birds; c) to identify main resting areas with a focus on wintering and moulting season; d) to characterise winter movements and home ranges aiming to describe core resting areas and the exchange between these areas in the context of the presence of offshore wind farms ; and e) to analyse site fidelity to areas outside the breeding season.

5.2 Methods

5.2.1 Movement analysis

For detailed information about captures and tagging of red-throated divers see chapter 4.3. For the analysis of annual movements we received data of 31 red-throated divers migrating to their potential breeding grounds, of 22 red-throated divers migrating from their potential breeding grounds to their potential moulting sites, of 14 birds returning to their main wintering sites, of 10 birds for the whole wintering period (second winter after capture), and of 7 birds for a second spring migration.

We used Geographic Information Systems (ArcGISv.10.1 and QGISv2.18) and Lambert Azimuthal Equal Area': ETRS89 / ETRS-LAEA (EPSG: 3035) projection to inspect migratory patterns, quantify migration movements, and to map migratory routes To calculate distances to breeding and wintering sites we used the North poles azimuthal equidistant projection by summing the lengths of vectors created from point to point PTT transmissions between first day of departure from a wintering site to the first day at a breeding ground (spring migration) and from the first day of departure from a breeding ground to the first day at wintering site. We did not include movements within resting and staging areas into the distance calculation.

We used all positions from the years 2015, 2016, 2017 that remained after applying Freitas filter (Freitas et al. 2008) and manual inspection and removal of the remaining obvious outliers.

For mapping of migratory pathways we used all positions while birds were on migration and to characterise the use of staging and resting sites we selected just the first position (arrival) and the last position (departure) in the corresponding area. We separated the data set into breeding area specific sets to be able to display migration routes more clearly that were data set 1) migration to northern Russia (European part and Siberian part) and 2) migration to Scandinavia, Greenland and Svalbard.

We used R Studio Version 0.99.902 (R Core Team 2014) to analyse and plot migratory patterns.

Definition of terms and seasons:

We defined the positions after capture covering winter and spring season in the capture area as the first winter/spring after capture. We defined the following winter as the second winter and consequently the following spring migration as the second spring migration, the following breeding as the second breeding, the following autumn as the second autumn, the following moult as the second moult and the thereafter following winter as the third winter.

We used McCloskey et al. (2018) and Oppel et al. (2008) as a guideline to define seasons within the annual cycle.

The annual cycle of red-throated divers can be characterised by the following seasons:

- spring migration
- breeding
- moult migration
- moulting period
- autumn migration
- winter period

Because the seasonal utilisation of sites varied between individuals and among years, we chose not to define seasons or sites by specific date ranges or distance constraints, but instead defined such sites as locations where a given diver did not progress in the general migration direction for more than 5 days. Generally, we found that spring migration/staging occurred in the time period between March and June, utilisation of potential breeding sites occurred between June and September, moult migration occurred between August and October, utilisation of potential moulting sites occurred within the time period between September and December, autumn migration/staging occurred between October and January and wintering within the time period between December and May.

Duration of migration was defined as the number of days between the first day of departure from the capture, staging, wintering, breeding, moulting grounds to the first day at breeding, staging, moulting or wintering grounds.

We defined the beginning of all migrations as the date a diver left the corresponding site (wintering, breeding or moulting area). We defined the start of the first spring migration when an individual red-throated diver left the staging, wintering or capture area and started directional movements that were followed by another movement in the same direction.

We defined the end of spring migration and the beginning of the breeding season as the date the diver settled at a potential breeding location and did not progress any further in the general migration direction. We defined the end of the breeding season when an individual red-throated diver left the breeding area and started directional movements that were followed by another movement in the same direction. Some red-throated divers moved from the nest lake to adjacent marine waters following potential nest failure. We did not consider these as stagings as long the diver stayed in the potential breeding area.

Most red-throated divers moult their primary feathers simultaneously in autumn after having left the breeding area (Mendel et al. 2008). This moulting period in autumn (usually between September and December) includes a flightless period of about three weeks, possibly in areas located along the migration route between breeding and wintering areas (Berndt & Drenckhahn 1990). Hence we followed Oppel et al. (2008) and defined migrations in autumn as moult migration (trajectory from breeding area to moulting area) and autumn migration (trajectory from moulting area into wintering area). Accordingly we defined moult migration when an individual red-throated diver left the potential breeding area and started directional movements that were followed by another movement in the same direction. We defined the beginning of the moulting period (Berndt & Drenckhahn 1990; Mendel et al. 2008) as the first location after a long-distance directional movement in autumn followed by short movements in a particular area and a minimum stay of 21 days.

We defined autumn migration as directional movements that were initiated before January after moult when an individual red-throated diver left the potential moulting area and started directional movements that were followed by another movement in the same direction. If autumn migration was not evident, the start of the winter period was defined as the end of either moult migration or if movements between moulting period and wintering period were distinguishable e.g. more local coastal movements versus more large-scale/offshore movements. Individual movements were analysed with regard to potential moulting times and range of movements. Small-range coastal movements were considered to be moulting movements and first larger movements indicating birds being more mobile as start of wintering movements.

We defined wintering areas when a diver did not continue directional movement and stayed in the corresponding area for at least 4 weeks. If more than one core area was utilised within wintering season we defined movements between wintering areas as wintering movements. We used the first week of January and clear movements into wintering areas as a cut off for the latest date for autumn migration because decreasing day length generally is considered to trigger its end (Berthold 1996; Oppel et al. 2008).

We defined the end of spring, moult or autumn migration as the date the diver settled in a potential breeding, moulting or wintering area and a given diver did not progress in the general migration direction. PTTs were deployed over three separate years so ordinal date (month and day only) was used as the temporal variable allowing comparisons to be made across years.

We defined staging areas along migration routes as areas where an individual diver spend ≥ 5 days. Short stop overs < 5 days were not considered in separate analyses.

Bird mobility in the wintering area was evaluated by measuring distances that individual birds moved at equal periods. Because valid telemetry locations are often clustered due to position logging schedule; we applied an iterative sub-sampling procedure to control the number of bird locations used in the analyses and avoid overrepresentation of certain periods where several positions with short time intervals between them were logged. We stratified the collected data into weekly intervals and one position per bird was randomly drawn from each week when selecting the dataset for calculations. All locations used for calculation of home ranges in the wintering area that passed Freitas filter were used, and distances between the extracted weekly positions were measured. The re-sampling procedure was repeated 50 times for each individual, and weekly relocation distances were finally obtained by averaging all 50 measurements for every weekly relocation of each bird. This iterative sub-sampling procedure is conducted aiming to reduce the bias in otherwise arbitrary selection of several satellite telemetry locations for analyses. Actual number of subsampling iterations was determined by testing different number of iterations on actual data and inspecting mean values and variability relative to the number of iterations used. Sufficient sample size is considered reached when averaged values and standard deviation stabilise and do not vary if sample size is further increased.

5.2.2 Red-throated diver home ranges in the wintering area

Different metrics and their settings could be used to measure home ranges of tracked animals (LAVER & KELLY 2008). The commonly used minimum convex polygon (MCP) draws a simple minimum polygon around the outermost recorded locations. While this is the easiest method to use, it usually over-represents the area used as MCPs often also include areas of unsuitable habitat, especially if a bird uses more than one core wintering site over the same season. The other method that is frequently used is kernel home range analysis. However, kernel analysis also has its biases: kernels are drawn around the “cloud” of positions without accounting for their temporal distribution and spatial accuracy. Also, results of kernel analysis are sensitive to the parameter settings, and due to different software packages allowing to perform such calculations, application of the same set of rules is rarely achievable, which often restricts the comparability of the results between different studies and their interpretation.

Recently developed dynamic Brownian bridge model addresses some of the biases of the traditional kernel analysis by accounting for temporal distribution of data points, autocorrelation between the points and position error (WORTON 1989; KRANSTAUBER et al. 2012). The dynamic Brownian bridge model enables to estimate a probabilistic model of animal home range, presented as utilisation distribution (UD) in a two dimensional space. Extracting different contours from an estimated continuous distribution raster allows the assessment of different level home range use. Considering the advantages offered by the dynamic Brownian bridge modelling we used this method instead of kernel density estimators. We extracted the 95% UD contour encompassing 95% of the volume of an animal distribution in its wintering area, which is intended to represent the overall winter home range of an individual. We also extracted 50% UD, which is considered as representing the core area of the distribution. It was not assumed that the 95% UD represents equal usage of the area within it, but rather that it indicates the potential range of bird movements on wintering grounds. The 95% UD corresponds to the area in which the probability to find the tagged bird is 0.95. The 50% UD is considered as representing the core range of animal distribution with a 0.50 relocation probability.

All bird positions within a birds’ wintering area, which passed the filtering, were used for calculating home ranges using dynamic Brownian bridge models. We excluded the first two weeks following bird release after tagging from home range analyses. Also, home ranges were only calculated for individuals providing locations for at least 30 days during the wintering season. For the second and third winters all data were used from when the bird had arrived in its general wintering area. Thus, for some individuals home ranges calculated also represent autumn staging and moulting periods, which took place in the same area as wintering. The length of the wintering season represented in the home ranges varied among individuals and years and lasted between 30 and 231 days. Figure 5.1 shows all bird locations used for home range analyses.

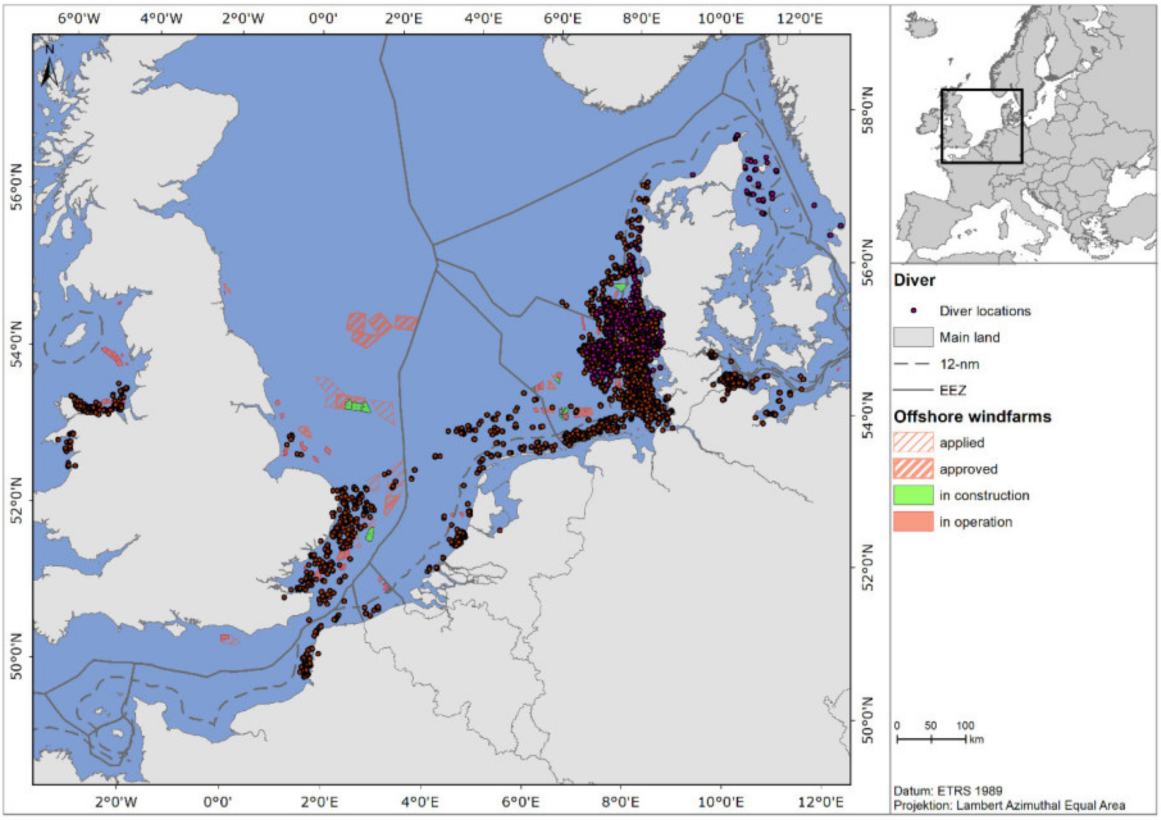


Figure 5.1 Red-throated diver locations in wintering areas as used for home range analyses.

Estimates of home range areas applying dynamic Brownian bridge model were run using the “move” package (Kranstauber & Smolla 2013) in R software (R Core Team 2018). We estimated winter home ranges separately for each individual which was tracked for at least 30 days while on wintering grounds and applied the same parameter settings for all individuals: raster resolution was set to 500 meter cell, window size of 7 locations, margin of 3 locations, time-step of 15 hours. When calculating home ranges with dynamic Brownian bridge modelling we did not expect that the algorithm would identify changes in bird behaviour based on movement patterns, because diver utilisation distribution was only assessed for the wintering stage of the annual cycle. Instead of using constant location error, we assigned mean errors to each location based on Argos location quality class as suggested by Douglas et al. (2012) and the same was also used by Gray et al. (2017) when calculating home ranges of red-throated divers tracked in North America (Table 4.2).

Table 5.1 Argos location classes and their mean errors (according to Douglas et al. 2012) used in the dynamic Brownian bridge models.

Argos location class	Mean error, m
3	1,500
2	3,300
1	7,600
0	17,200
A	15,000
B	20,900

Having calculated individual home range rasters, we extracted 95% and 50% UD contours for each individual and converted them to polygons. Prior to calculating home range areas, these polygons were intersected with land polygon and only the aquatic part of diver home ranges was retained.

5.2.3 Site fidelity analysis

The initial intention was to asses wintering site fidelity of red-throated divers using Kaplan-Meyer procedure, as suggested by Iverson & Esler (2006) and, for instance, applied by some of the authors of this study when assessing site fidelity of common eiders (*Somateria mollissima*) during the winter period in the Fehmarn Belt (FEBI 2013). However, shorter than expected lifetime of the transmitters did not allow to perform such an analysis in an unbiased way and with sufficient sample size. Instead, we calculated simple percentage of returning individuals that were tracked long enough over two winters. Also, we compared the 95% and 50% UD home ranges by assessing the percentage of overlap of these areas for individual birds relative to the previous winter season.

5.2.4 Stable isotope analysis - Additional analysis

The ratio of stable isotopes differs regionally throughout the world and leaves distinct patterns in animal tissues which allow to determine the area where a specific tissue is built up and thereby offers a wide range of options to study animal movements (Rubenstein & Hobson 2004; Hobson & Wassenaar 2019). Ratios of stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) are widely used to characterise trophic relationships within marine food webs. Stable isotope ratios of a consumer are related to those of its prey. Depending on the area where the consumer is foraging the carbon and nitrogen values can vary in relation to the food chain and primary producers so that area specific signatures are accumulated which can be distinguished.

We sampled neck feathers of all red-throated divers captured during this project (Table 4.2) aiming to determine the potential moulting regions of these birds in the previous year by using stable isotope analysis. Neck feathers of red-throated divers are particularly suitable for this purpose as they are changed at the same time as primary feathers in autumn when divers moult into wintering plumage. This ensures that the feather sample was built in the autumn moulting area. The tracking data served as a reference to assign isotope signatures to corresponding moulting locations.

The isotope signatures aim to distinguish between the North Sea and the Baltic Sea and present information about moulting sites from the season previous to feather sampling (captures). The data can be compared with tracking data that present information about moulting areas after captures in a higher resolution and thus information on moulting areas of two consecutive seasons is available. This allows some insight into moulting site fidelity by combining the results of both methods.

Feather samples were stored in plastic bags until analysis. To remove surface contaminants, feathers were individually cleaned in a chloroform/methanol solution (2/1, v/v), dried and cut into tiny fragments with stainless steel scissors. One feather per individual was analysed. To perform stable isotope analysis, a subsample of 0.3 to 0.5 mg was placed into tin cups (Table 5.2). Samples were analysed at LIENSs Stable Isotope Facility University of La Rochelle. Carbon and nitrogen ratios were determined with a continuous-flow mass spectrometer (Delta V Advantage or Delta V Plus, Thermo Scientific, Bremen, Germany) coupled to an elemental analyser (Flash EA 1112 or Flash 2000, Thermo Scientific, Milan Italy). Measurements of internal laboratory standards were conducted using acetanilide (Thermo Scientific) and peptone (Sigma-Aldrich), and indicated an experimental precision of ± 0.15‰ for both elements. Results are expressed in parts per thousand (‰), in the usual δ notation relative to Vienna Pee Dee Belemnite for δ13C and atmospheric N2 for δ15N, following the formula: δ13C or δ15N = [(Rsample/Rstandard) - 1] x 103, where R is 13C/12C or 15N/14N, respectively.

Table 5.2 Sample ID (Argos ID) of sampled diver and weight of feather sample used for stable isotope analysis (d 13C/12C (‰); d 15N/14N (‰)

ARGOS-ID	Weight (mg)	ARGOS-ID	Weight (mg)	ARGOS-ID	Weight (mg)
146437	0.46	146437_2	0.40	158320	0.42
146438	0.43	158326	0.37	158321	0.43
146439	0.41	158331	0.40	158322	0.41
146440	0.38	158332	0.44	158323	0.41
146441	0.37	158327	0.42	158324	0.42
146442	0.40	158328	0.45	158325	0.40
146443	0.39	158333	0.39	52062	0.35
146444	0.36	158329	0.40	56572	0.37
146445	0.38	158330	0.42	57332	0.36
146446	0.40	158316	0.40	57346	0.45
146449	0.41	158317	0.41	57345	0.40
146450	0.40	158334	0.39	52063	0.40
146451	0.40	158318	0.43	57331	0.33
156452	0.38	158335	0.40	57339	0.34
146453	0.42	158319	0.45	57335	0.35

5.3 Results

5.3.1 Origin of divers wintering in the German Bight, migration routes and migration characteristics

5.3.1.1. Spring migration

Red-throated divers captured during this study originate from four different breeding regions: northern Russia (European part and Siberian part), Scandinavia (Norway), Greenland and Svalbard (for all individual bird tracks see Appendix A.1). The majority of tagged birds migrated to northern Russia (n = 25; 73.5%; Figure 5.2). Of these 25 birds, 76% migrated to the Siberian part (Yamal, Gydan and Taimyr peninsulas and West Siberian Plain) and 24% in the European part of northern Russia (Kola Peninsula, Kanin Peninsula, Pechora Sea and Novaya Zemlya). Four red-throated divers migrated to Norway, two to Greenland and two to Svalbard. (Figure 5.3). Divers migrated to Siberia mainly along the Baltic Sea via the Gulf of Finland or via the Gulf of Bothnia to the White Sea or to the Barents Sea. One individual migrated along the Norwegian coast around the North Cape. The two birds that migrated to Greenland followed two different migration routes: one individual moved to northern Norway and then to East-Greenland and the other one moved first to Scotland, then to Iceland and then to West-Greenland. Out of the three birds that migrated to Norway two performed just short stop overs of less than 5 days and no stagings of minimum 5 days along their migration, and one moved straight to the Sognefjord and stayed there 30 days before moving inland to the potential breeding location. Of the two individuals that migrated to Svalbard one moved straight and one stayed 6 days about 300 km east of the North Cape. Red-throated divers migrating to northern Russia showed individual variance and two different patterns. Some individuals departed from the eastern part of the German Bight directly to the Baltic Sea while crossing land (Denmark and Schleswig Holstein) and the other part moved along the coast of Schleswig Holstein and Denmark. Of the birds migrating to Norway we also found two patterns of either staying coastal and moving around the southern tip of Norway or migrating north through Oslofjord and taking an about 400 km flight over land. Most of the migration routes followed coastlines and land masses were usually crossed at shortest possible distance. The longest inland flight was accomplished by a diver breeding east of the Ural and to reach the breeding ground the birds flew about 1,400 km inland, most likely in non-stop flights.

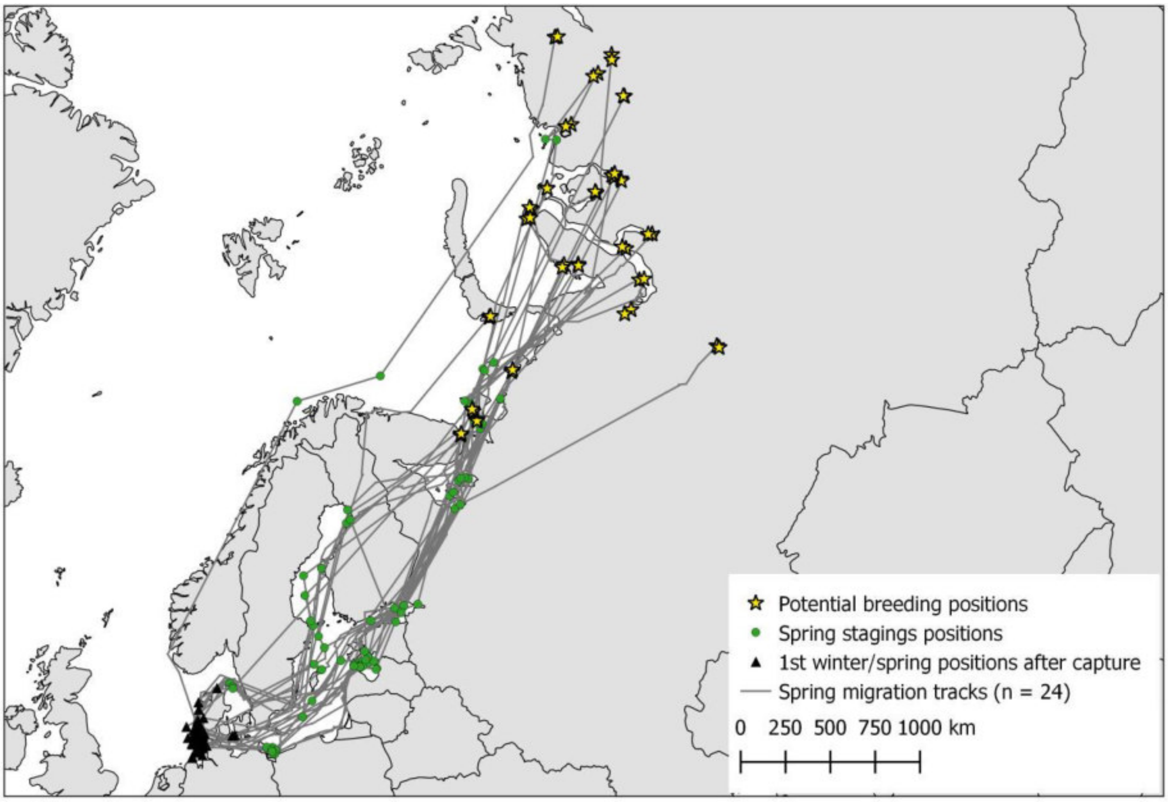


Figure 5.2 *Spring migration tracks and positions of staging and breeding areas of red-throated divers migrating to northern Russia. Black triangles indicate positions after capture in the eastern German Bight until start of spring migration. Green dots indicate positions in staging areas and yellow stars indicate positions in potential breeding areas. For each identified area of stay only the first and last position in the corresponding area is displayed per individual.*

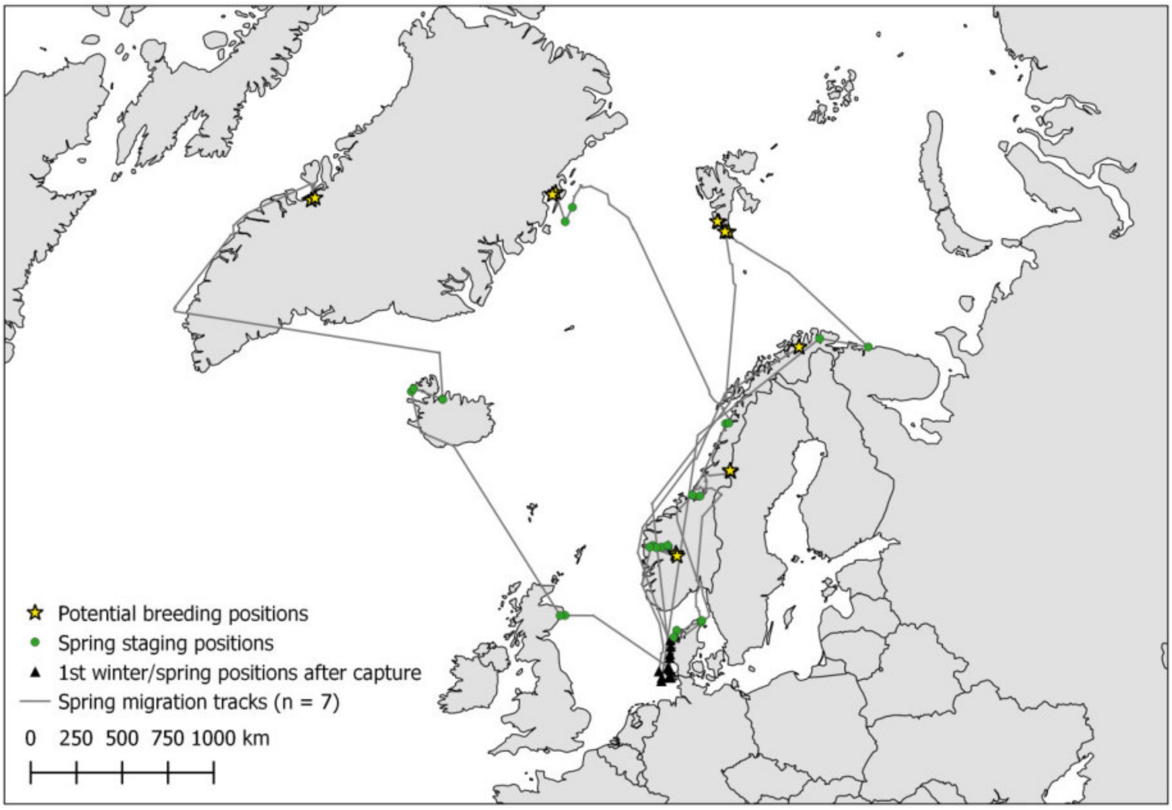


Figure 5.3 *Spring migration tracks and positions of staging and breeding areas of red-throated divers migrating to Norway (n = 3), Svalbard (n = 2) and Greenland (n = 2). Black triangles indicate positions after capture in the resting/wintering area until start of spring migration. Green dots indicate positions in staging areas and yellow stars indicate positions in potential breeding areas. For each identified area of stay the first and last position in the corresponding area is displayed per individual.*

5.3.1.2. Moult and autumn migration

Autumn migration followed more or less the same routes as spring migration (Figure 5.4, Figure 5.5). Birds from northern Russia moved along the Baltic Sea to their moulting sites (n = 17) and then further on to their wintering areas (n = 13) with the exception of one bird that moved along the Norwegian coast to its moulting site in the North Sea. One individual from West-Greenland followed a similar route as in spring via Iceland and probably moulted in Scotland, however, while the bird passed Iceland on spring migration, it flew along the east coast in autumn. Contrary to spring migration one individual from Svalbard moved without any longer stagings and just short stop overs of less than 5 days to its moulting location in the North Sea. In our data set the North Sea (eastern German Bight) represents the main wintering area for 54% of red-throated divers tagged in the German Bight (n = 7 of 13; six breeding in northern Russia and one in Svalbard). The remaining birds used other areas such as the southern Bight, the Irish Sea or the Baltic Sea as main wintering areas. These birds used the capture area (eastern German Bight) either as a staging area or a short stop over site during migration (spring or autumn) and one individual that used the Baltic Sea for wintering did not return to the capture area at all. Another individual commuted back and forth between the Baltic Sea and the North Sea (capture area) during wintering time.

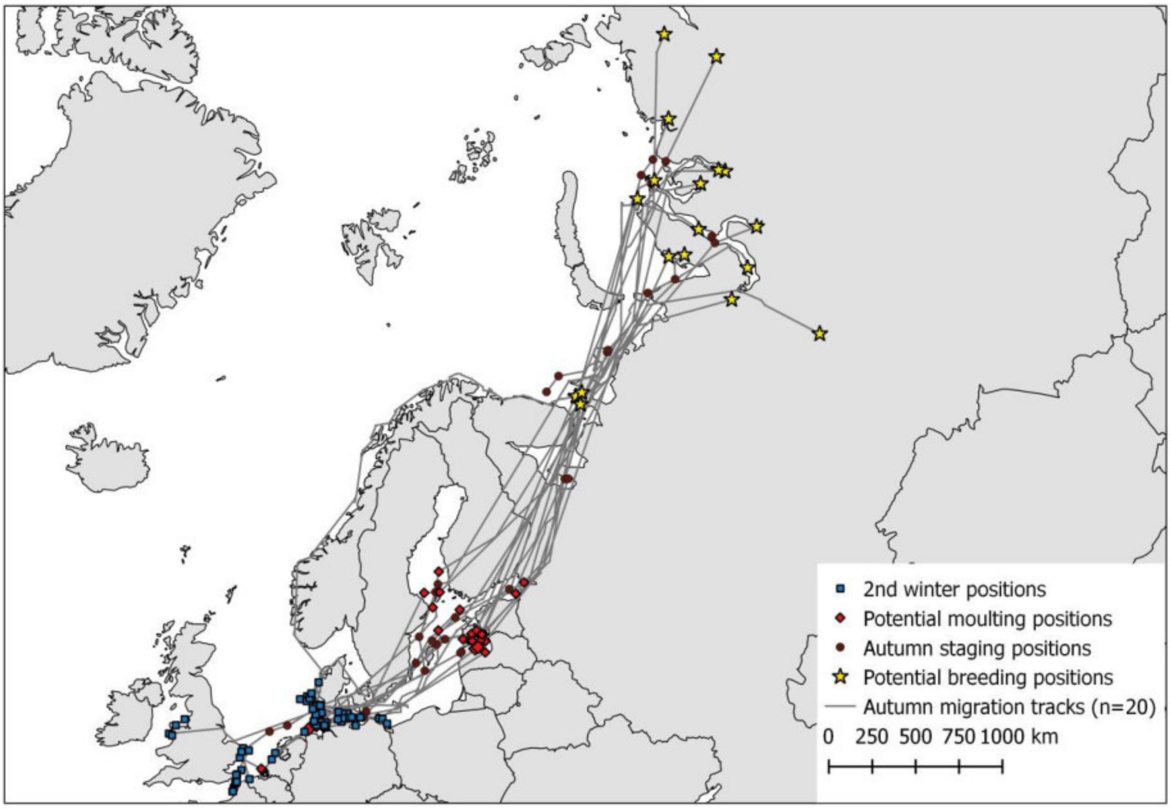


Figure 5.4 *Autumn migration tracks and positions of breeding, staging, potential moulting and wintering areas (2^nd^ winter) of red-throated divers originating from northern Russia. Yellow stars indicate positions in potential breeding areas. Brown dots indicate positions in autumn staging areas, red diamonds indicate positions in potential moulting areas and blue squares indicate positions in wintering areas (2^nd^ winter). For each identified area of stay the first and last position in the corresponding area is displayed per individual.*

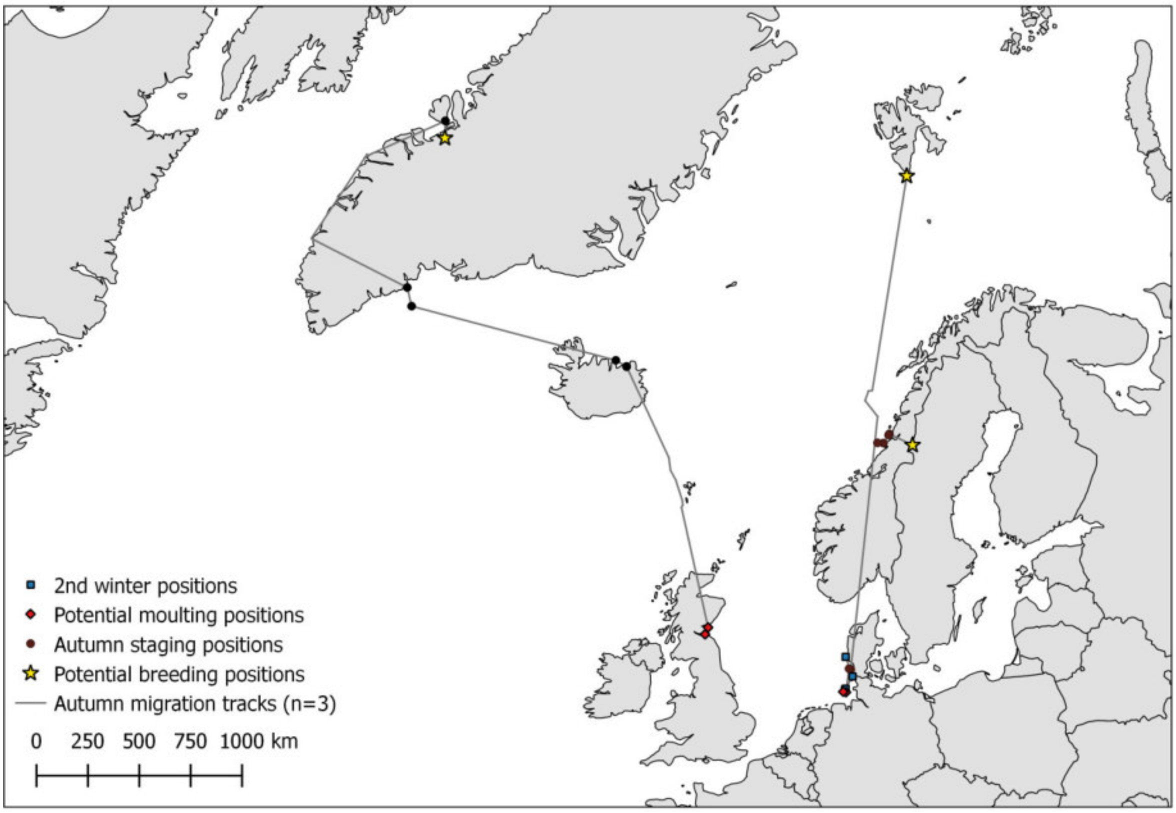


Figure 5.5 *Autumn migration tracks and positions of breeding, staging, potential moulting and wintering areas (2nd winter) of red-throated divers originating from West-Greenland (n = 1), Svalbard (n = 1) and Norway (n = 1). Yellow stars indicate positions in potential breeding areas. Brown dots indicate positions in autumn staging areas, red diamonds indicate positions in potential moulting areas and blue squares indicate positions in wintering areas (2nd winter). For each identified area of stay the first and last position in the corresponding area is displayed per individual.*

5.3.2 Migration distances

5.3.2.1. Spring migration

Red-throated divers captured in the North Sea moved long distances to potential breeding sites. Migration distances can only be given as minimum estimates assuming straight flight paths between consecutive Argos positions. The average distance to potential breeding sites in northern Russia was 4,000 km with a maximum of 4,980 km to the Taimyr Peninsula in Siberia and a minimum distance of 2,200 km to the Kola Peninsula. The overall furthest distance amounted to more than 5,000 km to Greenland and the shortest with 850 km to Norway.

5.3.2.2. Moult and autumn migration

Starting at the breeding location the furthest documented distance to the wintering area added up to more than 5,000 km. This diver (ID 146442) headed from northern Russia to the Irish Sea. Birds that wintered in the North Sea had moved on average 3,250 km (min. 2,900 km; max. 4,250 km).

5.3.3 Migration timing

5.3.3.1. Spring migration

Starting from the North Sea, red-throated divers spent on average 42.3 days for spring migration to northern Russia (n = 24), 31 days to Norway, 34.5 days to Greenland and 12.5 days to Svalbard with a maximum time of 60 days to Pechora Sea (Russia) and a minimum time of 4 days to the North Cape (Norway). Analysing migration patterns for the first winter after capture, the earliest departure from the eastern German Bight-North Sea took place in the last week of March (6.3%) with most birds (31.3%) departing in the first two weeks of May and none later than mid-May.

5.3.3.2. Autumn migration

The average period spent on autumn migration (between last position in the breeding area and first position in wintering area), including moulting period added up to a mean of 97 days (SD ± 23.76) with a minimum period of 66 days and a maximum period of 124 days.

Thirteen red-throated divers could be tracked until arrival in their wintering area. 53% returned to the German Bight and 47% utilised other areas for wintering and used the German Bight during autumn migration as a staging or stop-over area. Most birds (52%) arrived between beginning and mid-October (05.10. – 17.10.) and the earliest arrived in the second week of September to the potential moulting area. Considering birds that used the German Bight only as a wintering area in the second winter after capture, most birds (40%) arrived in the first week of January with the earliest start of wintering in this area in mid-November (Figure 5.6–Figure 5.8).

Beside the North Sea, the Gulf of Riga was identified as an important spring staging area and moulting area in autumn for red-throated divers originating from northern Russia.

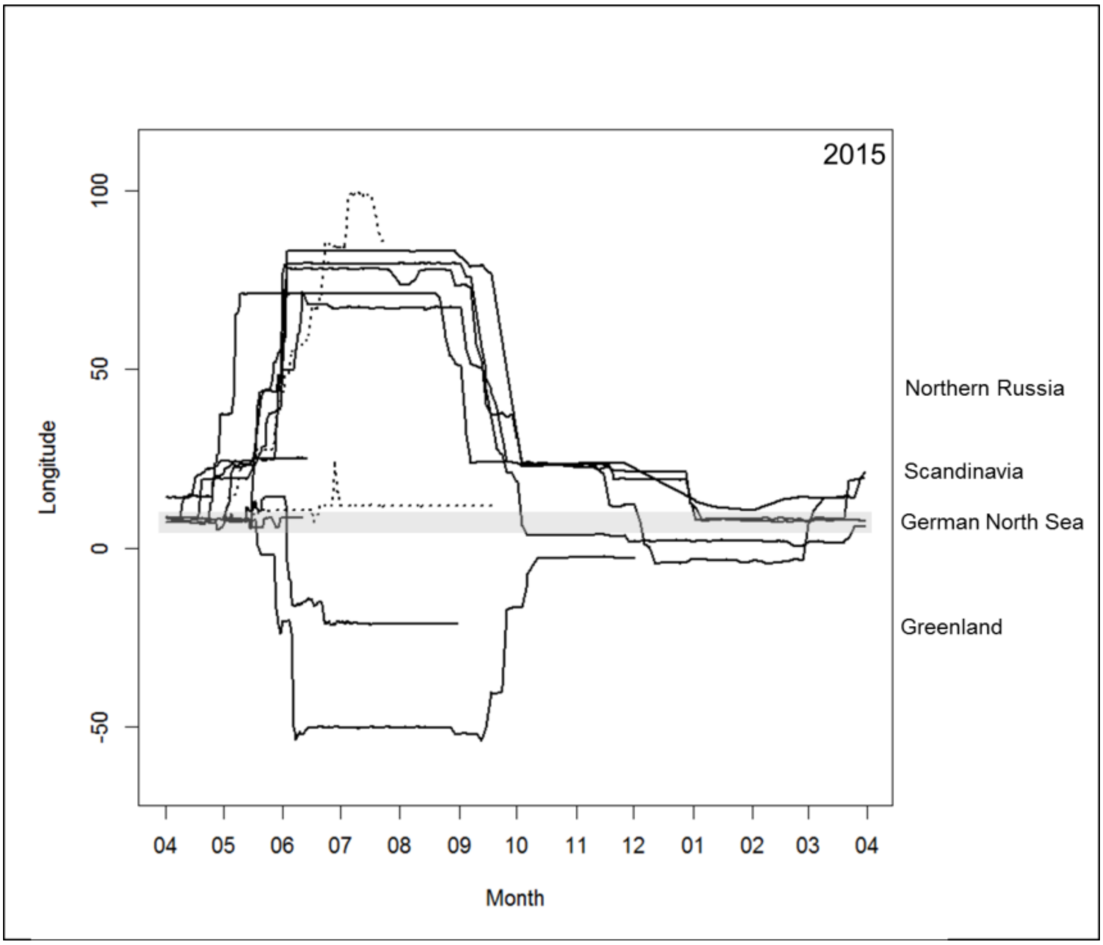


Figure 5.6 Migration patterns of red-throated divers tagged in the German North Sea in 2015 (n = 11) throughout their annual cycle along the longitude. The grey box represents the capture and wintering area in the German North Sea. The blue dotted line indicates the potential breeding regions. Individual migrations are indicated as black lines and migrations of non-breeders or failed breeders are indicated as black dotted lines.

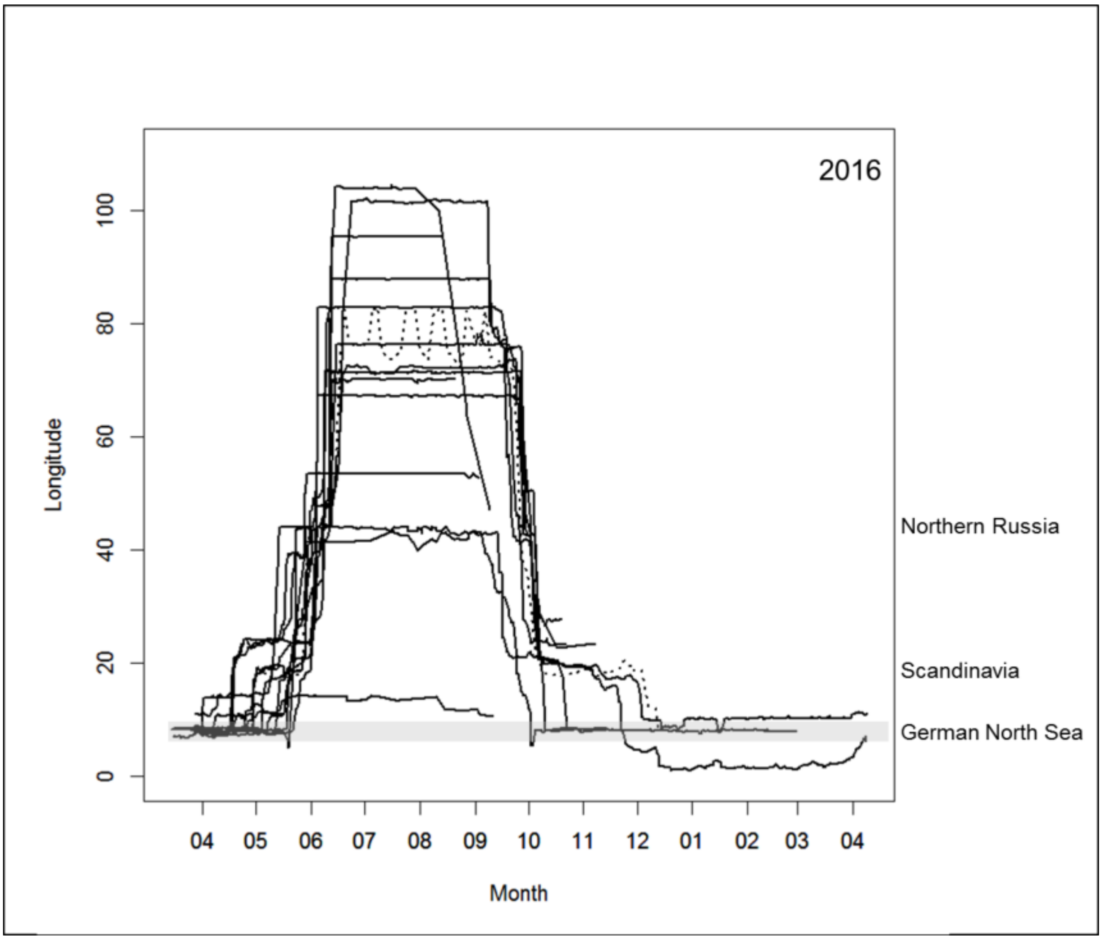


Figure 5.7 Migration patterns of red-throated divers tagged in the German North Sea in 2016 (n = 15) throughout their annual cycle along the longitude. The grey box represents the capture and wintering area in the German North Sea. The blue dotted line indicates the potential breeding regions. Individual migrations are indicated as black lines and migrations of non-breeders or failed breeders are indicated as black dotted lines.

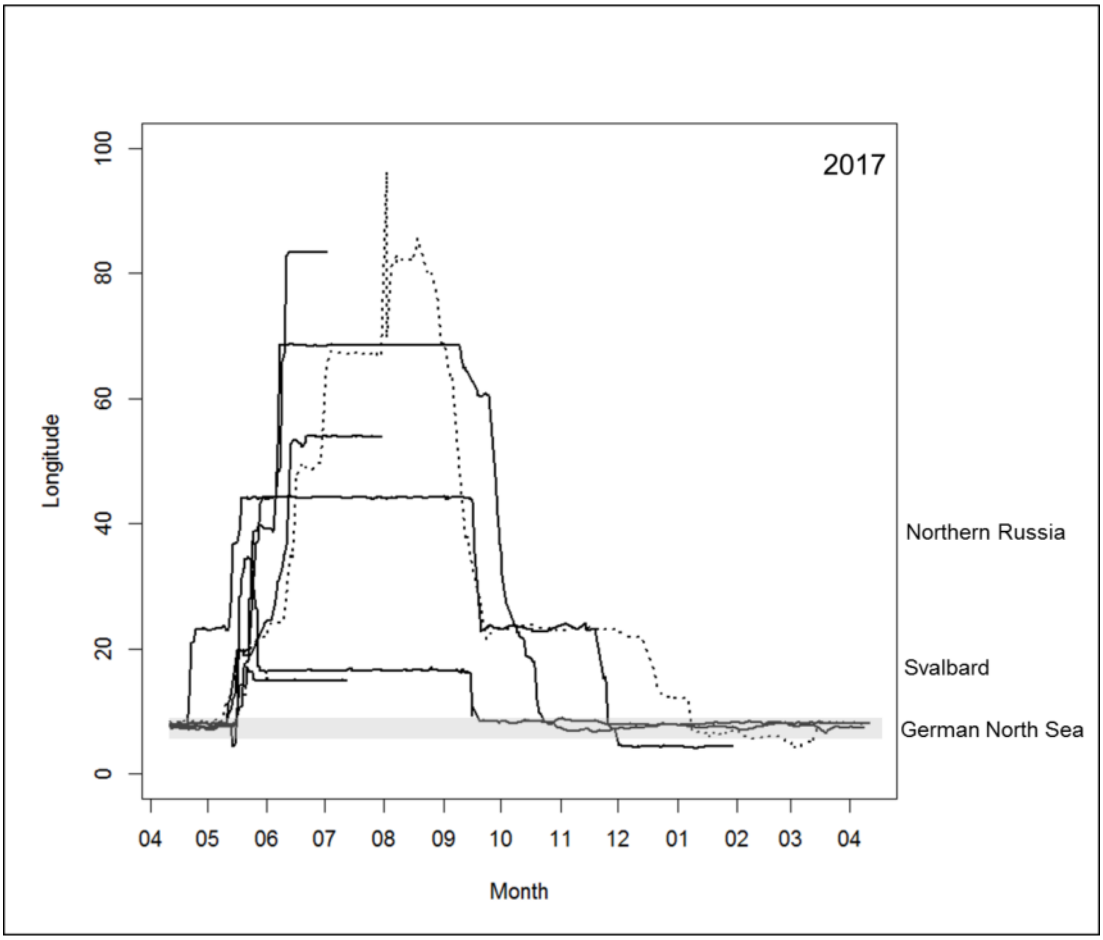


Figure 5.8 Migration patterns of red-throated divers tagged in the German North Sea in 2017 (n = 7) throughout their annual cycle along the longitude. The grey box represents the capture and wintering area in the German North Sea. The blue dotted line indicates the potential breeding regions. Individual migrations are indicated as black lines and migrations of non-breeders or failed breeders are indicated as black dotted lines.

5.3.4 Fidelity to migration routes and different sites used during the annual cycle

Red-throated diver tracking data of individuals which could be tracked for another season were analysed with regard to the species fidelity to migration routes and sites used during the annual cycle. Tracking data indicate that individual red-throated divers use the same general routes and areas year after year, however showing some flexibility and variation when looking at detailed tracks. For example diver ID 146444 used different routes when passing the Baltic during spring migration with migrating via the Gulf of Finland during the first spring and choosing the Gulf of Bothnia during the second spring (Figure 5.13). Also some variation in the use of different staging sites was observed, e.g. diver ID 146440 staging in the Gulf of Riga during the first spring, but skipping this area during the second spring migration (Figure 5.11). Some unexpected individual patterns in migration routes indicate that birds may stick to an individually learnt migration routes even if it includes detours of several hundred kilometres as observed for one bird migrating to Svalbard via a detour to Kola Peninsula (Russia) (Figure 5.15).

Winter site fidelity analysis results are displayed in chapter 5.3.6.3.

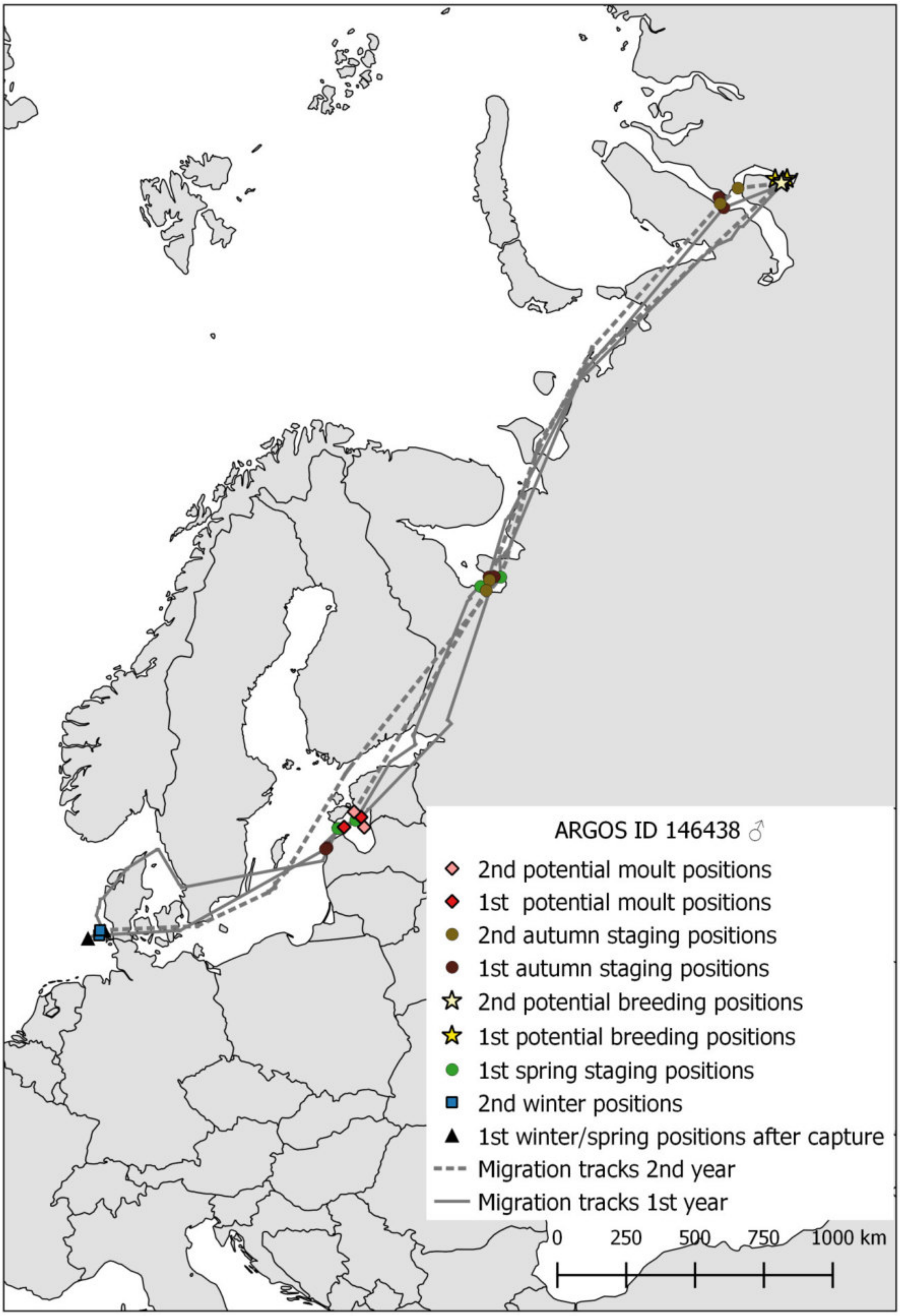


Figure 5.9 *Migration tracks and positions of breeding, staging, potential moulting and wintering areas of two years presented for red-throated diver ID 146438 For each identified area of stay only the first and last position in the corresponding area is displayed per individual.*

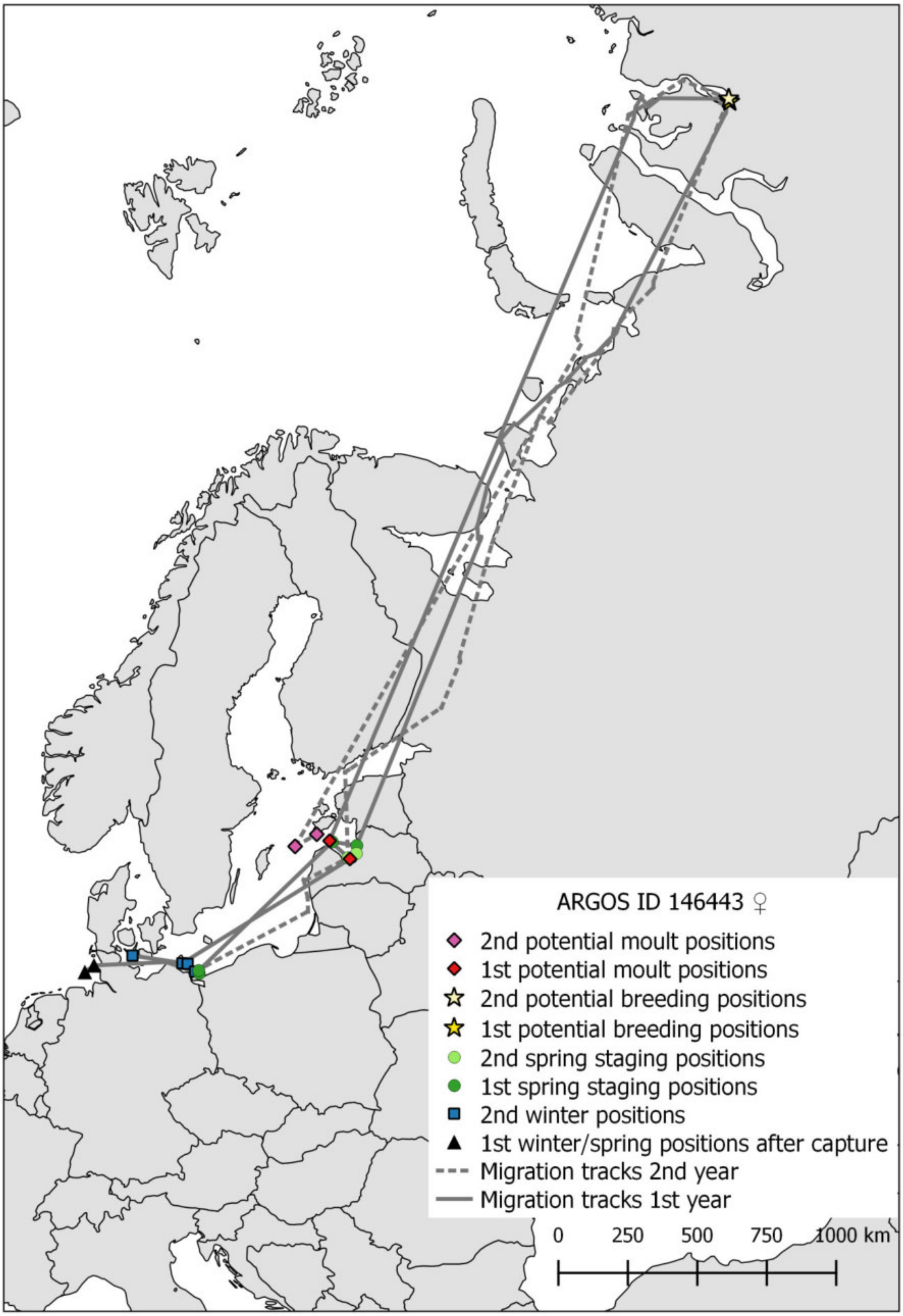


Figure 5.10 Migration tracks and positions of breeding, staging, potential moulting and wintering areas of two years presented for red-throated diver ID 146443. For each identified area of stay only the first and last position in the corresponding area is displayed per individual.

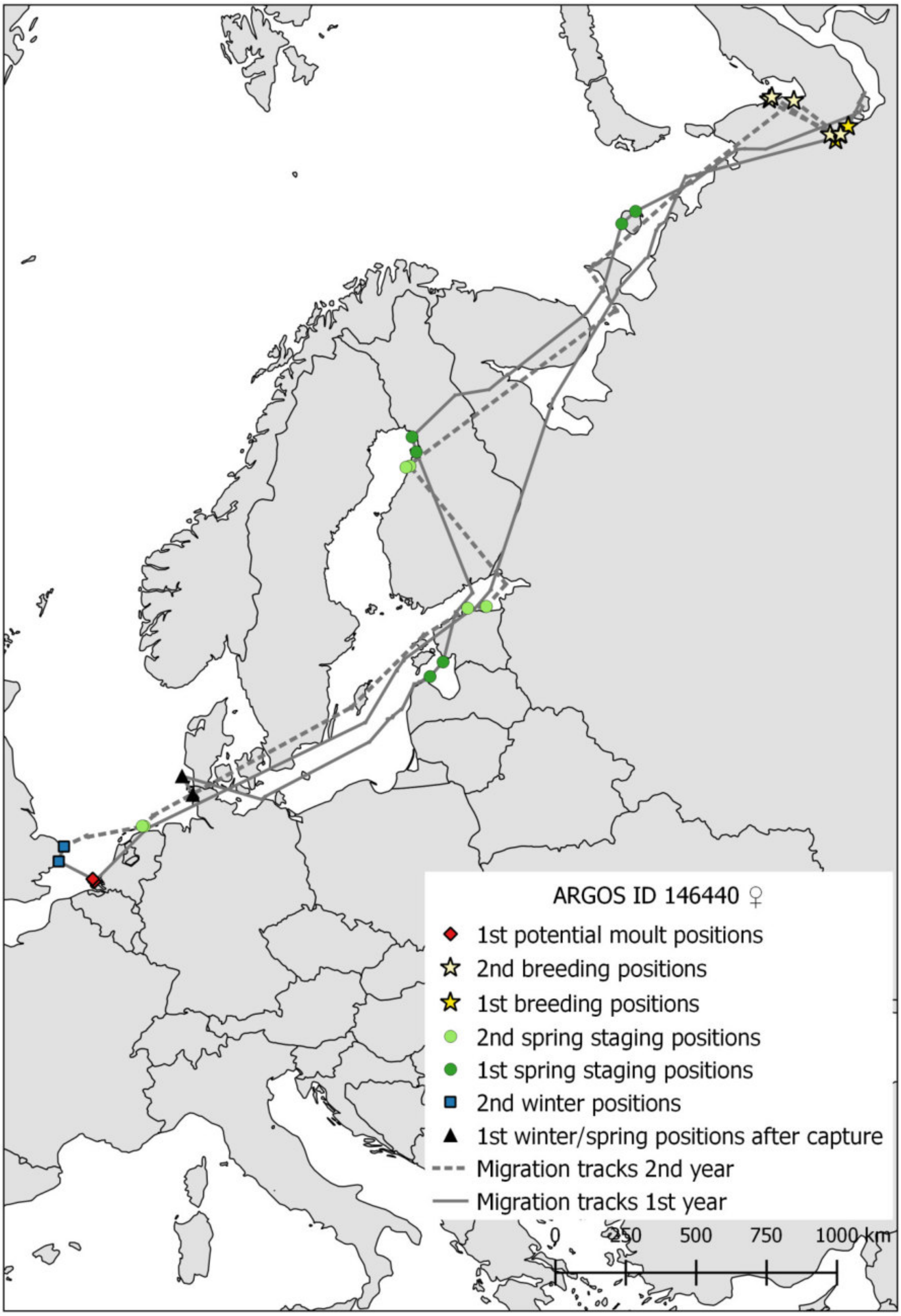


Figure 5.11 *Migration tracks and positions of breeding, staging, potential moulting and wintering areas of two years presented for red-throated diver ID 146440. For each identified area of stay only the first and last position in the corresponding area is displayed per individual.*

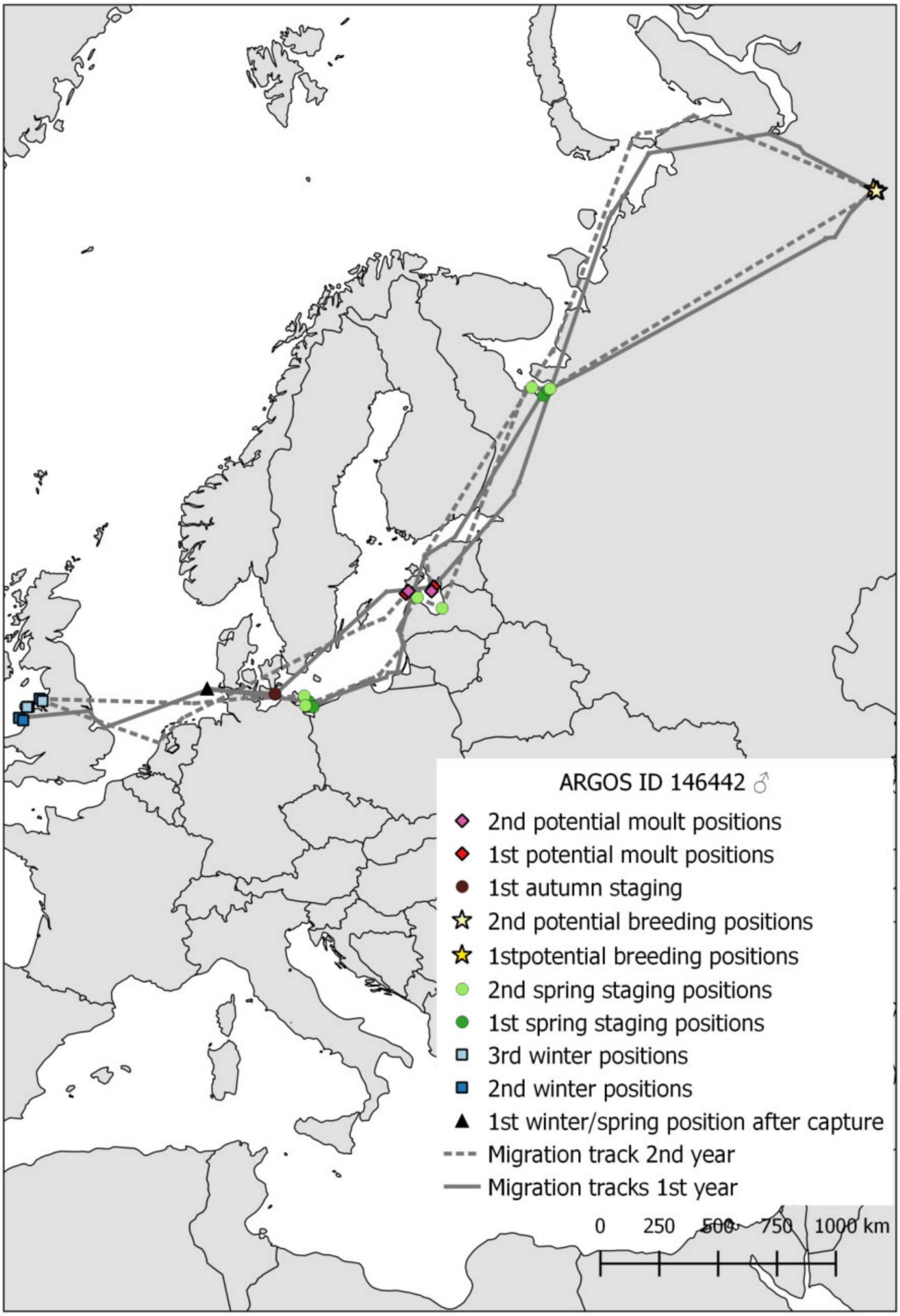


Figure 5.12 Migration tracks and positions of breeding, staging, potential moulting and wintering areas of two years presented for red-throated diver ID 146442. For each identified area of stay only the first and last position in the corresponding area is displayed per individual.

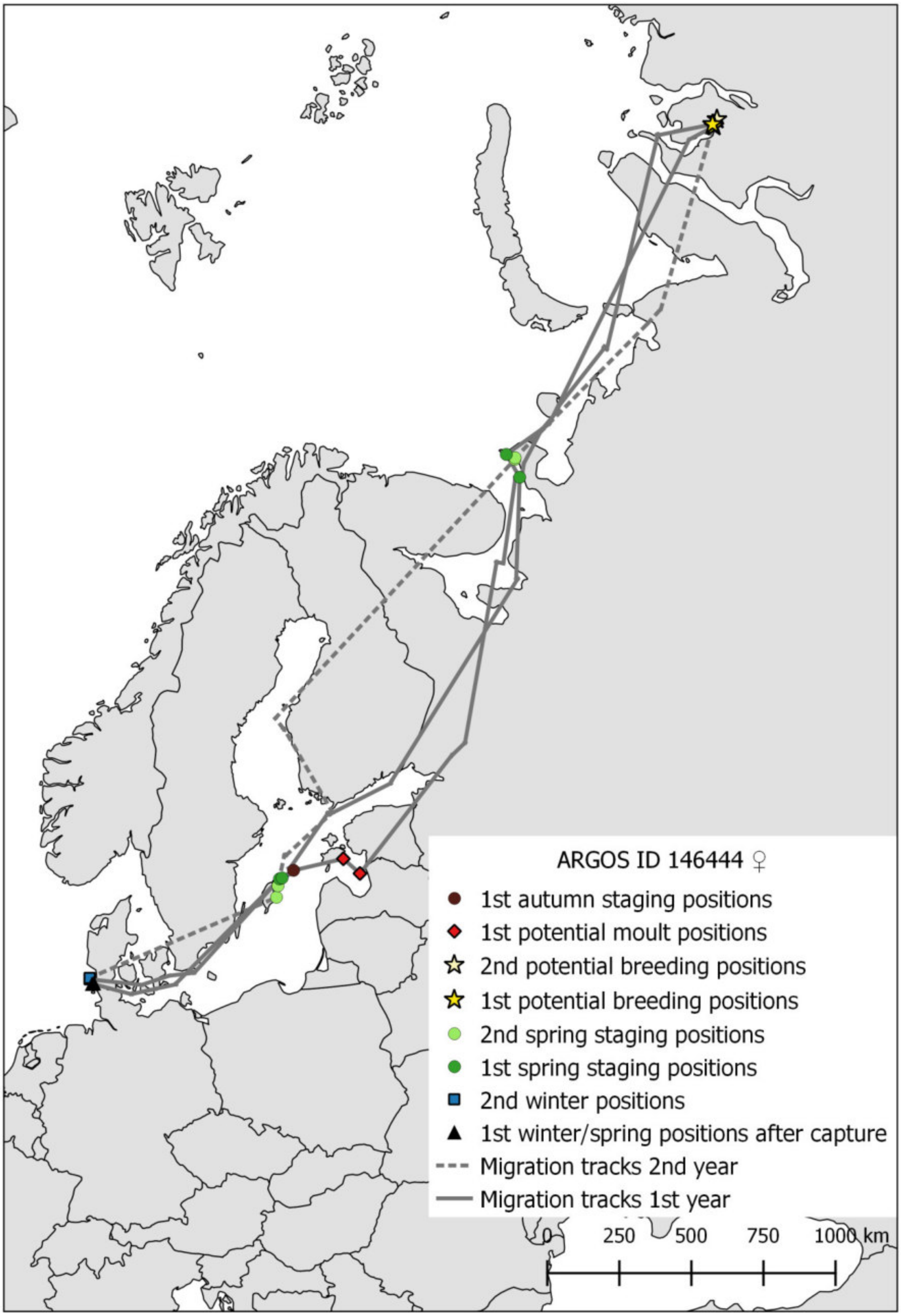


Figure 5.13 Migration tracks and positions of breeding, staging, potential moulting and wintering areas of two years presented for red-throated diver ID 146444. For each identified area of stay only the first and last position in the corresponding area is displayed per individual.

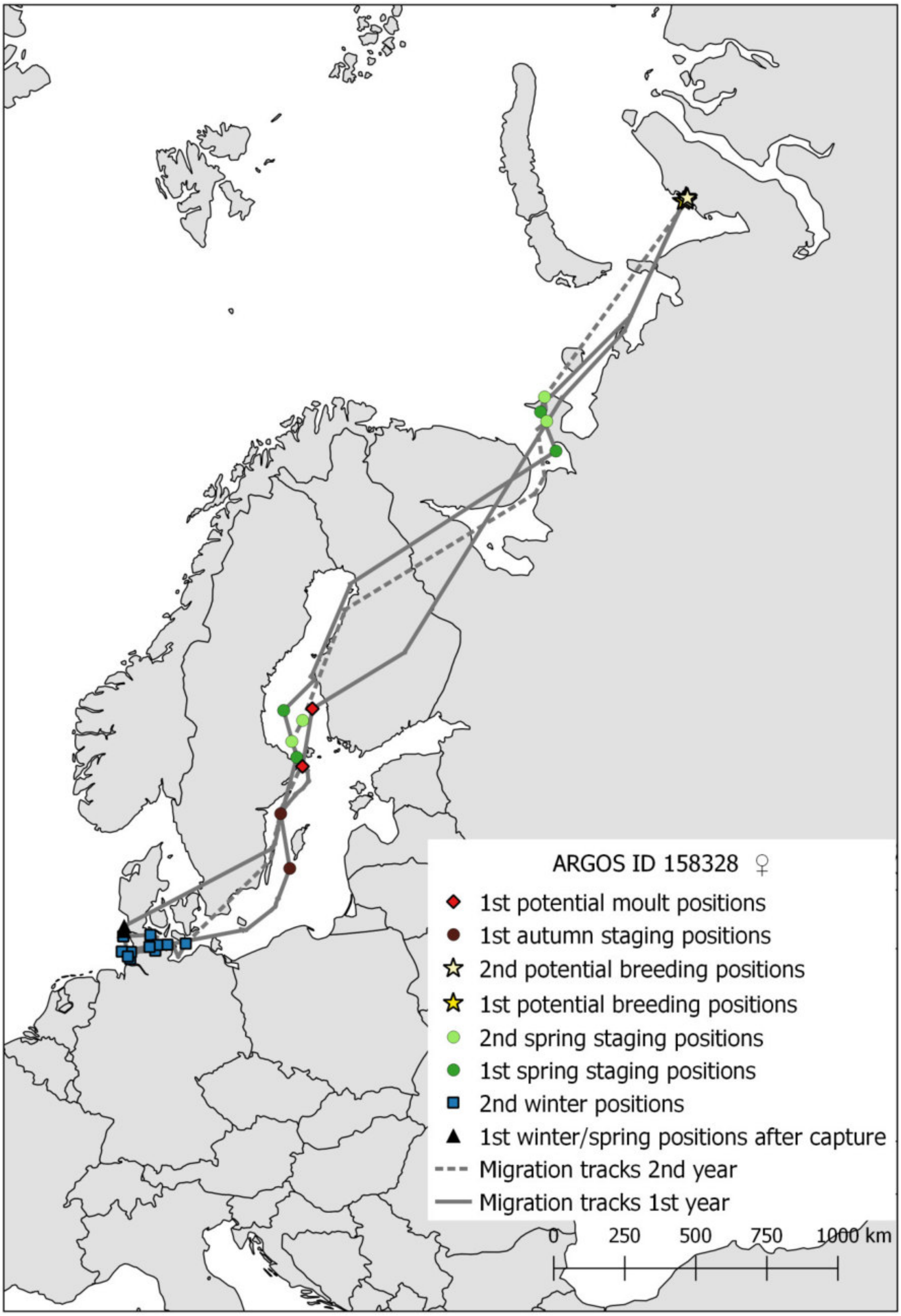


Figure 5.14 Migration tracks and positions of breeding, staging, potential moulting and wintering areas of two years presented for red-throated diver ID 158328. For each identified area of stay only the first and last position in the corresponding area is displayed per individual.

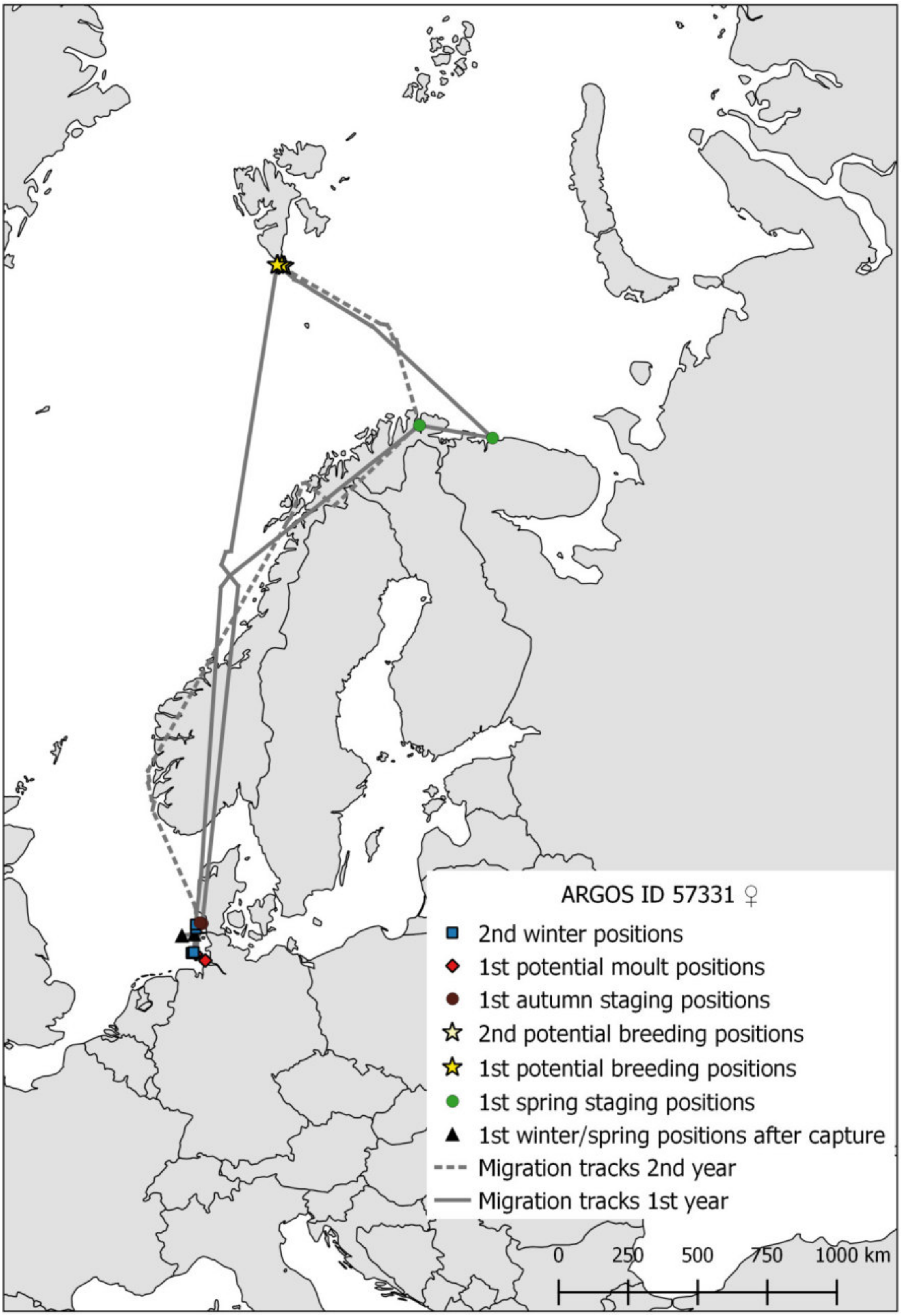


Figure 5.15 *Migration tracks and positions of breeding, staging, potential moulting and wintering areas of two years presented for red-throated diver ID 57331. For each identified area of stay only the first and last position in the corresponding area is displayed per individual.*

5.3.5 Stable isotope analysis

We received clearly distinguishable isotope signatures from red-throated divers that either moulted in the North Sea or birds moulted in the Baltic Sea. Of 45 individuals sampled, 53.3% (n = 24) performed their autumn moult in the Baltic Sea and 46.7% (n = 21) in the North Sea. Birds use the area as staging or wintering area and for their autumn moult. Apart from one individual all locations identified by isotope signature for the season prior to tagging matched the area identified by satellite tracking for the season after tagging (n = 17) and for the second year after tagging (n = 2).

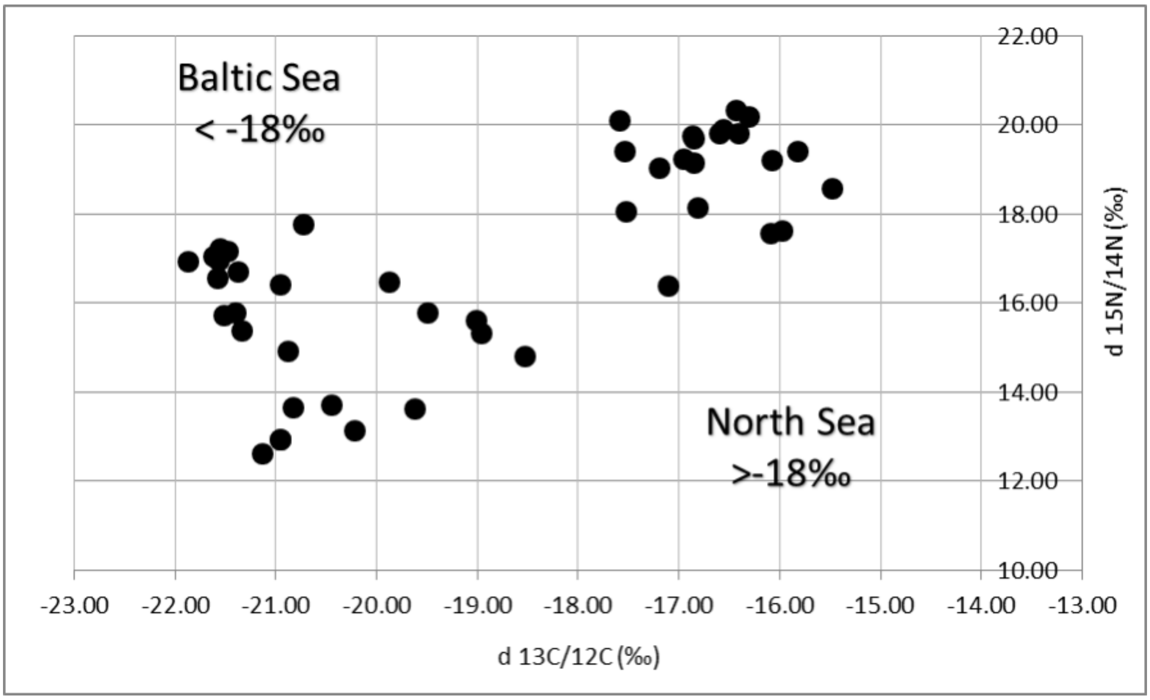


Figure 5.16 Stable isotope signatures of 45 red-throated diver feather samples assigned to the region where they were moulted. Data points showing feathers of 24 individuals moulted in the Baltic Sea and 21 individuals that moulted in the North Sea.

Table 5.3 Isotope signatures (carbon and nitrogen values) of 45 analysed red-throated divers, assignment to moult area previous to tagging and comparison with first moulting area after satellite tagging (n = 17) and second moult after tagging (n = 2).

Identifier	ARGOS-ID	Sex	d 13C/12C (‰)	d 15N/14N (‰)	Moult-area by stable isotopes	Moult-area by satellite tracking 1st year	Moult-area by satellite tracking 2nd year
Diver_2015_01	146437	♀	-19.62	13.62	Baltic Sea	n/a	n/a
Diver_2015_02	146438	♂	-21.47	17.17	Baltic Sea	Baltic Sea_ Gulf of Riga	Baltic Sea_ Gulf of Riga
Diver_2015_03	146439	♀	-16.31	20.18	North Sea	n/a	n/a
Diver_2015_04	146440	♀	-17.52	18.05	North Sea	North Sea_ Southern Bight	n/a
Diver_2015_05	146441	♀	-21.14	12.63	Baltic Sea	n/a	n/a
Diver_2015_06	146442	♂	-21.57	16.95	Baltic Sea	Baltic Sea_ Gulf of Riga	Baltic Sea_ Gulf of Riga

Identifier	ARGOS-ID	Sex	d 13C/12C (‰)	d 15N/14N (‰)	Moult-area by stable isotopes	Moult-area by satellite tracking 1st year	Moult-area by satellite tracking 2nd year
Diver_2015_07	146443	♀	-21.88	16.93	Baltic Sea	Baltic Sea_ Gulf of Riga	n/a
Diver_2015_08	146444	♀	-21.34	15.39	Baltic Sea	Baltic Sea_ Gulf of Riga	n/a
Diver_2015_09	146445	♂	-18.53	14.80	Baltic Sea	n/a	n/a
Diver_2015_10	146446	♀	-16.43	20.33	North Sea	n/a	n/a
Diver_2015_11	146449	♀	-16.09	17.56	North Sea	n/a	n/a
Diver_2015_12	146450	♀	-15.47	18.55	North Sea	n/a	n/a
Diver_2015_13	146451	♀	-21.55	17.22	Baltic Sea	n/a	n/a
Diver_2015_14	146452	♀	-16.56	19.88	North Sea	n/a	n/a
Diver_2015_15	146453	♀	-17.10	16.37	North Sea	n/a	n/a
Diver_2015_16	146437_2	♀	-15.98	17.61	North Sea	North Sea_ Scotland_ Firth of Tay	n/a
Diver_2016_01	158326	♂	-16.60	19.79	North Sea	n/a	n/a
Diver_2016_02	158331	♀	-21.52	15.73	Baltic Sea	n/a	n/a
Diver_2016_03	158332	♀	-16.85	19.14	North Sea	n/a	n/a
Diver_2016_04	158327	♀	-17.19	19.03	North Sea	North Sea_ German Bight_ North Frisia	n/a
Diver_2016_05	158328	♀	-16.87	19.74	North Sea	Baltic Sea_ Gulf of Bothnia	n/a
Diver_2016_06	158333	♀	-20.22	13.14	Baltic Sea	n/a	n/a
Diver_2016_07	158329	♀	-16.95	19.24	North Sea	n/a	n/a
Diver_2016_08	158330	♂	-21.37	16.69	Baltic Sea	n/a	n/a
Diver_2016_09	158316	♀	-21.40	15.78	Baltic Sea	n/a	n/a
Diver_2016_10	158317	♀	-20.44	13.70	Baltic Sea	n/a	n/a
Diver_2016_11	158334	♀	-20.95	12.94	Baltic Sea	Baltic Sea_ Gulf of Bothnia	n/a
Diver_2016_12	158318	♀	-16.85	19.70	North Sea	n/a	n/a
Diver_2016_13	158335	♀	-20.88	14.90	Baltic Sea	n/a	n/a
Diver_2016_14	158319	♀	-16.40	19.80	North Sea	n/a	n/a
Diver_2016_15	158320	♀	-21.61	17.06	Baltic Sea	Baltic Sea_ Gulf of Riga	n/a
Diver_2016_16	158321	♀	-21.58	16.57	Baltic Sea	Baltic Sea_ Gulf of Riga	n/a
Diver_2016_17	158322	♀	-16.81	18.15	North Sea	n/a	n/a
Diver_2016_18	158323	♀	-15.81	19.40	North Sea	n/a	n/a
Diver_2016_19	158324	♂	-19.01	15.61	Baltic Sea	Baltic Sea_ Northern Baltic Proper	n/a
Diver_2016_20	158325	♀	-20.82	13.64	Baltic Sea	n/a	n/a
Diver_2017_01	52062	♀	-17.54	19.41	North Sea	n/a	n/a
Diver_2017_02	56572	♂	-20.73	17.77	Baltic Sea	n/a	n/a
Diver_2017_03	57332	♀	-18.96	15.32	Baltic Sea	n/a	n/a

Identifier	ARGOS-ID	Sex	d 13C/12C (‰)	d 15N/14N (‰)	Moult-area by stable isotopes	Moult-area by satellite tracking 1st year	Moult-area by satellite tracking 2nd year
Diver_2017_04	57346	♀	-20.96	16.40	Baltic Sea	Baltic Sea_Gulf of Riga	n/a
Diver_2017_05	57345	♂	-17.59	20.09	North Sea	North Sea_German Bight_East Frisia	n/a
Diver_2017_6	52063	♂	-19.88	16.47	Baltic Sea	n/a	n/a
Diver_2017_7	57331	♀	-16.89	20.17	North Sea	North Sea_German Bight_North Frisia	n/a
Diver_2017_8	57339	♂	-19.49	15.78	Baltic Sea	Baltic Sea_Gulf of Riga	n/a
Diver_2017_9	57335	♀	-16.07	19.20	North Sea	n/a	n/a

5.3.6 Winter area use and movements

5.3.6.1. Winter home ranges

In total 28 winter home ranges were assessed for 22 individual divers; home ranges of six individuals were calculated for two different consecutive winter seasons (Table 5.4). Home ranges of 16 individuals were calculated for the first winter season, soon after they have been tagged but not including the first two weeks following bird release. The majority of birds, however, did not stay on wintering grounds right after tagging long enough for home range estimates (minimum 30 days) due to spring migration.

Table 5.4 List of bird ID (Argos ID), winter seasons, dates and region characterising when and where winter home ranges were calculated. Winter season in this analysis includes the full period a bird stayed in the wintering area, partly including autumn staging and moulting periods; winter 1 only represents the late winter period after bird tagging and not a full winter season.

Bird ID	Winter 1: dates from - to		Winter 2: dates from - to		Winter 3: dates from - to		Region
id-52062	2017-04-08	2017-05-09					North Sea
id-57331	2017-04-12	2017-05-13	2017-09-20	2018-05-08			North Sea
id-57332	2017-04-08	2017-05-09					North Sea
id-57335	2017-04-11	2017-05-11					North Sea
id-57339			2018-01-09	2018-04-20			North Sea
id-57345	2017-04-08	2017-05-14	2017-10-26	2018-05-16			North Sea
id-57346			2017-11-25	2018-02-07			North Sea
id-146438	2015-04-03	2015-05-03	2016-01-06	2016-04-27			North Sea
id-146440			2015-12-02	2016-03-23			North Sea
id-146442			2015-12-16	2016-03-02	2016-12-04	2017-02-06	Irish Sea
id-146444			2016-01-09	2016-03-23			North Sea
id-158317	2016-03-26	2016-05-02					North Sea
id-158318	2016-03-26	2016-05-20					North Sea
id-158323	2016-03-27	2016-05-16					North Sea

Bird ID	Winter 1: dates from - to		Winter 2: dates from - to		Winter 3: dates from - to		Region
id-158324			2016-11-22	2017-04-08			North Sea
id-158325	2016-03-28	2016-05-17					North Sea
id-158327	2016-03-13	2016-05-04	2016-10-22	2017-02-28			North Sea
id-158328	2016-03-14	2016-04-28	2016-12-03	2017-04-14			North – Baltic
id-158329	2016-03-14	2016-05-09					North Sea
id-158331	2016-03-13	2016-05-14					North Sea
id-158332	2016-03-13	2016-05-14					North Sea
id-158334	2016-03-27	2016-04-28					North Sea

We report diver winter home range sizes separately for the first winter, when the birds were tagged, and the second and third winters when the birds returned to the wintering area after the breeding season and moulting. As bird captures took place at the end of the first winter, the first winter period represented in home range analysis (mean 43 days, range 30–62 days) is shorter than for the second and third winter (mean 127 days, range 74–231 days) and therefore also the size of home ranges is expected to be smaller for the first winter.

Generic winter space use by birds was characterised by the 95% utilisation distribution (UD) calculated using dynamic Brownian bridge model and core distribution area was assessed using 50% UD of the same Brownian bridge model.

Average 95% UD home range during the first winter season was 8,418 km^2, with variability among individuals being quite high and ranging from 3,033 km^2 to 20,783 km^2 (Figure 5.17). Core distribution areas of 50% UD home ranges comprised on average 17% of the 95% UD home range size: averaged at 1,420 km^2 and ranged from 218 km^2 to 3,828 km^2 during the first winter (Figure 5.18).

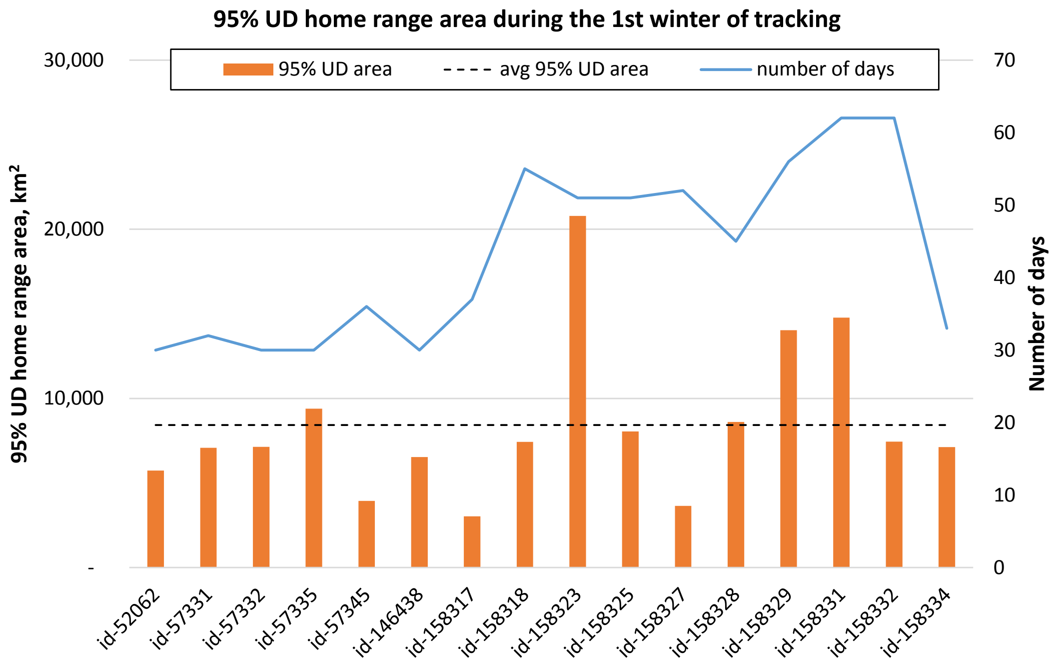


Figure 5.17 Area size of 95% UD home ranges of divers that were recorded during the first winter season of individual tracking. Blue solid line shows tracking duration in days which was used for estimating home range size. Black dashed line shows average size of 95% UD home range.

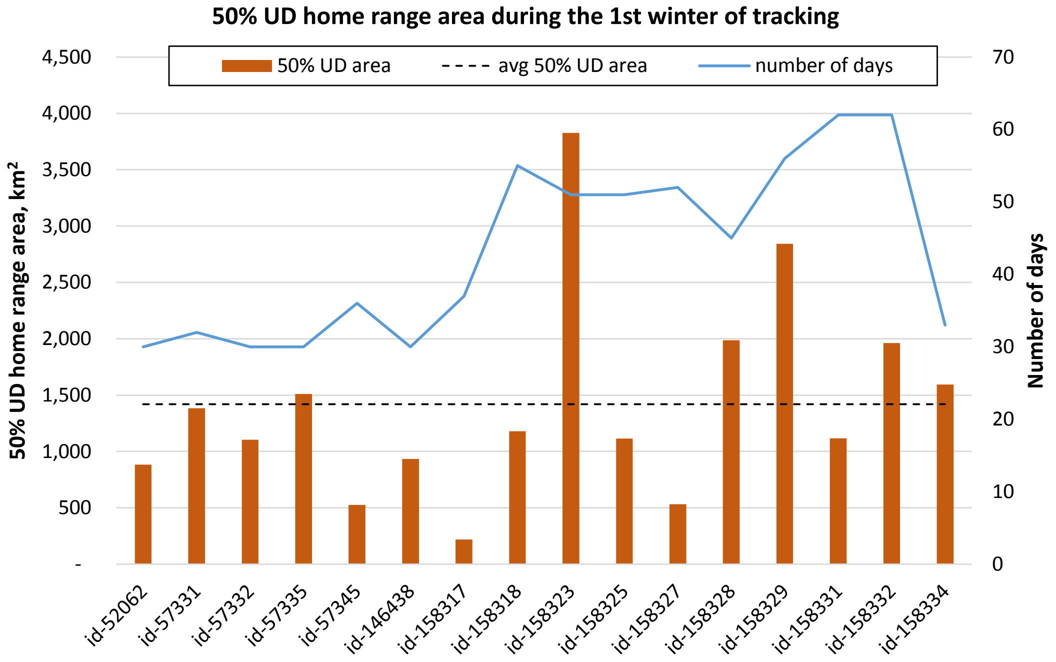


Figure 5.18 *Area size of 50% UD home ranges of divers that were recorded during the first winter season of individual tracking. Blue solid line shows tracking duration in days which was used for estimating home range size. Black dashed line shows average size of 50% UD home range.*

During the second winter season of individual tracking, the average 95% UD home range was nearly twice larger than during the first winter – 15,368 km^2, with variability among individuals also being high and ranging from 4,243 km^2 to 37,274 km^2 (Figure 5.19). While the average value was inflated by three very mobile individuals (id-57339, id-57345, and id-158324), the majority of individual 95% UD home ranges were smaller, at or below 10,000 km^2.

Core distribution areas represented as 50% UD home ranges comprised on average 14% of the 95% kernel home range size: averaged at 2,148 km^2 and ranged from 417 km^2 to 5,462 km^2 during the second winter (Figure 5.20).

Larger home range areas during the second winter of tracking are related to the longer duration of tracking and thus higher likelihood of moving around. The first winter in all cases represented late winter season following the birds after they have been tagged (tagging took place in the end of the wintering season in all project years.)

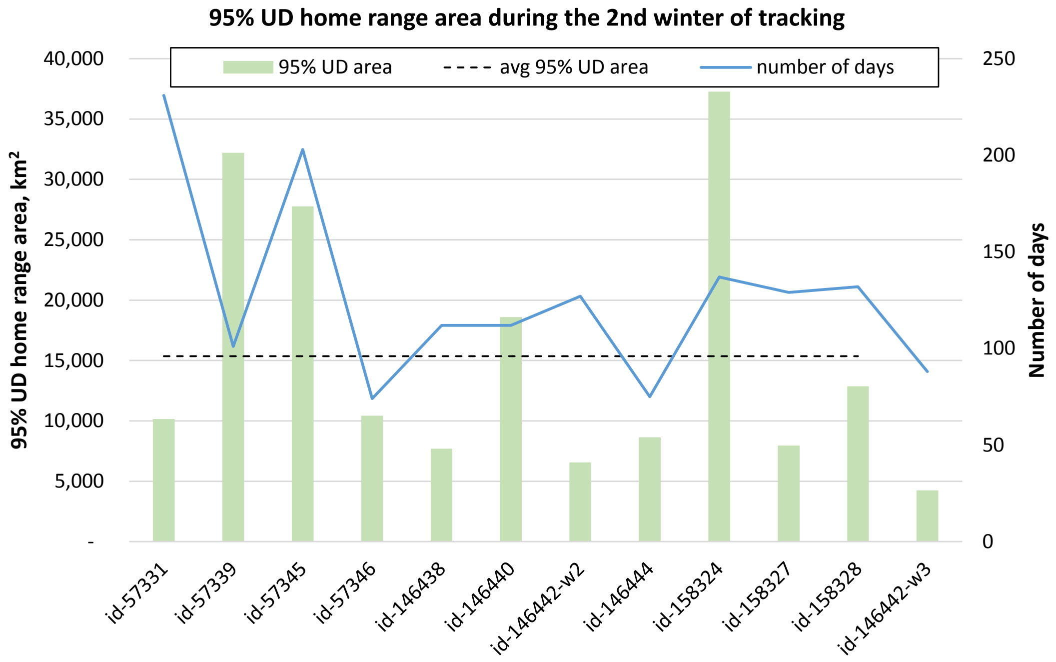


Figure 5.19 *Area size of 95% UD home ranges of divers that were recorded during the second winter season of individual tracking. Blue solid line shows tracking duration in days which was used for estimating home range size. Black dashed line shows average size of 95% UD home range.*

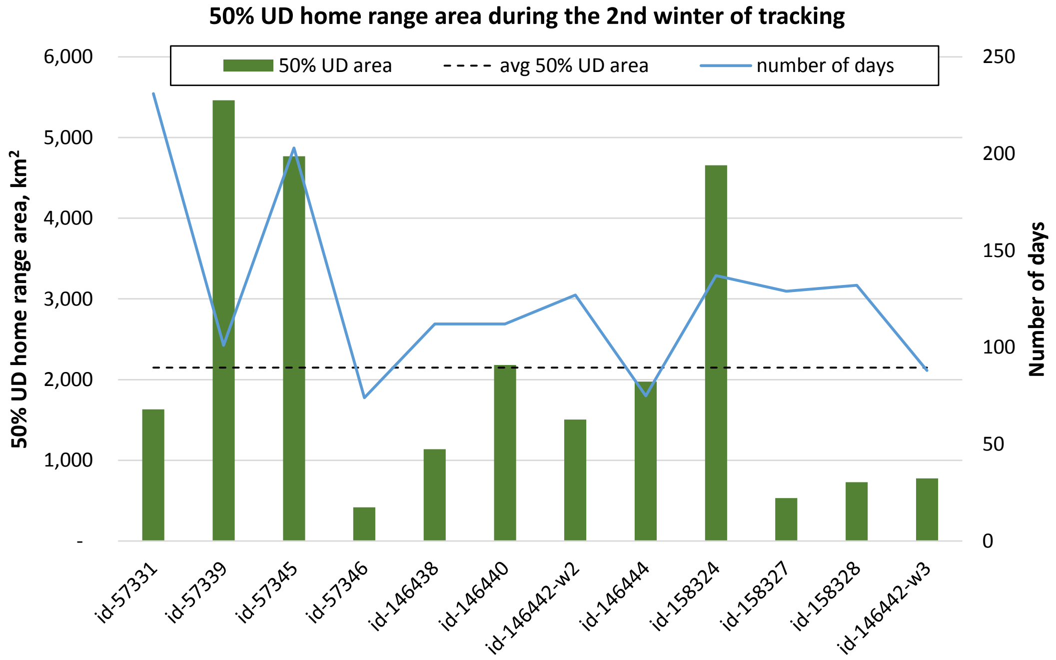


Figure 5.20 *Area size of 50% UD home ranges of divers that were recorded during the second winter season of individual tracking. Blue solid line shows tracking duration in days which was used for estimating home range size. Black dashed line shows average size of 50% UD home range.*

Selected winter home ranges derived from utilisation distributions of individual birds are presented in Figure 5.21 through Figure 5.30 (all winter home ranges to be found in Appendix

A.2). It can be seen that after accounting for possible uncertainty in Argos position accuracy, 95% UD areas in most cases cover substantially larger areas than actual telemetry positions recorded. It represents the potential area of distribution. The 50% UD areas highlight the core usage areas within the winter distribution of each individual.

Based on the inspection of 50% UD home ranges, the majority of birds used only one or two discrete wintering sites outlined as separate 50% UD polygons during one wintering season (Figure 5.21 – Figure 5.30). However, a few individuals could be singled out, which used large areas and were quite mobile during the wintering season. Bird id-158324 stayed at the coast of France, Thames estuary and offshore waters of the Netherlands during the second winter of tracking (Figure 5.28); birds id-57339 and id-158331 used several core offshore areas across the entire German Bight (Figure 5.26, Figure 5.27). Bird id-158328 used wintering areas in the German Bight and in the Kiel Bight (Baltic Sea) and commuted several times between the two areas in the course of the second winter of tracking (Figure 5.25).

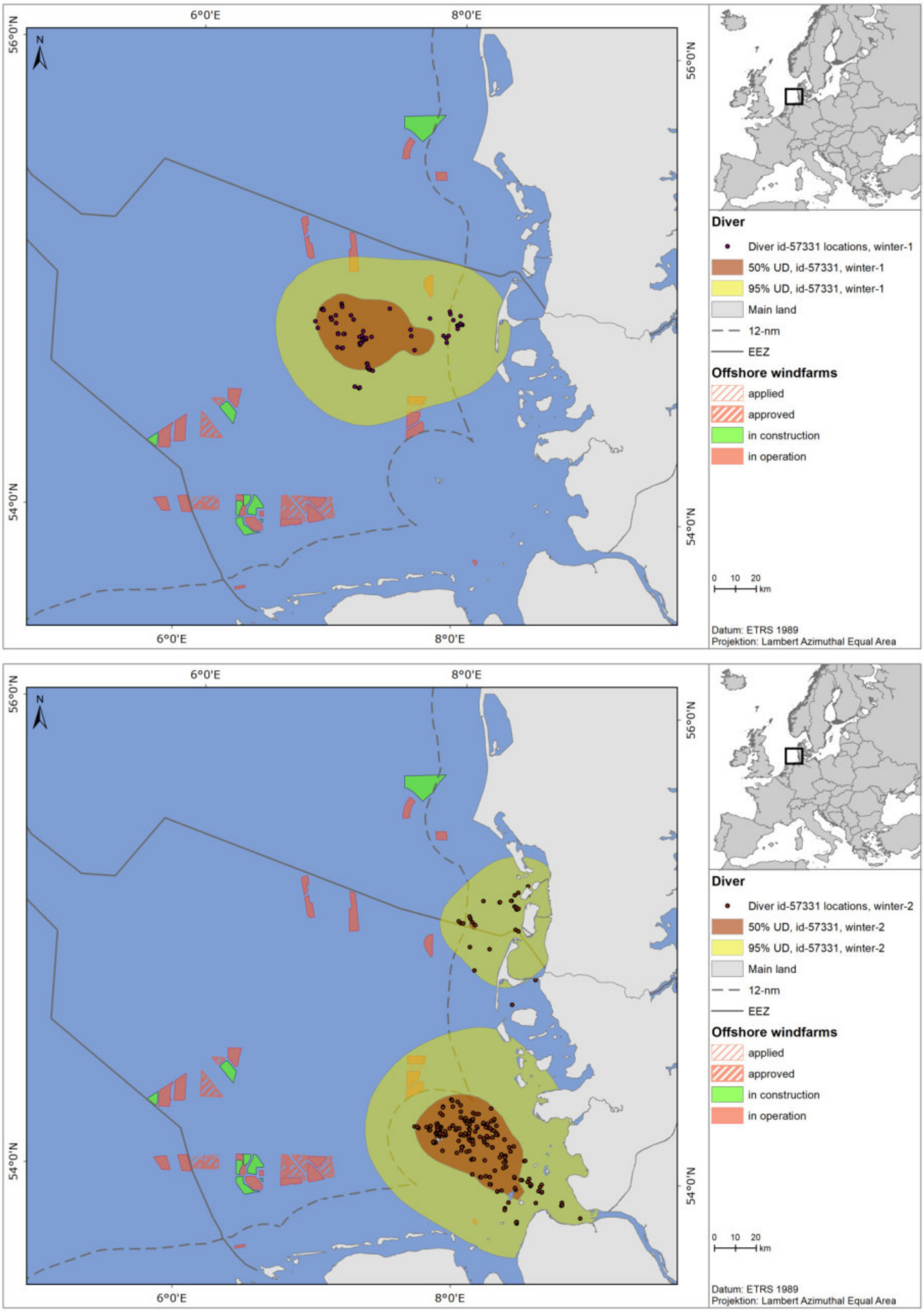


Figure 5.21 Distribution of diver id-57331 in the German Bight presented as 95% UD winter distribution and 50% UD core areas during the first winter (April 12 – May 13, 2017; upper map) and second winter of tracking (September 20, 2017 – May 8, 2018; lower map).

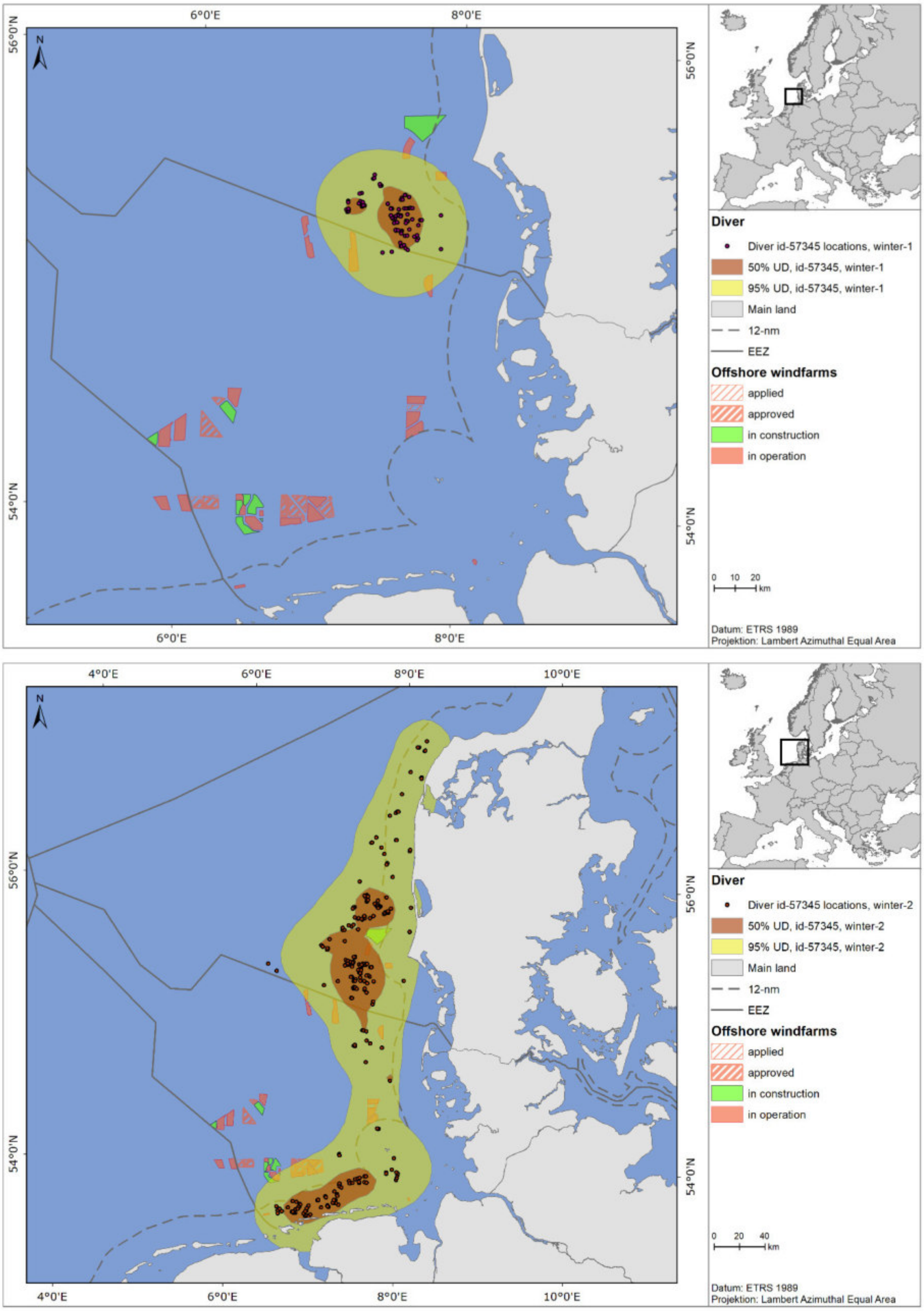
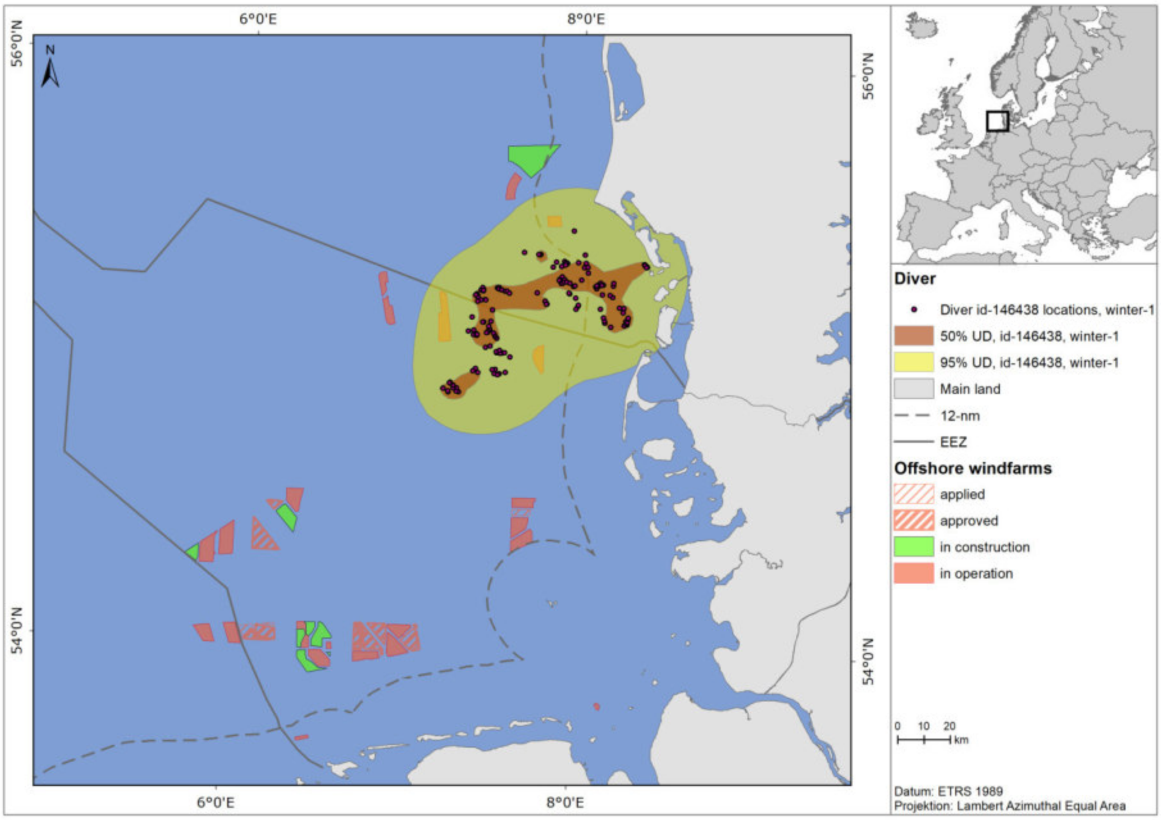


Figure 5.22 Distribution of diver id-57345 in the German Bight presented as 95% UD winter distribution and 50% UD core areas during the first winter (April 8 – May 14, 2017; upper map) and second winter of tracking (October 26, 2017 – May 16, 2018; lower map).



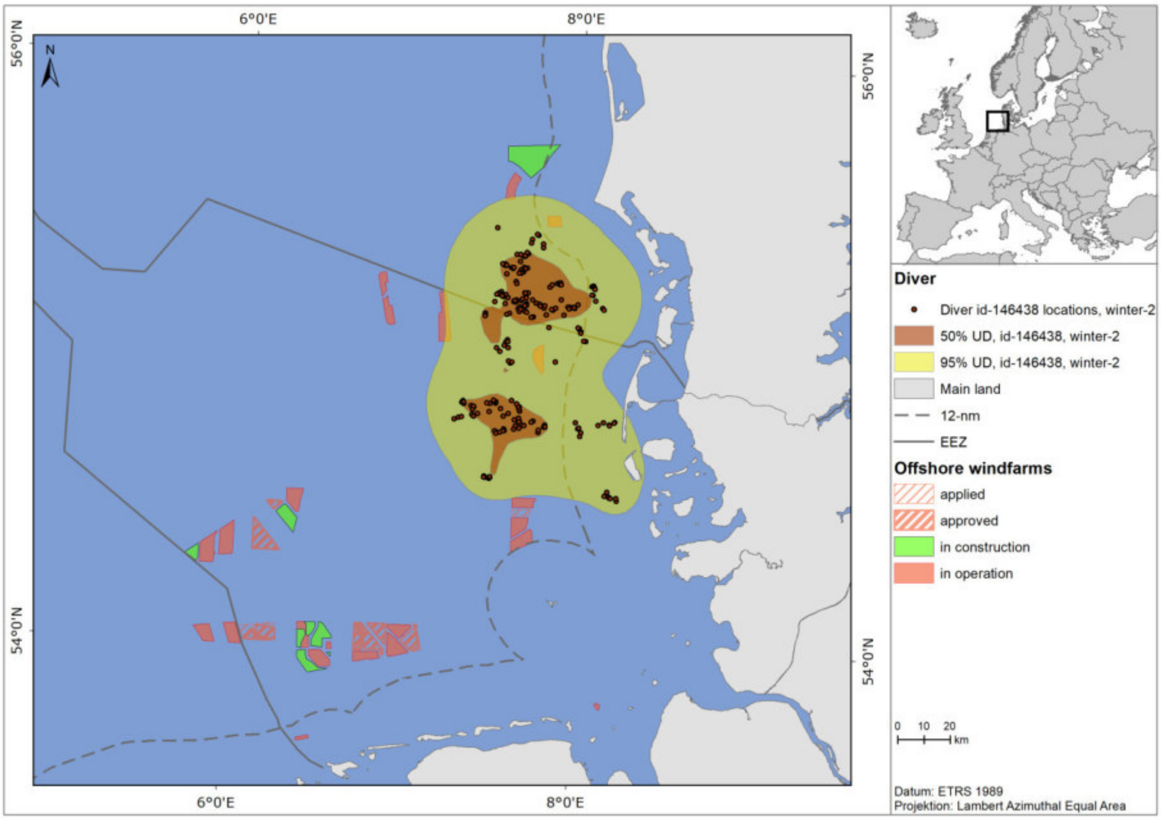


Figure 5.23 Distribution of diver id-146438 in the German Bight presented as 95% UD winter distribution and 50% UD core areas during the first winter (April 3 – May 3, 2015; upper map) and second winter of tracking (January 6 – April 27, 2016; lower map).

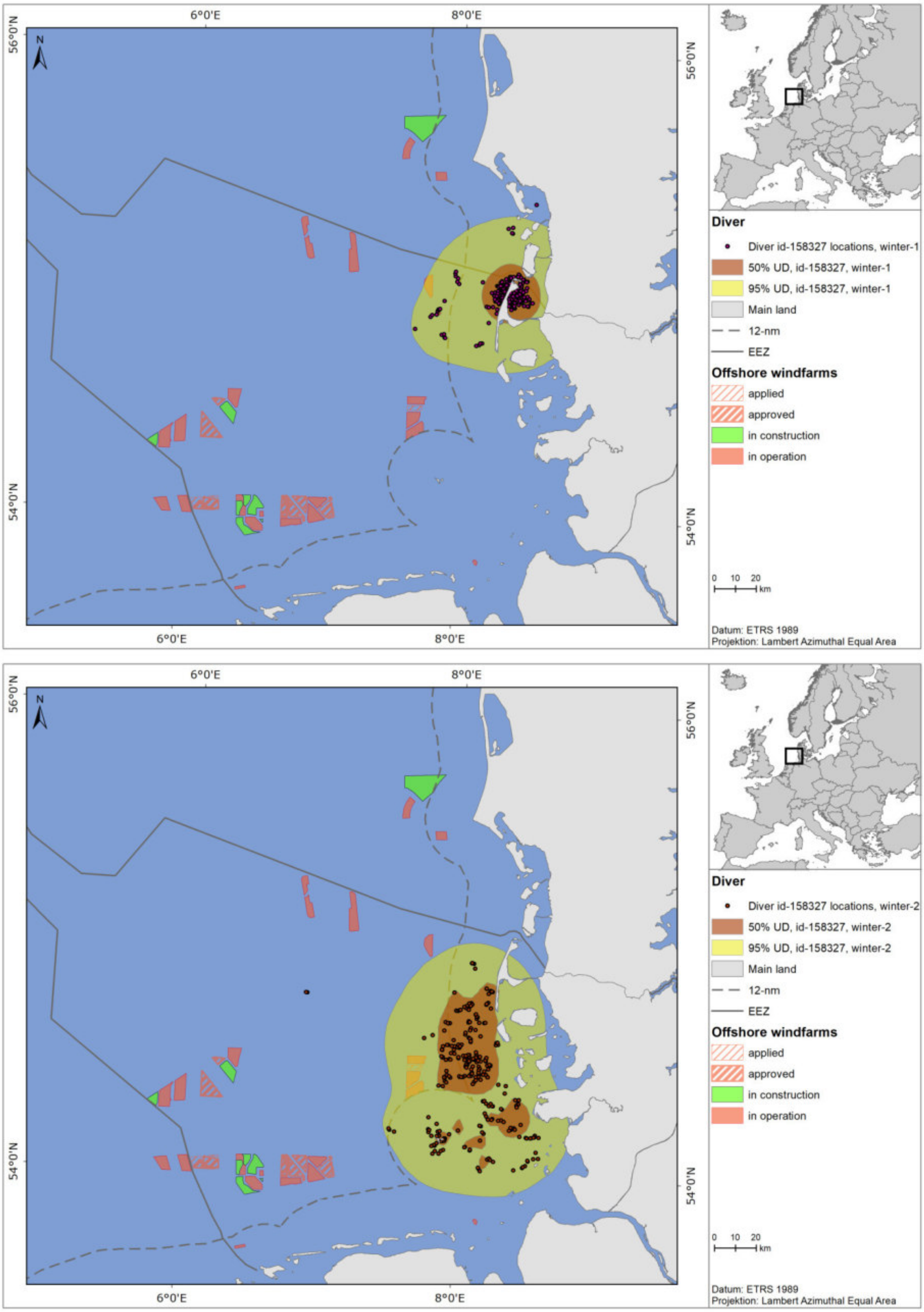


Figure 5.24 *Distribution of diver id-158327 in the German Bight and southern Baltic Sea presented as 95% UD winter distribution and 50% UD core areas during the first winter (March 13 – May 4, 2016; upper map) and second winter of tracking (October 22, 2016 – February 28, 2017; lower map).*

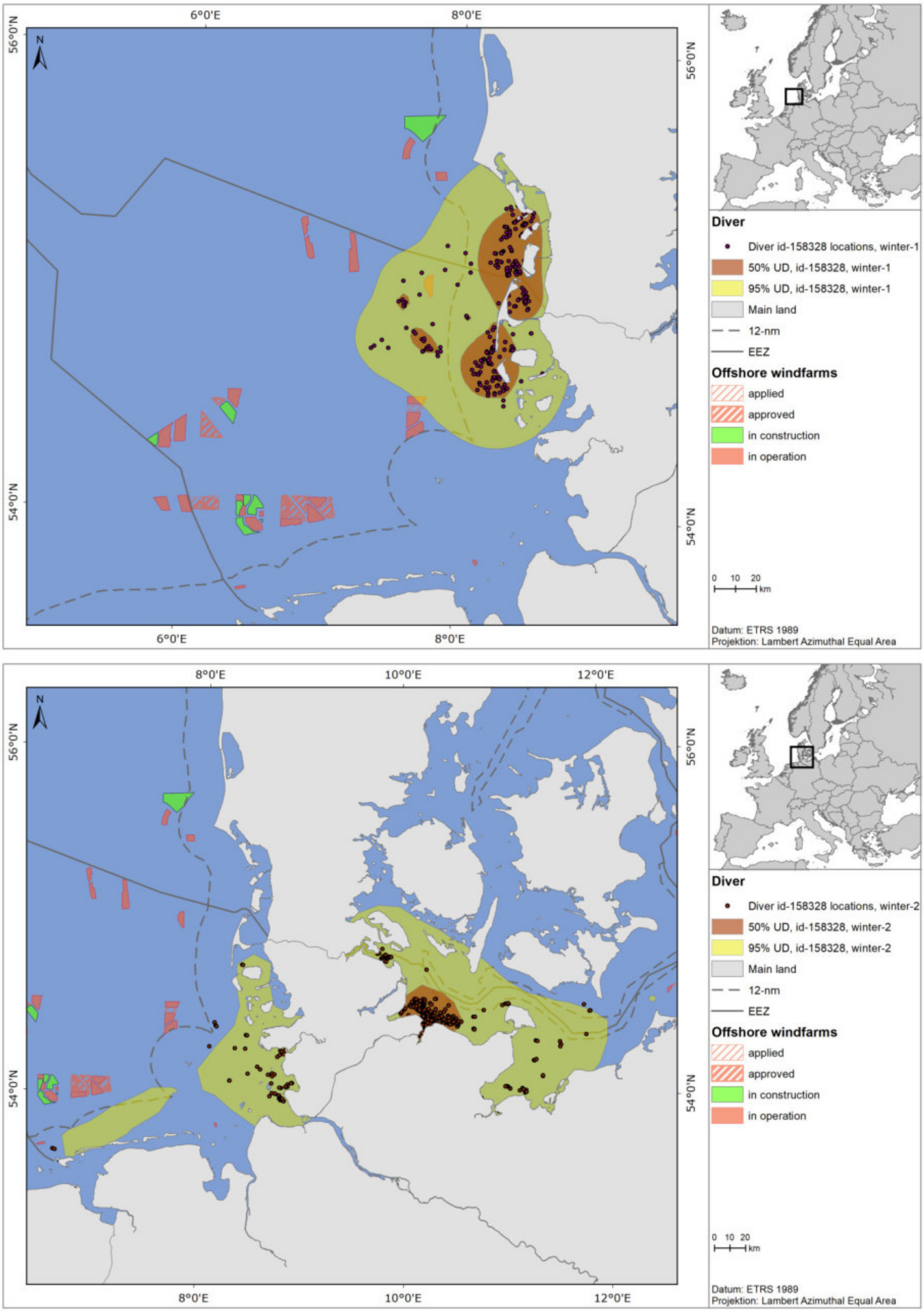


Figure 5.25 Distribution of diver id-158328 in the German Bight and southern Baltic Sea presented as 95% UD winter distribution and 50% UD core areas during the first winter (March 14 – April 28, 2016; upper map) and second winter of tracking (December 3, 2016 – April 14, 2017; lower map).

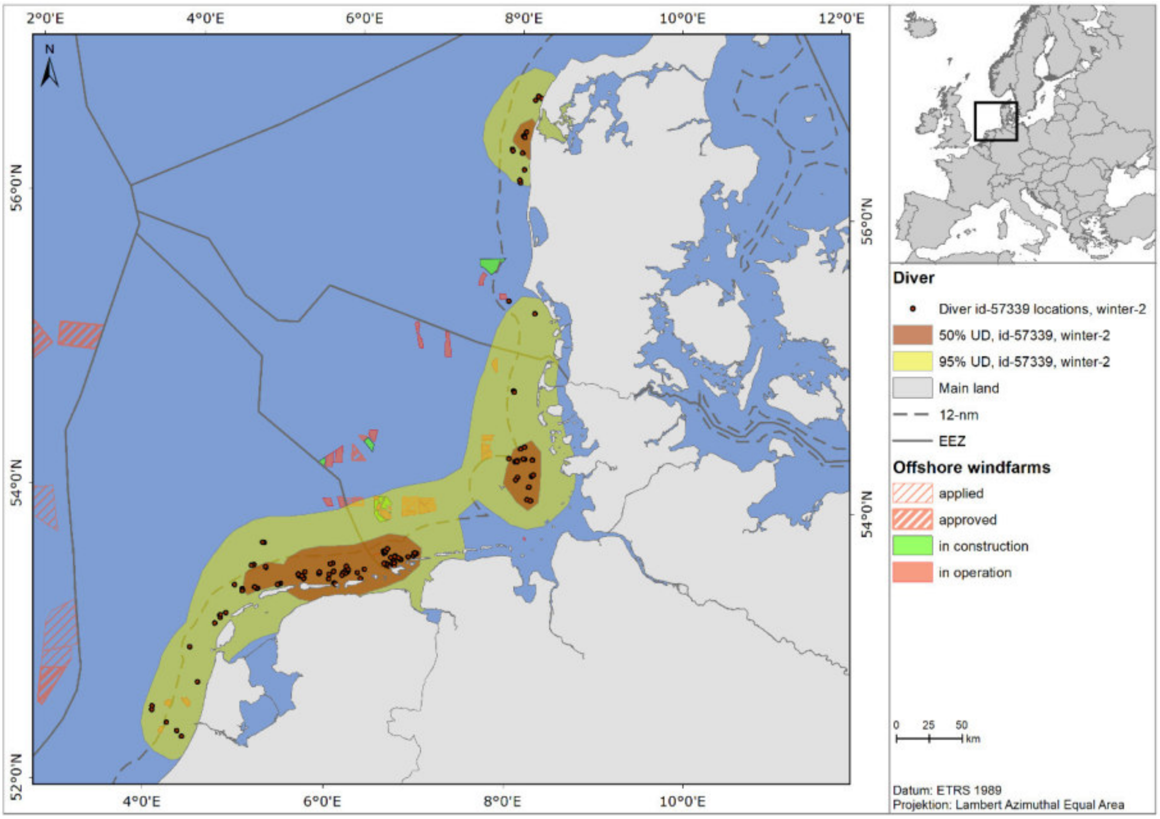


Figure 5.26 Distribution of diver id-57339 in the eastern North Sea presented as 95% UD winter distribution and 50% UD core area during the second winter of tracking (Jan 9 – Apr 20, 2018)

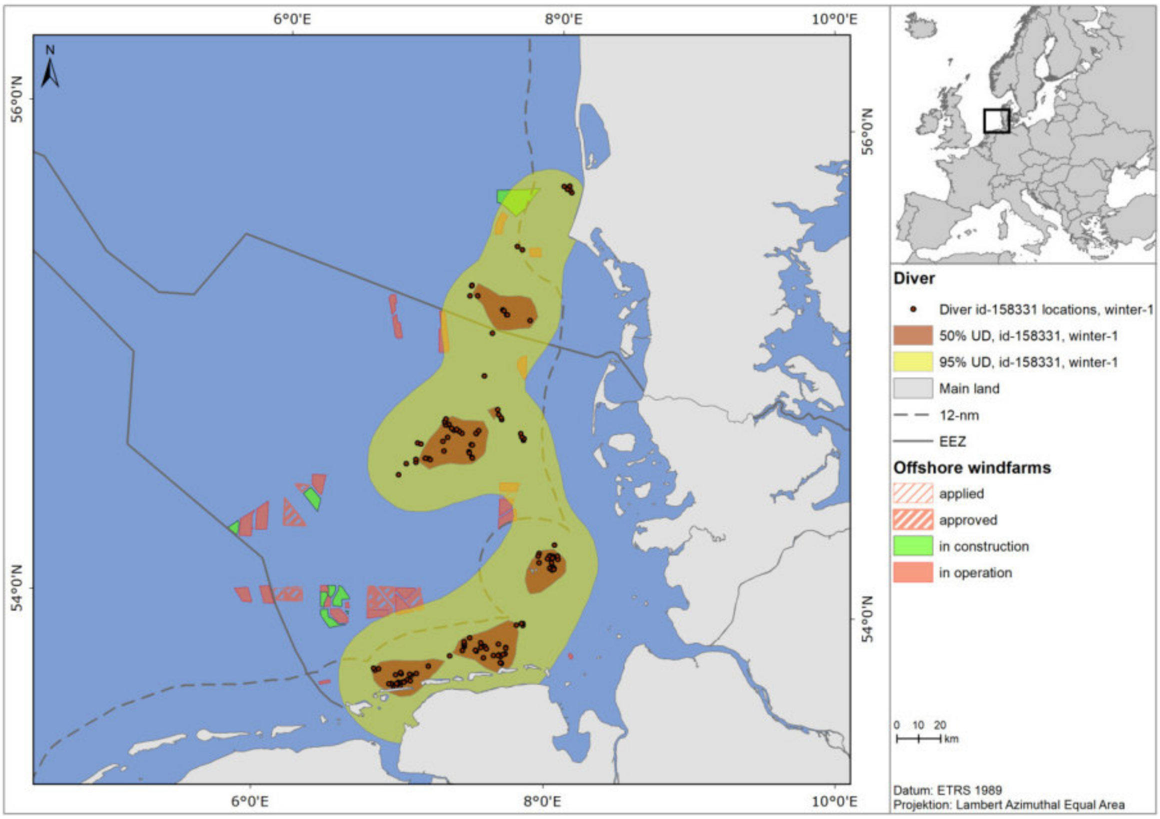


Figure 5.27 Distribution of diver id-158331 in the German Bight presented as 95% UD winter distribution and 50% UD core area during the first winter of tracking (Mar 13 – May 14, 2016).

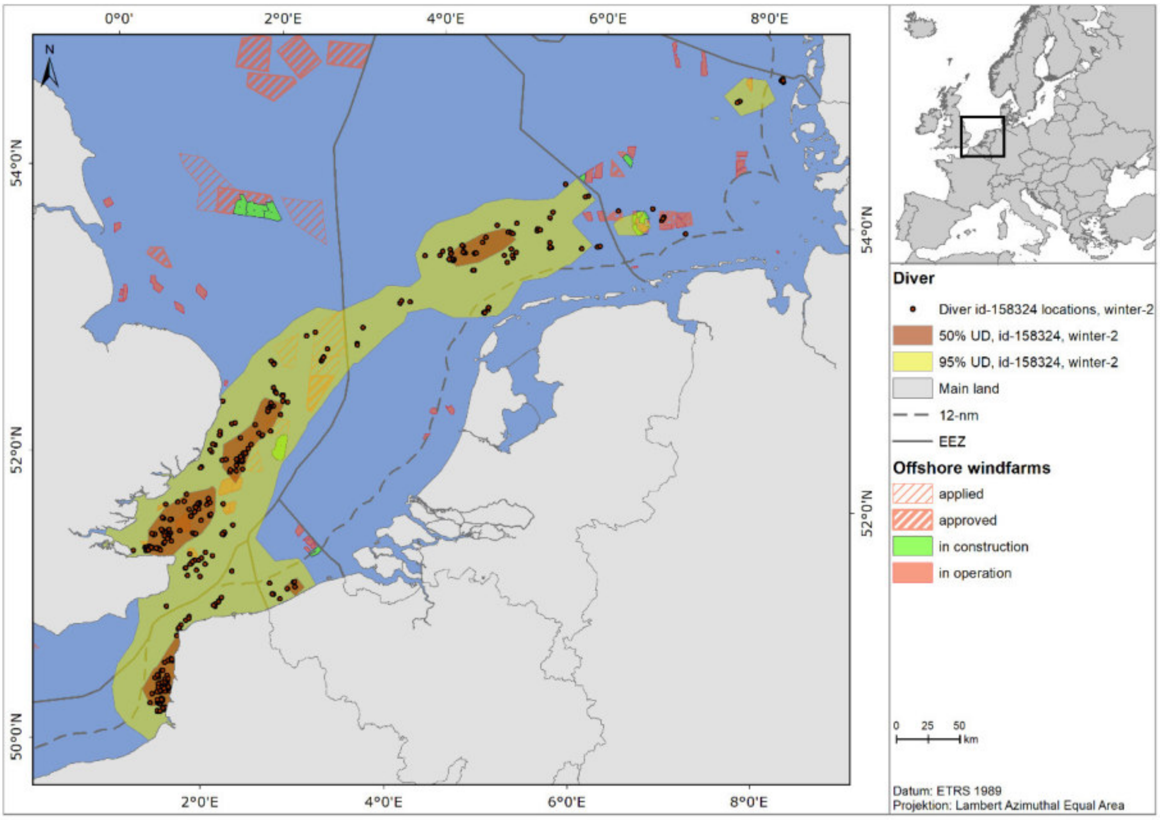


Figure 5.28 Distribution of diver id-158324 in the southern North Sea as 95% UD winter distribution and 50% UD core area during the second winter of tracking (Nov 22, 2016 – Apr 8, 2017).

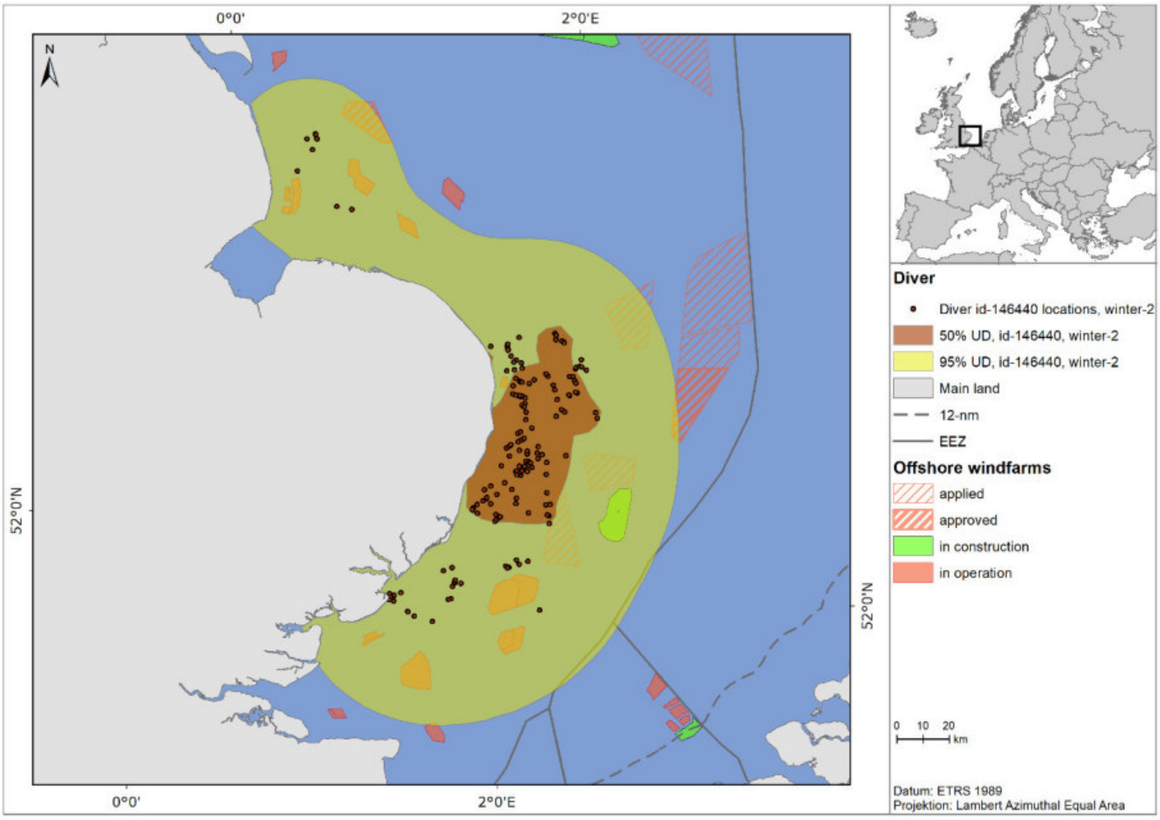
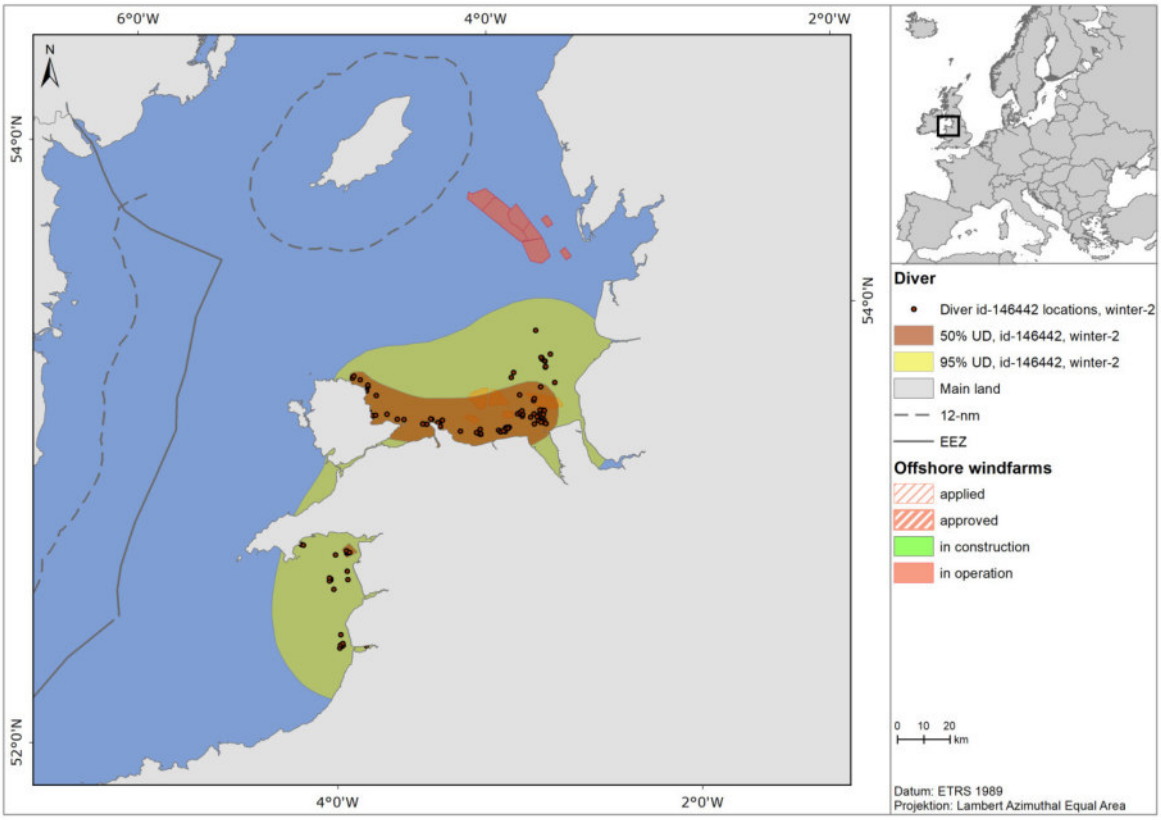


Figure 5.29 Distribution of diver id-146440 in the Southern Bight presented as 95% UD winter distribution and 50% UD core area during the second winter of tracking (Dec 2, 2015 – Mar 23, 2016).



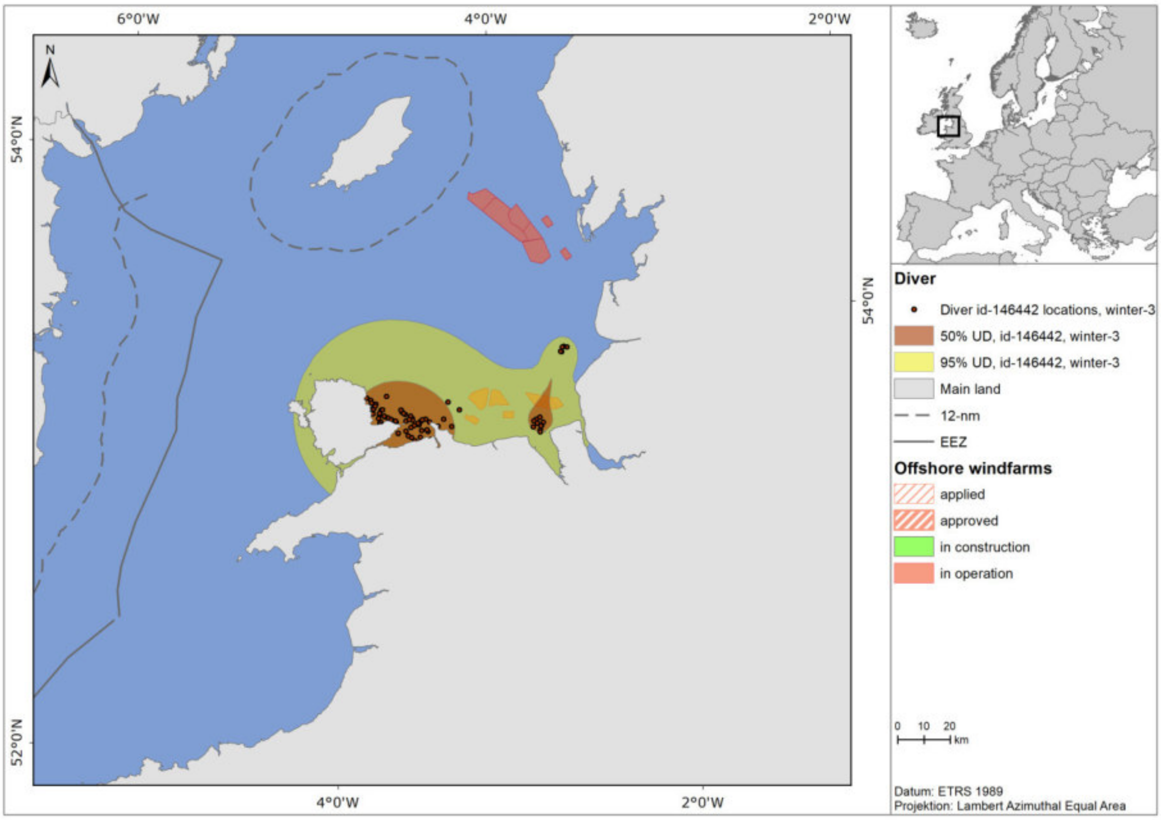


Figure 5.30 *Distribution of diver id-146442 in the Irish Sea presented as 95% UD winter distribution and 50% UD core areas during the second winter (December 16, 2015 – March 2, 2016; upper map) and third winter of tracking (December 4, 2016 – February 2, 2017; lower map).*

5.3.6.2. Characteristics of winter movements

Average distances between weekly location fixes of divers were relatively large and variable during the wintering season averaging at 35.8 ± 25.6 km (± SD, range 8.7–101.0 km, n = 28) among all individuals (Figure 5.31). Large variability in weekly relocation distances can also be observed within individual movements (examples in Figure 5.32, Figure 5.33). Closer inspection of weekly relocation distances revealed that distances between randomly drawn points were more variable during separate iterations (e.g. ranging from just 2.1 km to 71.1 km for individual id-158332, Figure 5.34).

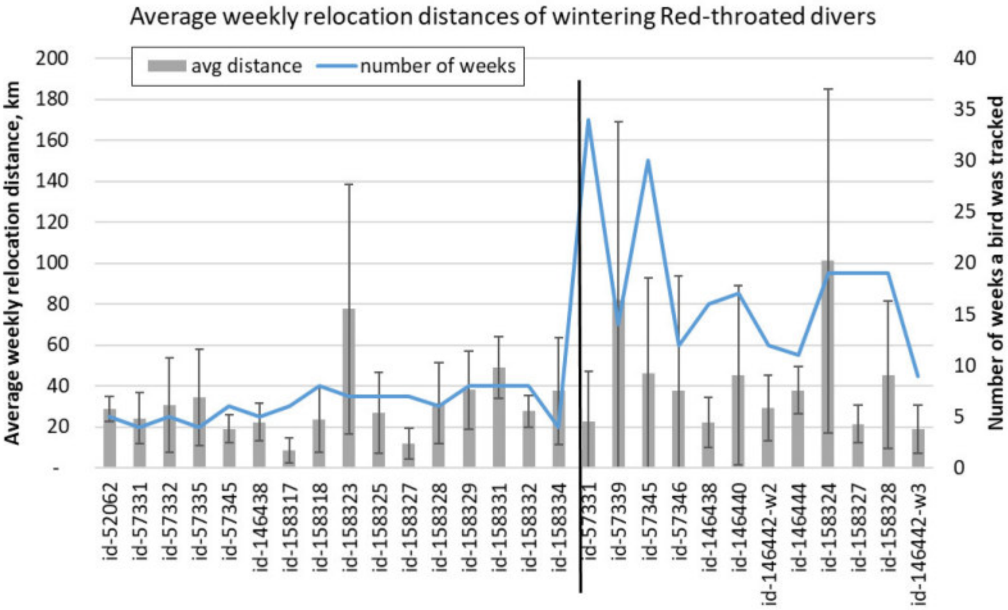


Figure 5.31 Average moving distances between weekly locations of individual Red-throated divers (22 individuals, 28 wintering seasons) as recorded by satellite telemetry. Vertical black line separates wintering areas assessed during the first winter season of tracking from wintering areas used during the second winter of tracking.

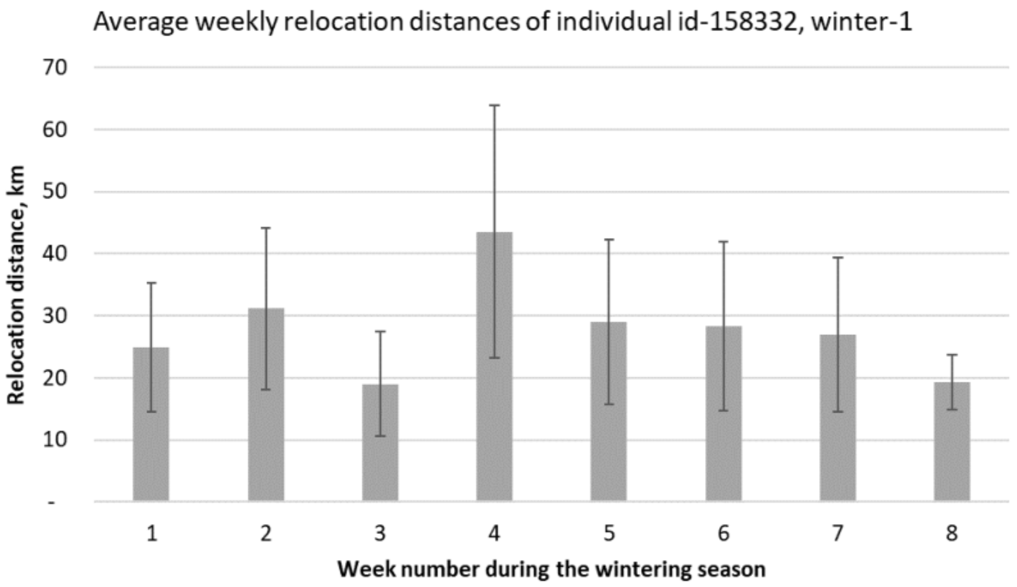


Figure 5.32 Average weekly relocation distances of Red-throated diver individual id-158332 during the first winter of tracking.

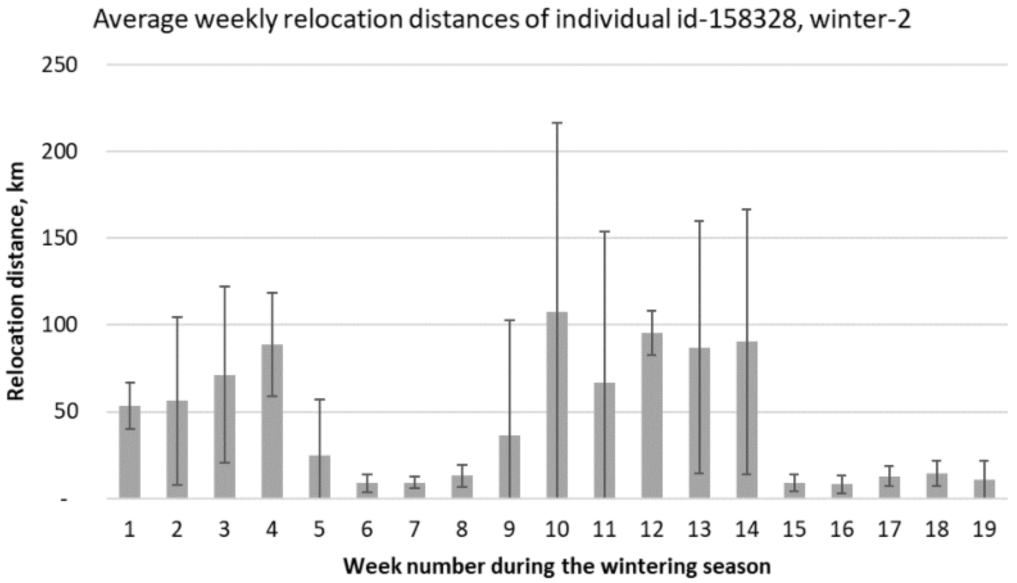


Figure 5.33 Average weekly relocation distances of Red-throated diver individual id-158328 during the second winter of tracking.

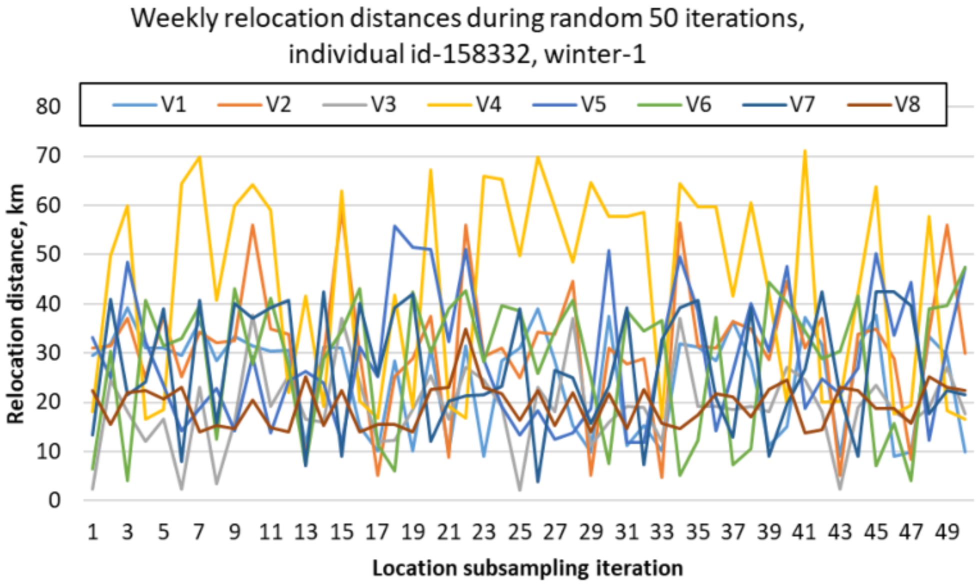
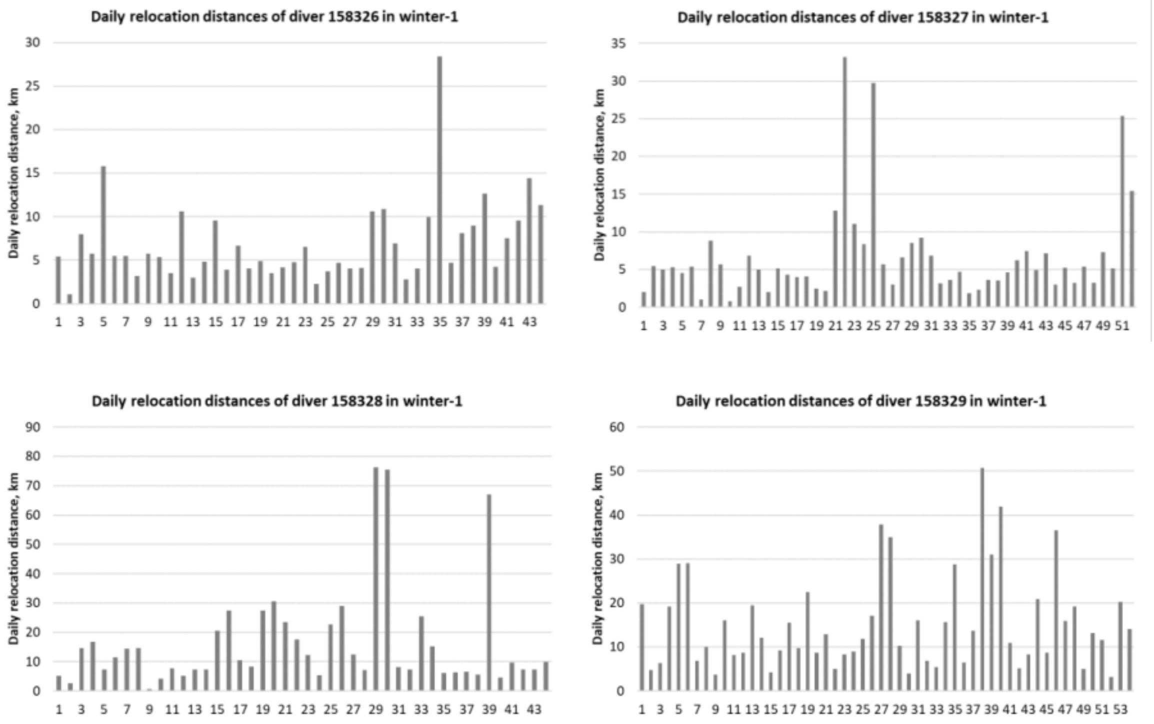


Figure 5.34 Relocation distances calculated for each of 8 weeks of tracking of individual id-158332 when randomly drawing weekly positions 50 times.

Daily relocations during the wintering season

Daily relocation distances were also measured for four individuals, which have been tracked using sufficiently frequent positioning schedule during the first winter season. An analogous approach was used as when measuring weekly relocation distances: a single daily location was randomly picked and then distances were measured. Five such replicates were conducted (because few daily positions have normally been recorded) and then average values calculated.

Average daily relocation distance of all four individuals pooled together was 11.26 km (±11.61 km (SD)). However, when taken separately, two individuals were twice less mobile compared to the other two birds: average relocation distance was 6.93 km (± 4.7 km (SD)) for bird id-158326; 6.61 km (± 6.4 km (SD)) for bird id-158327; 16.2 km (±17.34 km (SD)) for bird id-158328; and 15.25 km (± 10.78 km (SD)) for bird id-158329 (Figure 5.35).


Daily relocation distances of diver 158326 in winter-1

Daily relocation distances of diver 158327 in winter-1

Daily relocation distances of diver 158328 in winter-1

Daily relocation distances of diver 158329 in winter-1

Figure 5.35 Average daily relocation distances of red-throated diver individuals id-158326, id-158327, id-158328 and id-158329 during the first winter of tracking.

5.3.6.3. Winter movements in relation to offshore wind farms

This study was focussed on tracking divers inhabiting the areas where offshore wind farms are present. Thus, it is not surprising that 95% UD has often included several OWFs, but as stated above calculated 95% UD frequently extended far beyond the actual telemetry positions recorded. In contrast, 50% UD delineating core use areas almost never overlapped with OWF. From 28 individual winter home ranges that were calculated, 50% UD overlapped with OWF in only three cases (Figure 5.22 lower map, Figure 5.28, Figure 5.30). Only the first of those cases was in the German Bight, where OWF Horns Rev 2 fell within the core area even though the bird id-57345 has not been recorded within the wind farm, only in the waters around it (Figure 5.22 lower map). The second case was in the Thames Estuary, where the bird id-158324 stayed in the vicinity of several OWFs (Figure 5.28), and similarly the bird id-146442 wintered in the vicinity of several OWFs in the Liverpool Bay (Figure 5.30).

For many other individuals, particularly those wintering in the German Bight, it can be observed that the core distribution area (50% UD) was often squeezed in-between offshore wind farms.

5.3.6.4. Wintering site fidelity

Inter-seasonal wintering site fidelity was evaluated for individuals, which were tracked during two winter seasons. This was possible for six individuals, which all spent two wintering seasons (including moult and autumn period) in the same general area making general area site fidelity 100% (Figure 5.21 – Figure 5.25, Figure 5.30). The “same general area” is considered here as large geographic unit, such as the German Bight. Although one individual of the six spent the second winter season not only in the German Bight but also in the Kiel Bight, south Baltic Sea.

However, site fidelity assessments are scale dependent and at finer resolution the overlap gets smaller. We therefore compared the 95% and 50% UD home ranges by assessing the percentage of overlap relative to the first winter season. For those six individuals, the 50% UD home range area overlapped from 0% to 97%, averaging at 28%, when compared with 50% UD home range of the second winter season with half of the birds using completely non-overlapping core home range areas in the subsequent winter (Table 5.5). Overlap was greater for 95% UD home range area – on average 50%, ranging from 11% to 100% (Table 5.5).

Table 5.5 Total areas (km^2) and percent overlap between different winter seasons of individual divers using core winter areas (50% UD home range) and 95% UD home ranges.

Bird ID	50% UD home range			95% UD home range		
	winter-1	winter-2	% overlap	winter-1	winter-2	% overlap
57331	1,384	1,632	0%	7,074	10,149	15%
57345	526	4,767	97%	3,934	27,764	100%
146438	932	1,138	31%	6,528	7,709	77%
146442	1,505	777	38%	6,572	4,243	45%
158327	532	532	0%	3,648	7,965	50%
158328	1,987	729	0%	8,604	12,874	11%

There were more individuals (n = 15) that were tracked into the second winter season, but not long enough for making home range estimates either in the first winter of tracking or in the second winter. Of these 15 birds, 14 individuals came back to the German Bight next winter and either stayed there for wintering (n = 10) or staged briefly during seasonal migrations (n = 4). One individual (id-146437) which was not recorded back in the German Bight stopped transmitting early in the second winter season, on December 5, 2015, thus full winter movements of this bird remains unknown.

5.4 Discussion

5.4.1 Origin and movement patterns of red-throated divers captured in the eastern German Bight

We successfully identified the breeding regions of 31 red-throated divers captured in the eastern German Bight during winter and spring. We localised main resting areas along the migration routes and put particular attention on moulting and wintering sites. Our study shows that red-throated divers exhibit a relatively high fidelity towards all different areas visited during the annual cycle: migration routes, staging, breeding, moulting and wintering areas, however with some remarkable individual variation. With regard to wintering areas we specified area use and home range size during wintering season.

One of the main goals of this project was to determine the origin of red-throated divers occurring in internationally important numbers in the eastern German Bight in winter and spring. Four different distinct breeding regions were identified from birds tagged in this project: Scandinavian Peninsula (Norway), Svalbard, Greenland (western and eastern coast) and northern Russia (European and Siberian parts), with the majority of birds originating from northern Russia (73.5%). Though it is assumed that the eastern German Bight is used for wintering and staging also by red-throated divers originating from different parts of Scandinavia (Norway, Sweden, Finland) (OKILL 1994), this could be confirmed only for Norway. Red-throated divers breeding in the United Kingdom (Scotland, Shetland, Orkney, the inner and outer Hebrides are expected to winter in the Irish coastal waters (DILLON et al. 2009). Tracking data from our study give no indication for red-throated divers originating from the UK using the eastern German Bight for staging in late winter. Ringing recoveries of red-throated divers in Great Britain and Ireland showed that birds found at the British and Irish coasts were ringed on the Shetlands, Greenland, Sweden and Finland (OKILL 1994). Ring recoveries indicate a wide distribution range of Finish breeding birds including the Baltic Sea, UK, German Bight, French Atlantic coast and even Spain (BIRDLIFE FINLAND 2019). This indicates that red-throated divers from different breeding regions show different migration strategies in relation to short- or long-distance migrations and that red-throated divers breeding in Sweden and Finland mostly move short distances to spend the winter season in the Baltic Sea. The origin of divers caught in the eastern German Bight was mostly of Arctic breeding grounds from Greenland, Svalbard and Siberia, from closer distances only birds from Norway were recorded, leaving breeding grounds from Iceland, Scotland, Sweden, and Finland without a record. The migration patterns of red-throated divers thus resemble a classic leap-frog migration where birds of Arctic breeding origin winter further south than those breeding in temperate regions (ALERSTAM & HÖGSTEDT 1980). While this might be the case for Icelandic and Scottish birds, it seems unlikely for Scandinavian birds, because their more northern wintering areas would be located in the Baltic Sea, which is subject to regular freezing in the winter, at least until recently, and ice is likely forcing birds at least partly to move to the North Sea. Taking into account that the number of divers breeding in Finland and Sweden is much smaller than breeding numbers in Northern Russia (BIRDLIFE INTERNATIONAL 2019), it is also possible that birds from these countries were not caught for reasons of probability, thus the 45 tagged birds of our study may not represent the full range of breeding origins. Timing of captures (which all took place in late winter and spring) may also play an important role. Birds originating from Sweden and Finland could have left the capture area early and had already moved back to the Baltic Sea during that time.

Migration to breeding regions showed some individual variation. Most individuals migrating to Russian breeding grounds crossed the Baltic Sea but two patterns became apparent, one crossing land and thereby going straight and one moving coastal around land. One Individual migrated along the Norwegian coast to via the North Cape to northern Russia. These migration patterns show a similar migration direction but individually differing routes. Considering that the red-throated diver is a long living species, these patterns indicate that a general direction, where to migrate, could be innate, but the individual performance might be adaptive by learning and exploring (ÅKESSON & WEIMERSKIRCH 2005; PÉRON & GRÉMILLET 2013). We found that the migration route starting at the capture location in the eastern German Bight along the Baltic Sea contains several important staging areas that were consistently utilised in spring and autumn. In this respect, especially the Gulf of Riga is known to be one of the most important wintering areas for red-throated divers in the Baltic Sea (HELCOM 2013). Our tracking data reveal the importance of the Gulf of Riga as resting site for Russian red-throated divers that winter in the North Sea and adjacent waters.

Definitions of short or long-distance migrants vary. COX (2010) defines the range of short-distance migrants from local habitat shifts or altitudinal movements within a small geographical area to intracontinental movements of up to a few hundred kilometres. Accordingly long-distance migrations are defined as movements across major climatic zones, and often between continents or hemispheres. RAPPOLE (2013) classified different movement types such as local seasonal movements, facultative migration, partial migration, altitudinal migration or stepwise migration and defined short-distance migration as movements with a range less than 2,000 km and consequently long-distance migrations as movements greater 2,000 km and usually to a different continent. Regarding the distances covered from the capture location in the eastern German Bight to potential breeding areas the majority of red-throated divers travelled between 2,000 and 5,000 km (on average 4,000 km) and thus can be considered as long-distance migrants (87.9%). Just a small number of birds moved short distances to Norway (12.1%). For long distances the need to refuel is important and migratory behaviour critically depends on the ability to cover a given flight range and on the availability of suitable staging sites en route (WEBER & HOUSTON 1997). Most red-throated divers spent some weeks on migration and used 1.5 staging sites (min. 0 stagings; max. 3 stagings) with an average duration of stay of 15.03 days per staging (min. 6 days, max. 21 days) plus a higher number of shorter stops which indicates that they rather refuel in staging areas than rely on energy reserves obtained on wintering or spring staging areas. Single birds moved to or from their breeding areas without any longer stagings in a relatively short time and performed only short stop-overs of less than 5 days. These birds prove that red-throated divers are able to make long journeys in a few flights within a short time which either needs substantial body reserves or very good feeding conditions at the stop-over sites. In conclusion, the eastern German Bight holds populations of long and short distance migrating divers who use this area for moult, staging or wintering but have different strategies to migrate to their breeding sites and show a generally high variation between individuals.

We found that only about half of the birds captured in the German North Sea spent their following wintering time (defined as starting in December) in this area while the other half spent this time in adjacent waters, but used the eastern German Bight as staging area during autumn migration and moult. In this respect the ecological importance of the German Bight functions not only as a wintering habitat but also as a staging and moulting area. We analysed timing of red-throated divers of which our data covered two wintering seasons (first and second winter). In the second year red-throated divers arrived in the German Bight on average in January and departed between March and May with most birds departing between mid-April and end of April.

We found that the capture area in the German North Sea is a wintering, staging and moulting area for individuals originating from different breeding regions. These finding indicates a medium to low population connectivity (WEBSTER et al. 2002). Individuals captured in the eastern German Bight spread to four different breeding regions and individuals from one breeding region utilised different wintering areas in the second winter. For red-throated divers no fixed migration patterns could be evaluated from one breeding region or one wintering area but individuals showed a high variation in time and space. Thus, effects arising from the disturbance in this area can affect several breeding regions but only a proportion of individuals from the corresponding breeding region. In our data set mostly individuals breeding in northern Russia are concerned when it comes to disturbance in the eastern part of the German Bight.

Using stable isotope signatures we assigned moulting regions in the North Sea and the Baltic Sea to a similar amount between these two areas (53.3% and 46.7% respectively). Of these two areas the tracking data revealed a higher resolution and we could assign moulting areas in the North Sea to the Firth of Tay in Scotland, the Southern Bight and the German Bight and for the Baltic Sea to the Gulf of Riga, the Gulf of Bothnia.

5.4.2 Red-throated diver winter movements and habitat use

We found a relatively high site fidelity though individual patterns varied. Red-throated diver tend to follow consistently their migration routes and utilise the same wintering, spring staging, breeding and moulting areas between years. For one individual data transmission lasted for a third winter showing an identical wintering site as compared to the second winter. High site fidelity may result in a high sensitivity and susceptibility to disturbance and a longer time or several seasons to habituate to changes in the environment. The ability to adapt also depends on the availability of sufficient alternative habitats. For the eastern German Bight, the wide-ranged wintering areas of some individuals with more than one core area used indicate a relatively high exchange between various sites within one greater wintering area. Varying environmental conditions, e.g. wind drifts, can cause some individual flexibility in area use of stop-over sites along migration (CATRY et al. 2004) and similar patterns related to ocean productivity have been found for seabirds (PÉRON & GRÉMILLET 2013). We found red-throated divers also wintering in the Baltic Sea where in some years ice conditions make certain areas unavailable during cold periods. This happening leads to a use of alternative areas, to an extension or shift of wintering ranges and is likely to require some flexibility. However, some individuals in the eastern German Bight stayed consistently in an area with a moderate range for the entire wintering period.

Within the German Bight as a main wintering site, red-throated divers showed individual variable movement patterns ranging from a consistent site utilisation in an area and smaller home ranges to a mobile pattern with relatively large home ranges and more than one core area.

Winter site fidelity assessment reveals that red-throated divers are faithful to the general wintering area at large geographic scale, as all individuals that were tagged in the German Bight and tracked long enough, returned to the German Bight during the following autumn and winter. At small scale, however, birds were less faithful and their core home ranges often differed between wintering seasons.

Red-throated divers were highly mobile within their wintering areas and mostly moving constantly through and between their wintering areas. Throughout a winter individual divers roamed over up to almost the complete wintering area in the German Bight as identified from aerial surveys (SKOV et al. 1995; GARTHE et al. 2015). These findings point at limited differences in habitat quality over large areas. This is consistent with the findings that red-throated divers are feeding on widely distributed fish species with unstable local enrichments in the frontal systems (chapter 8). Movement patterns were similar over different wintering areas and also red-throated divers wintering in the mid-Atlantic coast of the US maintained large home ranges (GRAY et al. 2017). A high mobility in the wintering areas can be considered as a common pattern in red-throated diver habitat use. The high mobility may come as some surprise for a bird which does not explore its environment through foraging flights and may have limited benefit of travelling longer distances within the winter areas. The movements of red-throated divers are likely caused from drift by wind and current and compensatory movements to stay within a larger area of suitable habitats rather than active searching trips. Flushing from approaching ships also adds to diver daily movements. Red-throated divers usually occur solitary and move by swimming at low speed, within a dynamic hydrographic area where food enrichment at frontal zones is continuously changing in relation to tides, winds and river discharges. We thus suspect it to be difficult for red-throated divers to selectively exploit the most profitable food patches and presume that selection of wintering areas is rather driven by macro-selection of a larger suitable area with sufficient frequency of opportunistic encounters of suitable feeding conditions.

5.5 Effect of meteorological factors on the migration of red-throated divers

5.5.1 Background

Tracking red-throated divers revealed exceptional mobility of these birds during the migration periods. Environmental factors or intrinsic timing triggering migratory movements have always been of interest to biologists. Understanding how, why, and when divers initiate their migratory movements or large-scale mid-season relocations also has practical implications for conservation of this species. We therefore explored diver movements based on telemetry data in relation to a set of meteorological parameters. The key question was whether we can identify correlates with specific weather conditions triggering large-scale relocations of the species.

5.5.2 Methods

Sections of this chapter presented above on diver migration and movements during the annual cycle revealed well-defined periods of long-distance migrations and staging seasons. In order to relate diver movements several closely linked response variables were created, which were further explored: distance between successive location fixes, distance between successive location fixes over 50 km (binary), distance between successive location fixes over 100 km (binary), and distance between successive location fixes over 200 km (binary).

The same set of meteorological factors that was used in chapter 6.5 was tested when exploring environmental correlates associated with diver large-scale relocations: Charnock parameter, sunshine duration, total cloud cover, total precipitation, water vapor concentration, total atmospheric water, mean sea level pressure, wind U-component, wind V-component, wind speed and air temperature (Table 6.5). Environmental data were extracted using automated track annotation system available on Movebank portal to assign spatially and temporally matching data from European Centre for Medium-Range Weather Forecasts (ECMWF) (DODGE et al. 2013).

The assessment was done considering all valid telemetry positions that passed Freitas filter and subsequent manual screening (see chapter 4.3.3). We run separate model sets for spring and autumn periods by selecting all tracking data collected in April, May and June for the spring dataset and September, October and November for the autumn dataset.

Generalised additive mixed models (GAMMs) were fitted where individual bird ID was used as a random factor in order to account for individual effects. Tweedie distribution with log link was used when response variable was distance between successive locations in order to account for overdispersion in the data (CANDY 2004; SHONO 2008). Binomial distribution with logit link was used for binomial response variables (relocation distance exceeding 50 km, 100 km and 200 km). For GAMM fitting we used *mgcv* package (WOOD 2011) in software R (R CORE TEAM 2018).

5.5.3 Results

5.5.3.1. Effects of meteorological factors in red-throated diver spring migration

Out of considered response variables, it appeared that 'relocation distance of over 50 km' was the most consistent variable showing clear relationships with the predictor variables. However, all tested response variables showed generally the same patterns, as they were all closely related. Thus we report the results of the models where 'relocation distance of over 50 km' was used as the response variable.

First, we assessed the general patterns of spring migration by linking predictor variable to day of the year. The model was significant and the response curve showed general pattern of diver spring migration: the likelihood of diver migration is increasing starting from approx. day 105 (April 15), reaches its peak on day 145 (May 25), and declines steeply afterwards (Figure 5.36).

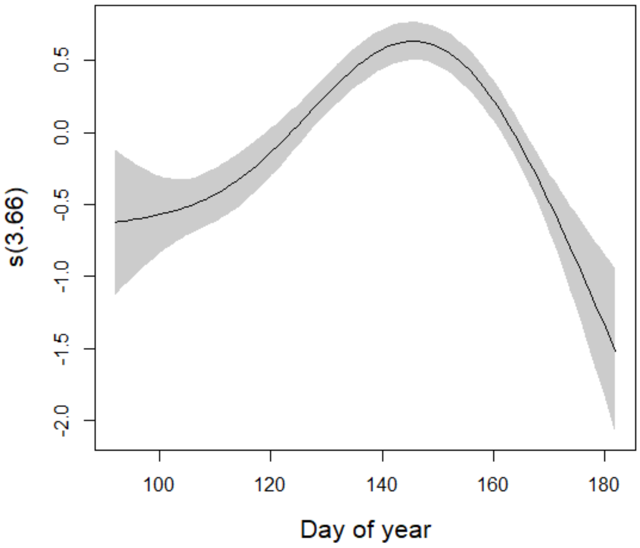


Figure 5.36 Response curve of the GAMM models showing general patterns of diver spring migration phenology when the only predictor variable is day of the year.

Further, the majority of the considered meteorological parameters were not significant explaining diver migration. Namely, no statistically significant relationship was found with sunshine duration, total cloud cover, total precipitation, water vapor concentration, total atmospheric water, mean sea level pressure, and air temperature. And only variables describing wind conditions were found being significant: Charnock parameter, wind U-component, wind V-component and wind speed.

Charnock parameter characterising sea surface roughness showed negative linear relationship with red-throated diver likelihood of spring migration (Table 5.6, Figure 5.37). This suggests that birds were less likely to initiate long-distance relocation in windy conditions (choppy sea surface), which are indicated by the higher Charnock parameter values.

Table 5.6 Parameter estimates and significance in the GAMM model relating the Charnock parameter to red-throated diver migration in spring.

Parameter coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	-3.019	0.102	-29.75	<0.001
	edf	**Ref. df**	**F**	**p-value**
Wind component-U	2.882	2.882	9.901	0.002

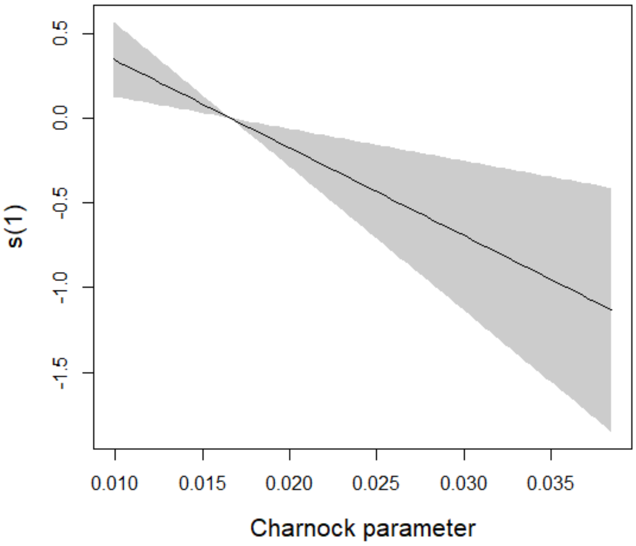


Figure 5.37 GAMM response curve showing that red-throated divers were less likely to migrate when Charnock parameter values, characterising sea surface roughness, were increasing during the spring migration period.

Wind component-U showed that divers were more likely to migrate in no wind or very light conditions of east-west wind (Table 5.7, Figure 5.38). Slight skewedness to the right of the bell-shape response curve can be noticed suggesting that divers migrating in spring tolerated slightly higher wind blowing from the west compared to the eastern direction (Figure 5.38). This observation seems sensible as the majority of divers tagged in the German Bight migrated to the north-east.

Table 5.7 Parameter estimates and significance in the GAMM model relating the wind component-U to red-throated diver migration in spring.

Parameter coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	-3.024	0.104	-29.16	<0.001
	edf	**Ref. df**	**F**	**p-value**
Wind component-U	2.882	2.882	6.106	<0.001

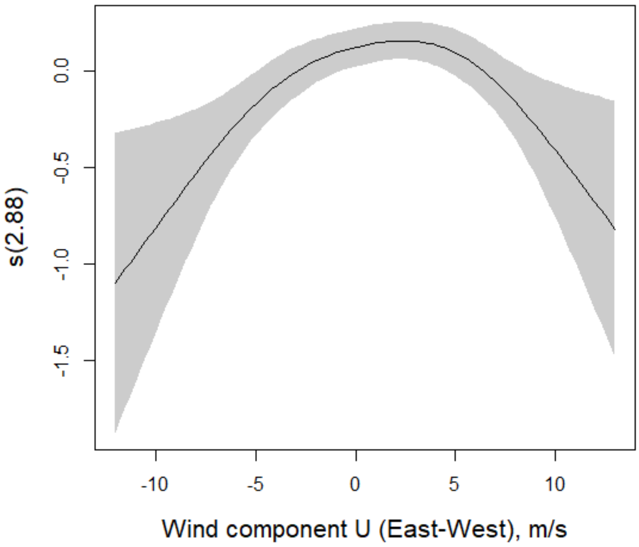


Figure 5.38 GAMM response curve showing that red-throated divers were likely to migrate in no wind or light winds from the west in relation to wind component-U during the spring migration period.

Wind component-V characterising north-south winds (negative values are for wind blowing from the north and positive – from the south) had positively linear relationship with red-throated diver spring migration and showed that divers were less likely to migrate at higher wind from the north and probability of spring migration was increasing with increasing wind strength from the south (Table 5.8, Figure 5.39). This suggests that birds were often using tail wind during the spring migration and were unlikely to initiate long-distance migration into the head wind.

Table 5.8 Parameter estimates and significance in the GAMM model relating the wind component-V to red-throated diver migration in spring.

Parameter coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	-3.014	0.103	-29.44	<0.001
	edf	**Ref. df**	**F**	**p-value**
Wind component-U	1	1	4.941	0.026

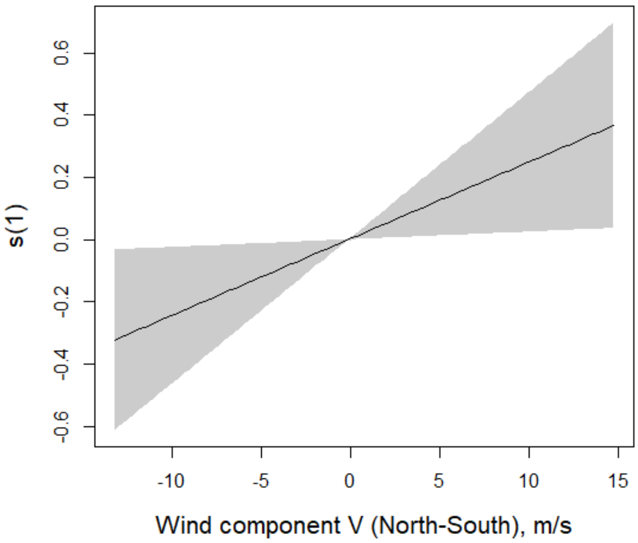


Figure 5.39 GAMM response curve showing that red-throated divers were likely to migrate in tail wind conditions from the south and unlikely to fly into the strong headwind blowing from the north, when assessed diver migration in relation to wind component-V during the spring period.

When assessing effects of overall wind speed calculated combining wind components U and V, it appeared that overall divers migrate in light wind conditions and migration probability starts declining as wind speed exceeds 5 m/s (Table 5.9, Figure 5.40).

Table 5.9 Parameter estimates and significance in the GAMM model relating overall wind speed to red-throated diver migration in spring.

Parameter coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	-3.018	0.102	-29.69	<0.001
	edf	**Ref. df**	**F**	**p-value**
Wind component-U	1.77	1.77	5.498	0.034

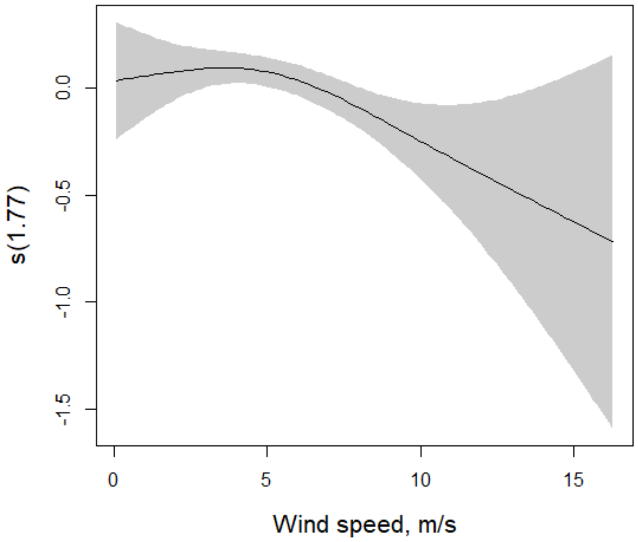


Figure 5.40 GAMM response curve showing that probability of red-throated diver spring migration was decreasing overall wind speed was exceeding 5 m/s.

5.5.3.2. Effects of meteorological factors in red-throated diver autumn migration

The same as in the assessment of spring migration, we first assessed the general patterns of autumn migration by linking the predictor variable to a day of the year. The model was significant and the response curve showed that the likelihood of diver migration in autumn is increasing until the day 270 (September 27), then declines until the day 310 (November 6) before starting to increase again (Figure 5.41).The two turning points of the curve indicate beginning and end of autumn moult period: birds migrate from the northern breeding grounds to the moulting areas, stay there for approx. 40 days and then migrate again to the wintering quarters.

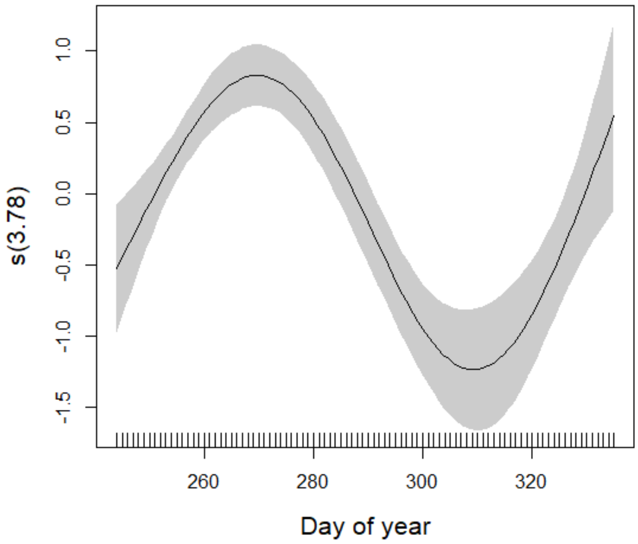


Figure 5.41 Response curve of the GAMM models showing general patterns of diver autumn migration phenology when the only predictor variable is day of the year.

Similarly as during the spring migration, the majority of the considered meteorological parameters were not significant explaining diver migration in autumn. Namely, no statistically significant relationship was found with Charnock parameter, sunshine duration, total cloud cover, total precipitation, water vapor concentration, total atmospheric water, mean sea level pressure, wind component-U and wind speed. Only variables describing air temperature and wind component-V were significant.

Air temperature was highly significant environmental variable and its response curve showed that probability of diver migration was highest at temperatures between 2 and 12 °C (Table 5.10, Figure 5.42).

Table 5.10 Parameter estimates and significance in the GAMM model relating the air temperature to red-throated diver migration in autumn.

Parameter coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	-3.122	0.220	-14.16	<0.001
	edf	**Ref. df**	**F**	**p-value**
Wind component-U	2.341	2.341	5.693	0.007

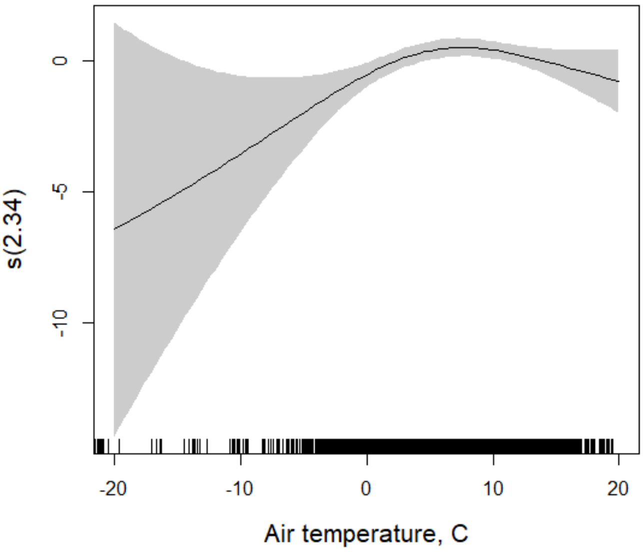


Figure 5.42 GAMM response curve showing that red-throated divers most likely migrate when air temperature was between 2 and 12 °C during the autumn migration period.

Wind component-V, characterising north-south winds (negative values are for wind blowing from the north and positive – from the south), had a negatively linear relationship with red-throated diver autumn migration suggesting that divers were more likely to migrate at higher wind from the north and probability of autumn migration was decreasing with increasing wind speed from the south (Table 5.11, Figure 5.43). This shows the exact opposite results compared to the spring migration and indicates that birds prefer using tail wind during the migration periods.

Table 5.11 Parameter estimates and significance in the GAMM model relating the wind component-V to red-throated diver migration in autumn.

Parameter coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	-2.923	0.192	-15.21	<0.001
	edf	**Ref. df**	**F**	**p-value**
Wind component-U	1	1	8.196	0.004

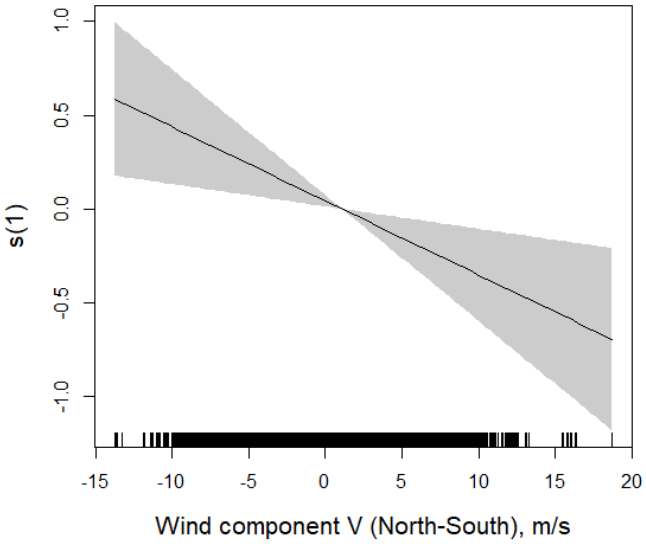


Figure 5.43 GAMM response curve showing that red-throated divers were likely to migrate in tail wind conditions from the north and unlikely to fly into the strong headwind blowing from the south, when assessed diver migration in relation to wind component-V during the autumn period.

5.5.4 Discussion

Migration timing of red-throated diver individuals is quite synchronous, which was shown by many individuals migrating to and from the same breeding regions at similar times. It is likely that migration timing is primarily defined by intrinsic factors (instincts, life experience, etc.) as it is unlikely that birds would be able to gauge conditions on e.g. nesting areas prior to migration initiation, which are often located thousands kilometres away.

It was shown in many bird species that in addition to the intrinsic urge to migrate, meteorological factors also influence migration timing (SHAMOUN-BARANES et al. 2017). Thus, it can also be expected that weather conditions play a role in diver migration. Rather few of the assessed meteorological variables showed correlates with red-throated diver migration. However, importance of wind conditions was clear and separate analyses for spring and autumn migration revealed that divers tend to migrate using tail wind conditions and are unlikely to migrate into the strong headwinds. Using tail winds and avoiding strong head winds helps saving energy during long-distance migration, which is particularly important for a species with heavy wing loading as the red-throated diver (ALERSTAM et al. 2007).

Importance of Charnock parameter in spring can be viewed as a proxy of wind speed, which was likely correlated with strong winds of unfavourable direction. Interpretation of air temperature influence in autumn is more difficult to interpret.

6 RED-THROATED DIVER HABITAT USE IN RELATION TO OWFS

This chapter contains a manuscript submitted for publication with the status of December 2019 and additional analyses, which are displayed in chapter 6.5 and 6.6.

Strong displacement of red-throated divers (*Gavia stellata*) from offshore wind farms confirmed by two independent data sets, satellite telemetry and digital aerial surveys

Stefan Heinänen[1,6], Ramūnas Žydelis[1,2], Birgit Kleinschmidt[3,4], Monika Dorsch[3], Claudia Burger[3], Julius Morkūnas[5], Petra Quillfeldt[4], Georg Nehls[3]

[1]DHI, [2]Ornitela, [3]BioConsult SH, [4]Justus Liebig University Giessen, [5]Marine Research Institute, Klaipėda University, [6]Novia University of Applied Sciences

Abstract

Expansion of offshore wind energy is vital for the reduction of CO_2 emissions. However, if not adequately planned there is a risk for environmental impacts. Here we assess the robustness of the conclusions that the strictly protected red-throated diver, *Gavia stellata*, is strongly displaced from wind farms. We modelled the distribution of divers based on two independent data sets, digital aerial surveys and satellite telemetry, in relation to the dynamic offshore environment and anthropogenic pressures. The model results based on both data types were consistent. Divers were strongly displaced from within and 5 km around the wind farms located in suitable habitat. The displacement effect gradually decreased with distance from the wind farms, but a significant effect could be detected up to 10 – 15 km away. The telemetry data further indicated that the displacement distance decreased with decreasing visibility. These findings should be taken into consideration in marine spatial planning to avoid cumulative impacts on the red-throated diver population.

6.1 Introduction

The pace of offshore wind farm construction particularly in Europe is rapid and plans for future developments are extensive (WINDEUROPE 2018). A similar expansion of offshore wind is expected for other parts of the world as well (see e.g. FIRESTONE et al. 2015). If this expansion is not adequately planned there is a risk for environmental impacts (BAILEY et al. 2014). The prevailing and recommended approach for avoiding conflicts between wildlife and wind farms is spatial planning, i.e. to avoid building wind farms in areas of high conservation value (see e.g. DREWITT & LANGSTON 2006). Planning of offshore wind farms thus requires sound knowledge about the spatial distribution, movements and response of species of concern.

The main potential effects caused by offshore wind farms on birds have been described to be collisions, displacement, barrier effect and habitat loss (DREWITT & LANGSTON 2006). If birds are strongly displaced the collision risk is naturally very small and displacement/disturbance can be regarded as the major effect. Spatial planning aiming to reduce cumulative impacts is important, not only regarding construction of offshore wind farms, but rather including the full range of anthropogenic offshore activities (KANNEN 2014).

The strictly protected red-throated diver (*Gavia stellata*) has a circumpolar summer distribution, breeding widely on lakes in the boreal and the high Arctic regions. During the non-breeding season the species is found broadly in coastal waters in the Northern Hemisphere. The species is listed in Annex I of the EU Birds Directive, in Annex II of the Bern Convention, in the African Eurasian Waterbird Agreement (AEWA) and is further listed by HELCOM (2013) as a critically endangered species, though as of least concern by IUCN (BIRDLIFE INTERNATIONAL 2016). The preferred non-breeding habitats of red-throated divers, characterised by relatively shallow waters not too far from the coast (SKOV & PRINS 2001), also overlap with suitable areas for offshore wind farms and other anthropogenic activities. The German Bight (North Sea) holds several offshore wind farms and a large concentration of red-throated divers in spring (March to May). The mean estimated spring population size for the years 2002–2013 in the area was about 20 000 (including 10% black-throated divers, GARTHE et al. 2015), which (considering imprecise population estimates) might represent around 5 – 15% of the total flyway population (WETLANDS INTERNATIONAL 2018). Diver species have been identified as particularly sensitive to anthropogenic disturbance on both breeding and non-breeding grounds (LOKKI & EKLÖF 1984; DIERSCHKE et al. 2012, 2016). Several studies have shown that divers are displaced from offshore wind farms, however, mostly published in “grey literature” (WELCKER & NEHLS 2016). In parallel to our study a coarse scale analysis based on interpolated long-term mean distribution patterns before and after construction of wind farms was conducted in the German Bight, showing a clear and long ranging displacement of diver species from offshore wind farms (MENDEL et al. 2019a). Divers have also been shown to be sensitive to shipping (BELLEBAUM et al. 2006; SCHWEMMER et al. 2011; BURGER et al. 2019).

Seabird displacement from offshore wind farms has been studied based on a range of different approaches, sampling design and statistics; by using a Before-After-Control-Impact (BACI) design (VANERMEN et al. 2015), or a gradient analysis design (Leopold et al., 2013) for example. Some studies include the wind farm effect (VANERMEN et al. 2015) and some compare interpolated density surfaces pre and post construction (PETERSEN et al. 2013). The data collection methods have also varied: ship surveys, visual and digital aerial surveys, radars and more recently also telemetry. However, it is still unclear whether different methods give similar results and thus provide robust evidence for displacement effects.

Relatively few studies have previously incorporated the dynamic environmental conditions in the displacement modelling approach (but see PÉREZ LAPEÑA et al. 2011). Shallow shelf seas, such as the North Sea, can be complex and animal distributions can partly be shaped by dynamic processes in frontal zones (COX et al. 2013, 2016; SKOV et al. 2016). Failing to account for the dynamic environment can lead to a wrongly defined displacement effect (Type I error) or an undetected effect of wind farms (Type II error). Including the hydrodynamic predictors should also enhance the power of detecting a displacement (PÉREZ LAPEÑA et al. 2011). Further, it is also important to understand the habitat relationships and thereby be able to assess the extent of alternative habitat (if birds are displaced). In case there is plenty of suitable habitat near the area where the birds are disturbed, the impact can be expected to be less severe than if the habitat is limited and density dependence therefore stronger.

The aim of this study was to assess whether the same displacement effect can be detected and described by two different state of the art data sets and a different modelling approach compared to the pre- and post-construction method used by MENDEL et al. (2019b) and thereby confirm the strong displacement effect previously found. Our analyses were based solely on high quality post-construction data describing the displacement as a result of a behavioural response, while accounting for the dynamic environment. We therefore provide an approach for analysing displacement without pre-construction data, which in many cases are lacking. We further hypothesized that the displacement range varies with decreasing visibility which we analysed based on the telemetry data.

6.2 Material and Methods

6.2.1 Study area

Red-throated divers were tagged and surveyed in the German Bight, eastern North Sea (Figure 6.1). The size of the study area is approximately 16,500 km^2 of which 270 km^2 is covered by wind farms. There are three wind farms in the northern part of the study area, Butendiek (80 turbines, 3.6 MW each), DanTysk (80 turbines, 3.6 MW each) and Sandbank (72 turbines, 4 MW each). The Sandbank wind farm was built during 2016 and was fully operational in 2017, during the time our study was taking place. In the analyses only fully operational wind farms were regarded as a pressure (i.e. Sandbank wind farms was only included in 2017). In the southern part of the study area there is a cluster (“Helgoland Cluster”) consisting of three wind farms, Amrumbank West (80 turbines, 3.6 MW each), Nordsee Ost (48 turbines, 6.15 MW each) and Meerwind Süd|Ost (80 turbines, 3.6 MW each). Shipping and fishing intensity is also relatively high in the area (VESPE et al. 2016; ALESSANDRINI et al. 2017).

The study area is located in a shallow shelf sea and strongly influenced by tidal motion (OTTO et al. 1990). There are two main water masses, the North Sea water mass and the continental coastal water mass (BECKER et al. 1992). The coastal water mass has lower salinity influenced by river outflows and the frontal zone between the two water masses is dynamic (BECKER et al. 1992). Red-throated divers have previously been shown to prefer the frontal zone between these two water masses (SKOV & PRINS 2001). The area is also highly productive in spring when the spring bloom takes place (VAN LEEUWEN et al. 2015).

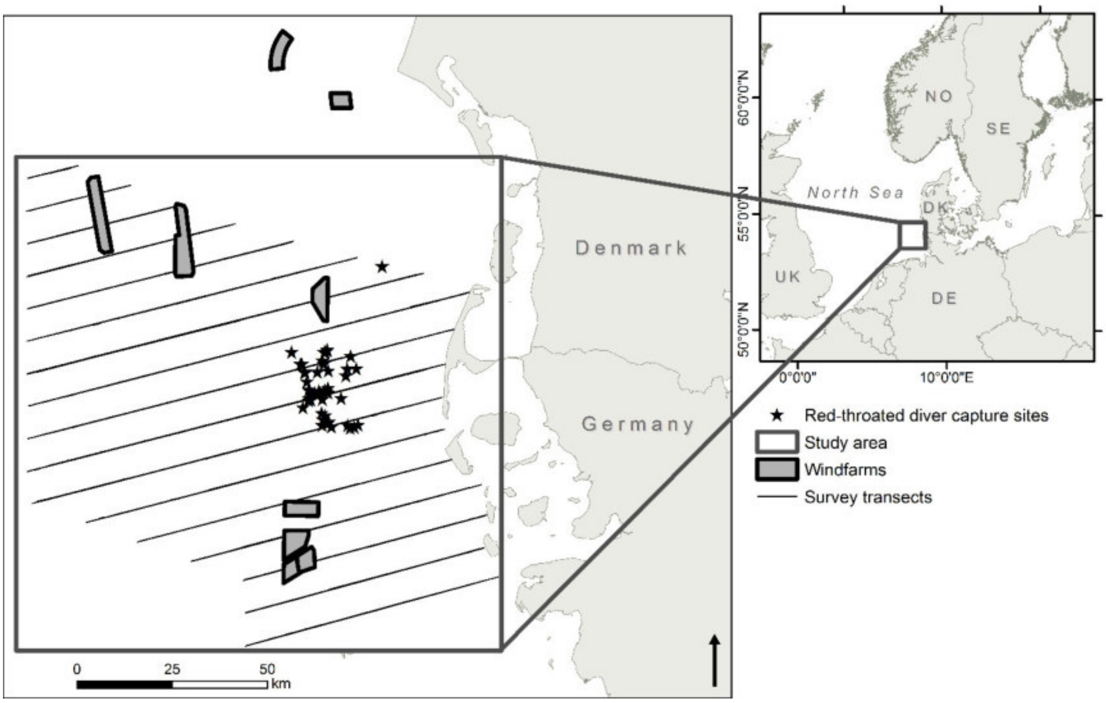


Figure 6.1 Study area, red-throated diver capture sites for fitting birds with transmitters and digital aerial survey transects. In total 45 birds were tagged and 33 individuals analysed. Operational wind farms present during the study period are shown.

6.2.2 Satellite telemetry

Birds were captured from a boat at sea using the “night lighting technique" (WHITWORTH et al. 1997). On dark nights birds were searched from a small boat using a bright light. We used two different types of lamps: a Hella hand held search lamp with a short range 55 W bulb and a long range 100 W bulb with an opening of 154 mm and a Acebeam X60M with three LED bulbs of 10 000 lm and an opening of 108 mm. Once found, divers were (often) disoriented by the light, which allowed the capture team to approach the diver close enough to catch it with a hand net attached to a pole.

Catching birds was done during three time periods: March to April 2015, February to March 2016 and March 2017. Birds were caught in the German North Sea between 54°30’ and 55°00’N and about 20 – 30 km off the coast (Figure 6.1).

The captured birds were placed into well ventilated and specially adapted kennels. The kennel floor was made from elevated mesh in order to keep birds dry and clean. The inner walls of the kennels were padded with soft material or cardboard making sure that there were no holes in the crate that were big enough for birds' bill to go through. Only one bird was kept in each kennel when transporting, and the kennels were stored outdoors to prevent birds from overheating. Within minutes after capturing the birds were sedated by injecting Midazolam, administering approximately 2 mg/kg. Sedation is necessary for this species as red-throated divers have a tendency of getting stressed.

The captured birds were delivered from the small capture boat to a larger ship. During the first tagging period in 2015 transmitter implanting was conducted in a temporary land-based surgery room with all required equipment. To reduce handling time, the surgeries during the following two tagging periods were conducted in a similar temporary surgery room on board the ship. Transmitters were abdominally implanted with percutaneous antenna following standard surgical technique used for diving birds (KORSCHGEN et al. 1996; MULCAHY & ESLER 1999). Birds were released 2 – 4 hours after surgery when they were assessed as having fully recovered from sedation. When possible, birds were released in the area of capture, only in 2015 three individuals were released from the shore due to stormy sea conditions. Captivity time from the moment of capture to release ranged from 5 to 27 hours. Surgeries were done by an experienced veterinarian and all fieldwork (animal capture, sampling and tagging) was conducted under appropriate ethics and approved by BfN (Federal Agency for Nature Conservation, Germany, 05.08.2014) and the Ministry of Environment and Food Denmark, Danish Veterinary and Food Administration (permit no. 2014-15-0201-00239, issued 18.12.2014).

We used implantable Argos satellite platform terminal transmitters (PTTs) manufactured by Telonics, Inc. IMPTAV-2635 (5 units), IMPTAV-2640 (20 units), IMPTAV-2645 (15 units) and Sirtrack, Ltd (K3I 171A, 5 units). PTTs weighing between 35 and 45 grams were implanted in birds weighing on average 1 729 grams (SD ± 174) and comprised on average 2.65% (SD ± 0.36) of the bird's body weight.

Transmitters were programmed using varying duty cycles with 3 or 4 transmission hours and 12–24 hour intervals between them when birds were expected to be on wintering grounds and longer intervals during the breeding season, 60 – 68 hour.

Collected ARGOS data was delivered by CLS France (CLS 2013). Received positions were classified into one of six Argos quality classes, with accuracy ranging from < 250 m to > 1 500 m, and there were also locations with unavailable accuracy information (Table B.11.1).

Satellite telemetry data requires filtering to reduce noise produced by location fixes with low or unknown accuracy. We applied a Freitas filter to eliminate unlikely locations based on the location quality class, calculated bird moving speed, distance between successive locations, and turning angles (FREITAS et al. 2008). When applying the Freitas algorithm, the maximum moving speed of divers was set at 20 m/s and other parameters were kept as default. The package 'argosfilter' (FREITAS et al. 2008) in the R statistical environment (R CORE TEAM 2018) was used to apply the filtering algorithm. Filtering successfully eliminated the majority of unlikely locations outside of the actual area used by the animal and removed 'spikes' along bird tracks. The filtered data set was further inspected visually and several obvious outlier positions were flagged and eliminated from the data set. Finally, positions recorded during the first two weeks after the release were excluded from all analyses due to possible unnatural behaviour during that period.

6.2.3 Digital aerial video surveys

Four digital aerial video surveys were conducted, during 10 April 2016, 1 May 2016, 25 March 2017 and 11 May 2017, using a transect design consisting of 17 transects with a spacing of about 8 km and a total length of roughly 1,300 km. The total area surveyed, as defined by a convex hull around the survey transects, was approximately 11,500 km^2 (Figure 6.1) of which approximately

720 km^2 were covered by the survey transect. The duration of a survey was 9–11 hours, of which approximately 7 hours were spent on transect. Surveys started in the morning around 1.5–2 hours after sunrise to ensure having enough daylight hours for completing the survey within one day, including a 2 – 4 hours break during midday. The surveys were conducted using the HiDef video camera system at 549 m flight altitude (Weiß et al. 2016; Žydelis et al. 2019). The camera system consists of a rig with four cameras with a ground resolution of 2 cm per pixel. The two outermost cameras in the row cover a strip of 143 m each while the innermost two cameras a strip of 129 m each and each strip is separated by 20 m (i.e. in total a video strip width of 544 m). The flight track was recorded in intervals (segments) of one second using a Garmin GPSMap GPS receiver 296 with a precision of 1 m. Image frames from the video footage were georeferenced to the corresponding survey segment. Bird identification was done by trained observers in the lab and divers were identified to species level in most cases. Only red-throated divers identified to the species level were retained for the analyses, i.e. black-throated divers (0.1%) and unidentified divers (3% of all divers) were discarded. The detection and identification of objects on the video footage was done in two steps. In the first step observers marked all birds and marine mammals occurring in the video footage. For quality assurance 20% of the video footage (for each camera strip) were randomly selected and analysed by an independent observer. If < 90% agreement was obtained the video footage was reanalysed. In the second step the marked objects (birds and marine mammals) were identified to the lowest possible taxonomic level by experienced ornithologists. Additionally, behaviour, age, sex and other potentially useful information was noted. Similarly to the first step, a quality assurance of 20% of all identified objects was conducted. If < 90% agreement was obtained bird identification was redone. The valid bird observations identified in the videos were spatially and temporarily combined with the flight effort (with effort meaning also zero observations were added). The red-throated diver observations were summed per segment of approximately 500 m (the length of the original 1 min survey segments were summed until 500 m was reached). Bird densities (birds/km^2) were calculated by dividing the number of observed birds by the area covered in each segment. The environmental data (described below) was finally extracted to the survey data based on position and time.

6.2.4 Environmental data and pressure layers

To describe the distribution of red-throated divers in the German Bight we included the following environmental variables in the modelling of digital aerial survey data: modelled surface salinity, a gradient index of chlorophyll a concentration and water depth. Distance to wind farms and shipping intensity (based on data from the automatic identification system of ships, AIS) were further included as anthropogenic pressure variables. In the model based on telemetry data the gradient index of chlorophyll a concentration and shipping intensity were not included because data on these two variables were not available for the whole study period.

Surface salinity (second modelled vertical layer from the top at ca. 1 m) was extracted from a DHI 3D hydrodynamic model (DHI 2016), covering the whole North Sea with a flexible mesh (unstructured triangular grid) with a mean resolution of approximately 7.7 km^2 and a temporal resolution of 1 hour. The layer was converted to a regular grid of 0.01 x 0.01 degrees. The hydrodynamic model was calibrated based on a range of input data, including bathymetry, initial water levels, current velocities and boundary conditions.

For calculation of the chlorophyll gradient, as a proxy for the frontal zone, a standard Aqua MODIS chlorophyll a concentration layer (OCI algorithm) was extracted, an 8 day composite 3-level raster with the standard 4 x 4 km resolution corresponding to the survey data period (https://oceancolor.gsfc.nasa.gov/cgi/l3). The slope tool in ArcGIS was used to calculate a gradient index with chlorophyll a concentration as input variable, depicting variability in chlorophyll concentration, based on the maximum change within a 3 x 3 cell neighbourhood. The resulting gradient layer should be regarded as an index as the slope tool requires x, y and z input variables of the same unit for the calculation of a gradient in degrees. An increasing index value is assumed to indicate a frontal area.

The water depth layer used in the models had a resolution of 500 x 500 m. Distance to wind farms was calculated as the Euclidean distance to the wind farm footprint. The distance variable was further classified into five categories; 0 – 5 km (footprint + 5 km buffer, n = 1,112), 5 – 10 km (n = 1 263), 10 – 15 km (n = 1,351), 15 – 20 km (n = 1,555), and > 20 km from the wind farm (n = 4,699). The indicated sample sizes are for the aerial survey data. Distance bands of 5 km ensured a reasonable sample size within each distance category. No divers were detected inside the wind farm during the surveys which caused analytical problems when including the footprint as a separate level in the model. The footprint was therefore combined with the 5 km buffer. Shipping intensity was calculated by creating ship tracks for each individual vessel from AIS positions of all vessels recorded in the area during the survey days (i.e. a temporal resolution of 24 hours). We did not distinguish between ship types in this analysis, i.e. variation due to ship type and sailing speed was not separated (see BURGER et al. 2019 for more details on this aspect). The tracks were further intersected with a 500 x 500 m grid and the length of all tracks within each cell was calculated (summed). Further, the sum within 1,500 m from each cell was calculated (using the Geospatial modelling environment, Beyer, 2015). The AIS data was purchased from www.marinetraffic.com. For predictions the finest grid was used (500 x 500 m), all other variables were intersected with this grid and mean values for the survey dates for dynamic variables were used.

For assessing the displacement distance (distance of individual divers to wind farms) in relation to weather conditions meteorological data from the European Centre for Medium-Range Weather Forecasts (ECMWF) was extracted to the telemetry data within the Movebank portal (Dodge et al. 2013). The following variables were extracted: charnock parameter, sunshine duration, total cloud cover, total precipitation, total atmospheric water, mean sea level pressure, wind U-component, wind V-component, wind speed, air temperature. These variables were all hypothesized to affect visibility and thereby the distance between divers and wind farms. We further also hypothesized that wind turbines are more visible to the birds during night because of the red safety lights. To assess the day-night effect on the displacement range the angle of the Sun in relation to the horizon was calculated using a custom-made R function that estimates sun’s position based on geographic location (longitude and latitude) and time of the position. Negative values of the angle indicate that the sun is below the horizon and positive values that it is above the horizon. As a threshold between day and night we used the angle value of -6 (the Sun is six degrees below the horizon) that refers to the end of civil twilight in the evening and beginning of civil twilight in the morning. Time was assessed both as a factor variable (day or night) or as a continuous variable.

6.2.5 Statistical analyses

To assess the displacement effect from offshore wind farms while accounting for other important factors a generalised additive mixed model (GAMM) approach was used for both data sets (telemetry and survey data). The two data sets are fundamentally different and were therefore analysed separately, which also allows for cross comparison of the results. The telemetry data is "presence only" (i.e. there are no records of absences) and to be able to model these data with a binomial distribution (logistic regression), pseudo-absences (availability positions) were generated. The digital survey data on the other hand have in addition to information about presences and absences also information on abundance. A typical characteristic of survey data is, however, zero inflation, i.e. there are many more zeros than positive observations. There are different approaches for dealing with the over dispersion caused by zero inflation (ZUUR et al. 2012), including e.g. zero inflated models and hurdle models. Hurdle models are two step-models where the probability of presence is modelled in the first step and in the second step the abundance or density is modelled conditioning on presence (i.e. all zeros are excluded). Red-throated divers generally occur in low densities, individually or in groups of a few birds only. Presence-absence models should therefore be able to describe most of the variability in the distribution pattern. GAMMs were fitted in R (R CORE TEAM 2018) using the mgcv package (WOOD 2011). Below the specific analyses for each data type are described in detail.

6.2.5.1. Displacement analyses based on telemetry data

Three pseudo-absence locations (availability points) for each presence position within the study area were randomly generated. The approximation of habitat availability improves with increasing number of absences and three absence locations were assessed to be suitable in this study (AARTS et al. 2008). The assumption is that a bird can easily reach any location within the area within a short timeframe and therefore the whole area is potentially available for the birds. We used Geospatial Modelling Environment 0.7.4 (http://www.spatialecology.com/) for generating pseudo-absence locations. Each pseudo-absence location received the same date-time stamp as the actual location it was associated with.

A binomial GAMM was fitted with telemetry presence points (defined as 1) and the generated pseudo-absences (defined as 0) as the response variable. One presence point per bird and day was randomly selected and included in the model and only points from within the study area were used (Figure 6.2). Data subsampling and the use of a single telemetry position per bird per day was done aiming to reduce over-representation of some individuals and autocorrelation between positions (AARTS et al. 2008). As predictor variables we included salinity (extracted based on position and time), water depth and distance to wind farms, the latter as a factor variable. The degrees of freedom for the continuous variables, smooth terms, were estimated based on cross-validation but were restricted to a maximum of 5 ($k = 5$) to reduce potential overfitting (REDFERN et al. 2008; GOWAN & ORTEGA-ORTIZ 2014). The default thin plate regression splines in the mgcv R package were used. Water depth and salinity were rather highly correlated with Pearson's correlation coefficient being 0.69, which is close to the maximum collinearity between the predictor variables that can be accepted (DORMANN et al. 2013). To account for residual autocorrelation in the data (which the predictor variables could not explain) a correlation structure (corARMA, $p = 1$, $q = 1$), grouped by individual bird-months, was included. Failing to account for potential residual autocorrelation could result in biased parameter estimates and therefore potentially wrong conclusions about the displacement effect. The predictive ability of the model was assessed by a split sample approach, 20% of the data was randomly selected and left out for evaluation. The model was refitted on the remaining 80% and tested on the 20% using the area under receiver operating characteristic curve (AUC, Pearce & Ferrier 2000). Potential residual autocorrelation was assessed using an autocorrelation function (ACF) plot and a variogram (Zuur et al. 2012).

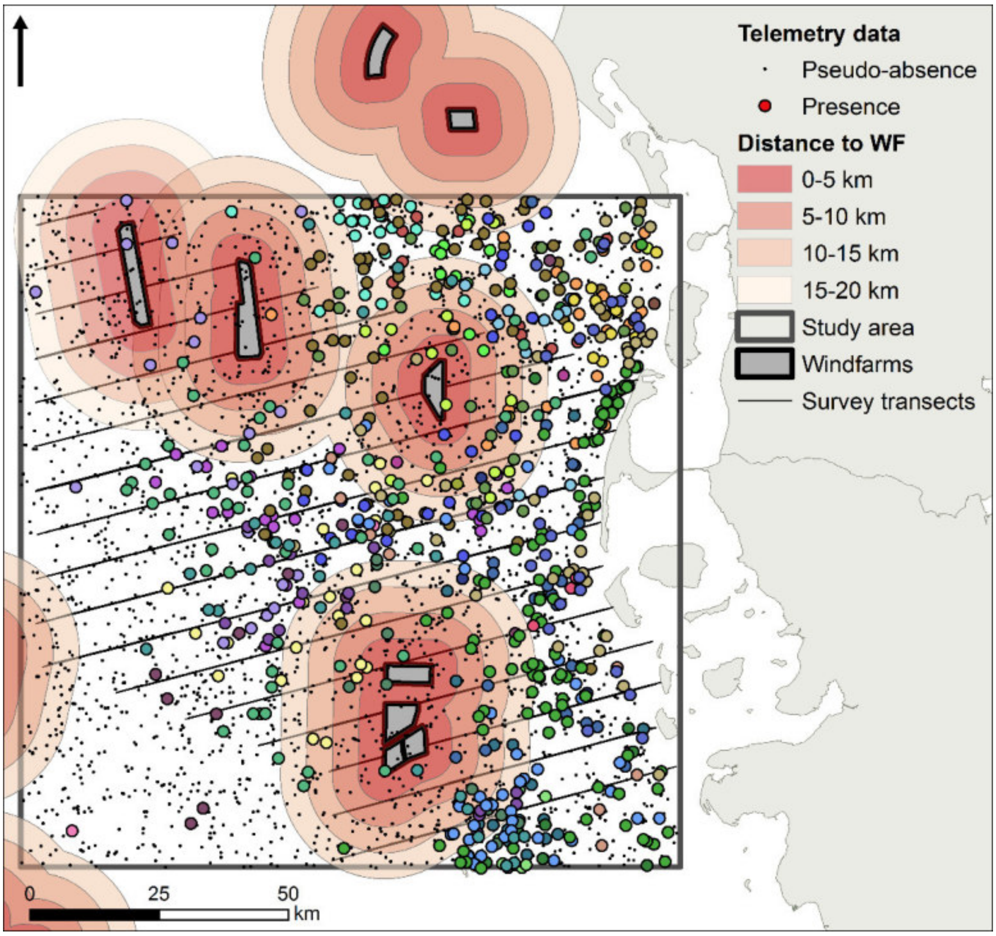


Figure 6.2 *Telemetry data included in the GAMM analyses, different colours (indicated as presence) indicate different individuals (n = 33) and black dots indicate pseudo-absence locations. The distance from wind farms categories used in the analyses are indicated as buffers.*

6.2.5.2. Effect of meteorological factors on displacement range based on telemetry data

To assess whether meteorological factors affect the distance of individual divers to offshore wind farms univariate GAMMs were fitted with distance to wind farms as a response variable and individual, meteorological or daytime variables as explanatory variables. The distance to wind farms variable was normally distributed and the models were therefore fitted with a Gaussian family distribution (with an identity link). A single location per bird per day was randomly selected from the full dataset to avoid overrepresentation of any specific individuals in the models. Individual bird ID was used as a random factor in order to account for individual effects.

6.2.5.3. Analyses of displacement based on digital aerial video surveys

The digital aerial video survey data was fitted using a two-step (hurdle) GAMM modelling approach. The model consisted of a binomial model part (presence-absence) and a positive density model part, fitted with a gamma distribution. To account for potential spatial or temporal autocorrelation a correlation structure (corARMA) grouped by transect ID was included. The permitted degrees of freedom were restricted to maximum 5 (k = 5) or were reduced to 3 (k = 3) if the response curves still showed possible model overfitting. Thin plate regression splines were used for the smooth functions. The predictions from both model parts were combined (multiplied) to yield the final density surface (HEINÄNEN et al. 2017). To illustrate a hypothetical situation, in a case without wind farms, the model was also predicted on the whole study grid assuming no wind farms and no shipping. Potential residual autocorrelation was assessed using an ACF plot and a variogram (ZUUR et al. 2012).

The models were evaluated for predictive accuracy by fitting the model on 80% of the data (randomly selected) and predicting on 20% withheld data. The presence-absence model part was evaluated using AUC (PEARCE & FERRIER 2000) and the overall density predictions obtained by combining both model parts were evaluated using Spearman’s correlation coefficient (POTTS & ELITH 2006). The evaluation procedure, for the aerial video survey data, was done 10 times to assess the effect of the random sample.

6.3 Results

6.3.1 Telemetry data

Of 45 red-throated divers tagged, 33 individuals were successfully tracked in the area selected for analyses (Figure 6.1). Bird positions recorded in the Wadden Sea were removed before analyses because of different environmental characteristics which were not covered by the survey transects. Overall, only 9 telemetry positions by only two individuals of all 2,682 data points were logged inside the wind farm footprints. After filtering and sub-sampling (randomly selecting one daily location per bird) 694 bird presence positions in the study area were retained for analyses (Figure 6.2), covering the periods: 3 April 2015 to 21 May 2015, 8 December 2015 to 17 May 2016 and 10 October 2016 to 14 May 2017. Of these presence locations only 1 position was recorded inside the operating wind farms (Figure 6.2). The proportion of presences versus randomly generated pseudo-absences in different distance bands from the wind farm indicated a preference for areas farther away from wind farms (Figure 6.3).

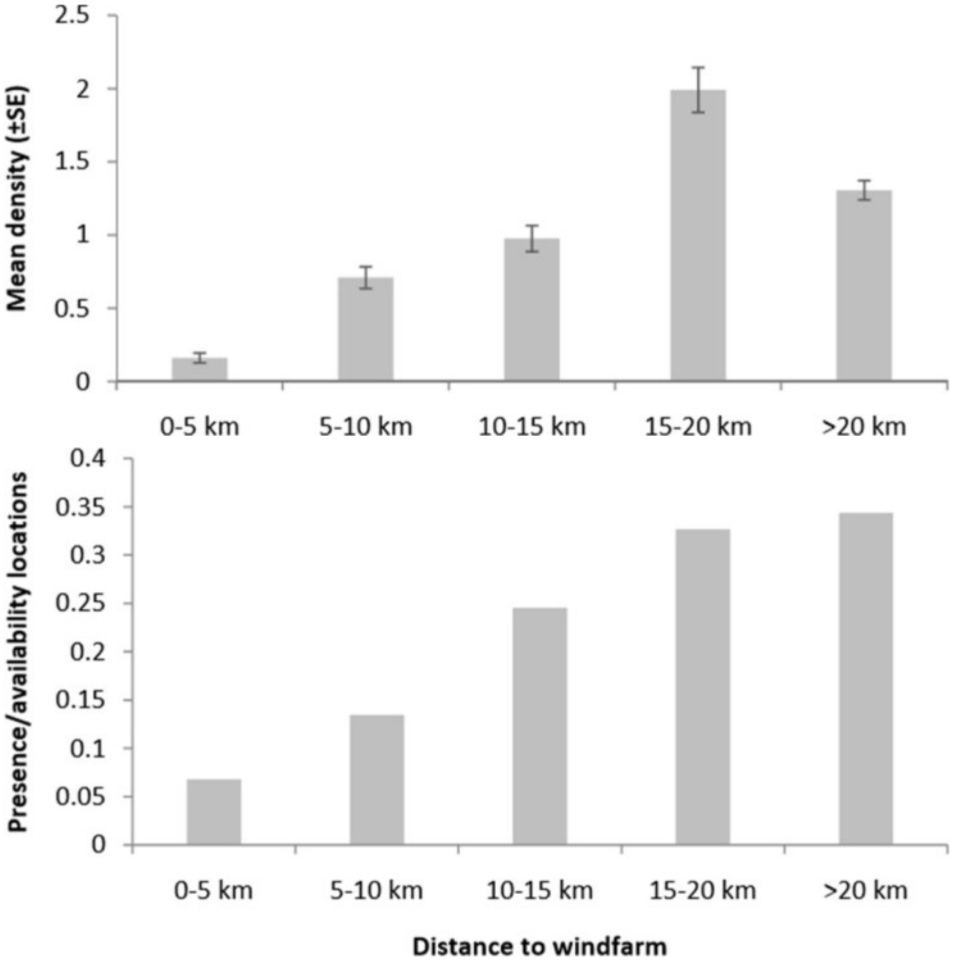


Figure 6.3 *Recorded distribution of tagged red-throated diver positions in relation to distance to offshore wind farms after accounting for area availability (lower chart) and mean density (birds/km²) of this species registered during digital aerial surveys within distance zones from offshore wind farms (upper chart).*

6.3.2 Digital aerial video survey data

The highest numbers of red-throated divers were observed during the survey conducted during 10 April 2016 (~ 1,400 birds) and slightly fewer during 1 May 2016 (~ 1,100 birds). In 2017, notably fewer birds were counted during 25 March (~ 570 birds) and 11 May (~ 330 birds). The mean densities in different distance bands from the wind farms indicate a reduced number of birds closer to the wind farm (Figure 6.3). No divers were recorded within wind farm footprints and few, 31 presences (during four surveys), within 5 km from the footprints (post-construction).

6.3.3 Displacement based on telemetry data

According to the GAMM model fitted on satellite telemetry data the tagged red-throated divers preferred areas with salinities around 30–32 psu and the preference decreased linearly with increasing water depth (Figure 6.4). The habitat preference (habitat suitability) was significantly lower within the wind farm including a 5 km buffer and up to 10 – 15 km away from the wind farm as compared to the areas farther away (Table 6.1, Figure 6.4). There was no residual autocorrelation and according to the evaluation statistics the model had a reasonable predictive ability (AUC = 0.73).

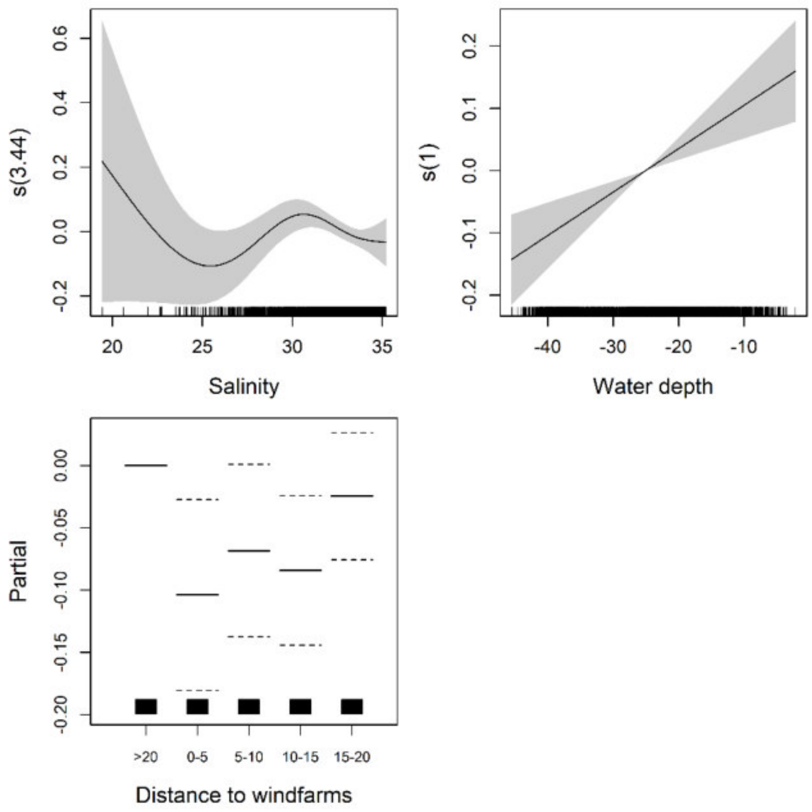


Figure 6.4 *Response curves of the GAMM based on telemetry data. The range of the predictor variables are shown on the X-axis and the response on the Y-axis in logit scale (scale of the linear predictor). The grey areas and the dotted lines show the 95% confidence intervals.*

Table 6.1 *Parameter estimates and significance for the parametric and smooth terms included in the GAMM based on telemetry data.*

	Estimate	**Std.-Error**	**T value**	**Pr(>|t|)**
(Intercept)	-0.658	0.163	-4.038	0
Distance to OWF 0–5 km (including footprint)	-0.104	0.038	-2.713	0.007
Distance to OWF 5–10 km	-0.068	0.035	-1.972	0.048
Distance to OWF 10–15 km	-0.084	0.030	-2.805	0.005
Distance to OWF 15–20 km	-0.025	0.026	-0.963	0.334
	edf	Ref.df	F	p-value
Salinity	3.437	3.437	2.915	0.046

	Estimate	Std.-Error	T value	Pr(>|t|)
Water depth	1	1	15.502	0
N	3,103			

6.3.4 Distance between tagged divers and wind farms

The different red-throated diver individuals were exposed to varying meteorological conditions in the study area during the whole study period. According to the univariate GAMMs the distance from the tagged divers to the closest wind farm decreased linearly with increasing wind speed and precipitation. Divers were also significantly closer to wind farms during day in comparison to night, based on both the categorical variable (day/night) and the continuous time variable (sun's angle; Table 6.2).

Table 6.2 Univariate GAMM fixed effect parameter estimates for parametric and smooth terms showing significant responses.

Model 1 Parametric terms	**Estimate**	**Std.-Error**	**T value**	**Pr(>|t|)**
Intercept	23,413	872.4	26.84	<0.001
Smooth term	**edf**	**Ref. df**	**F**	**p-value**
Wind speed	1	1	8.862	0.003
Model 2 Parametric terms	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
Intercept	23,484	871.2	26.96	<0.001
Smooth term	**edf**	**Ref. df**	**F**	**p-value**
Sun's angle	1	1	6.729	0.009
Model 3 Parametric terms	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
Intercept	23,004	896.3	25.665	<0.001
Factor "Night"	1,378	694.2	1.985	0.048

6.3.5 Displacement based on digital aerial video surveys

According to the binomial model part based on digital aerial surveys the probability of birds being present was lowest within the wind farm footprints including a 5 km buffer zone around them. The probability was also significantly lower within 5 – 10 km and 10 – 15 km in comparison to 15 – 20 km and > 20 km from the wind farm. This indicates that there is a displacement/disturbance effect up to 10 – 15 km, gradually decreasing with distance to the wind farm. The probability of presence increased also significantly with decreasing shipping intensity, increasing salinity, increasing index (slope) of chlorophyll concentration and at water depths around 20 m. The probability of presence was significantly lower in the survey conducted in May 2017, in comparison to the first survey in April 2016 (Figure 6.5a, Table 6.3). In the positive model part the displacement effect was similar, a decreasing density with decreasing distance to the wind farms, which was still significant in the category 10 – 15 km away from the wind farms. Density was peaking at about 25 m water depth and at higher salinities (Figure 6.5b). There were also some high densities in low salinity although the occurrences were fewer than more offshore in areas with higher salinity (Figure 6.5b, Figure 6.6). Chlorophyll gradient and shipping intensity were not significant in the positive model part and therefore excluded. There was not a significant difference in the positive diver densities between surveys (i.e. when present the abundance of divers were of a similar order of magnitude). No autocorrelation was found in model residuals. Evaluation statistics indicated a reasonable predictive ability, a mean AUC of 0.78 (± 0.003 SE) for the presence/absence part and a mean Spearman’s correlation of 0.38 (± 0.012 SE) for the final density predictions (based on combining both model parts).

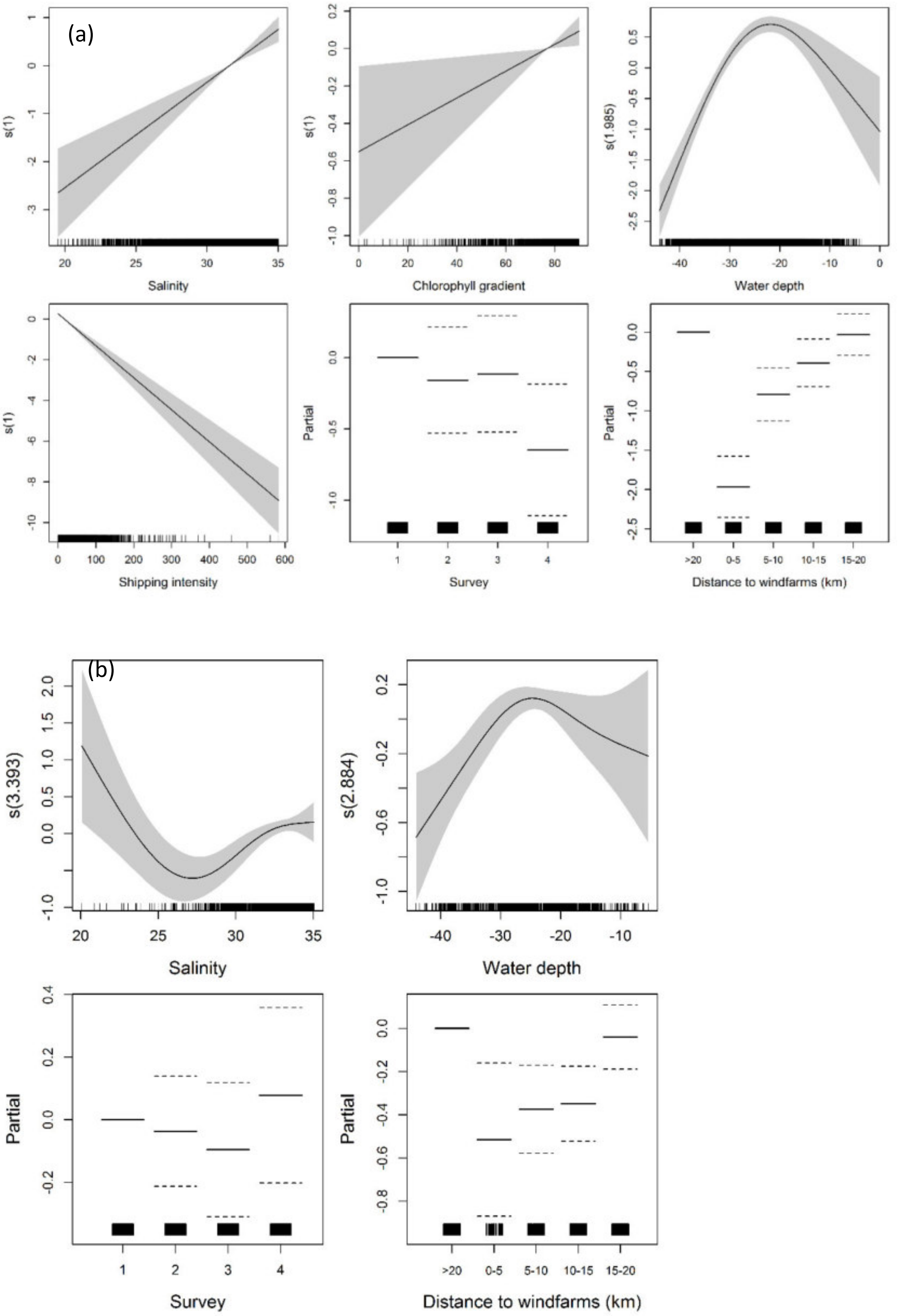


Figure 6.5 *Response curves of the GAMM based on digital aerial survey data, a) binomial model part and b) gamma model part. The range of the predictor variables are shown on the X-axis and the response on the Y-axis in logit or log scale (scale of the linear predictor). The grey areas and the dotted lines show the 95% confidence intervals. The levels in the factor variable for "Survey" are 1 = 10 April 2016, 2 = 1 May 2016, 3 = 25 March 2017 and 4 = 11 May 2017.*

Table 6.3 Parameter estimates and significance for the parametric and smooth terms included in both GAMM hurdle model parts (binomial and gamma) based digital aerial survey data.

	Binomial				**Gamma**			
	Estimate	**Std.-Error**	**T value**	**Pr(>|t|)**	**Estimate**	**Std.-Error**	**t value**	**Pr(<|t|)**
(Intercept)	-1.679	0.147	-11.395	0	2.217	0.072	30.991	0
Survey 1 May 2016	-0.158	0.186	-0.851	0.395	-0.037	0.088	-0.417	0.677
Survey 25 March 2017	-0.114	0.204	-0.56	0.575	-0.095	0.107	-0.889	0.374
Survey 11 May 2017	-0.647	0.23	-2.811	0.005	0.078	0.14	0.558	0.577
Distance to OWF 0–5 km (including footprint)	-1.966	0.194	-10.129	0	-0.514	0.177	-2.902	0.004
Distance to OWF 5–10 km	-0.792	0.168	-4.717	0	-0.374	0.102	-3.668	0
Distance to OWF 10–15 km	-0.39	0.152	-2.573	0.01	-0.349	0.087	-4.02	0
Distance to OWF 15–20 km	-0.032	0.132	-0.242	0.809	-0.04	0.074	-0.541	0.589
	edf	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**
Salinity	1	1	32.878	0	3.393	3.393	4.514	0.001
Chlorophyll gradient	1	1	5.823	0.016				
Water depth	1.985	1.985	58.622	0	2.884	2.884	6.853	0
Shipping intensity	1	1	121.44	0				
N	9,980				1,391			

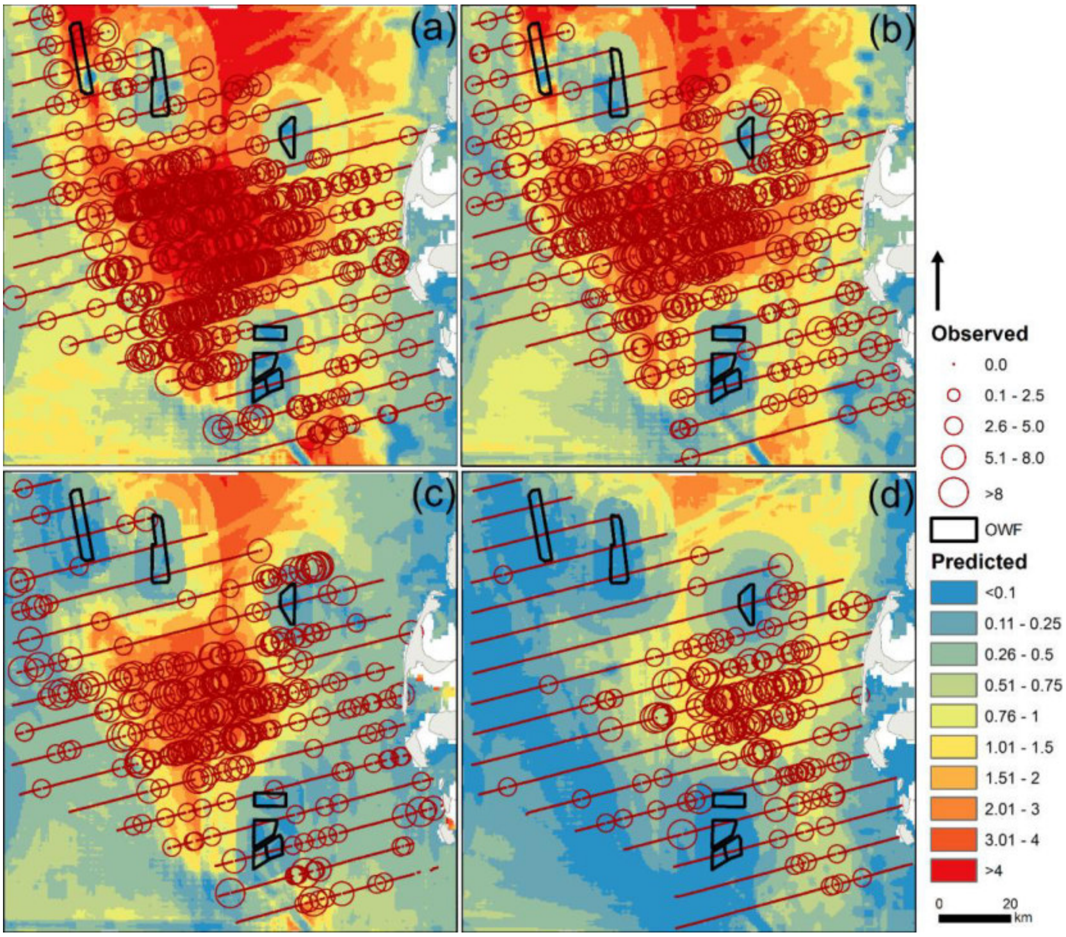


Figure 6.6 Predicted mean density (birds/km^2) distribution of red-throated divers based on digital aerial video survey data for average conditions in the whole study area during the specific survey days with observed densities overlaid, a) 10 April 2016, b) 1 May 2016, c) 25 March 2017 and d) 11 May 2017.

6.3.6 Predictions based on digital aerial surveys

The models were used to predict diver density distribution on the whole study grid based on mean environmental variables for the specific survey days. The predictions illustrate clearly a decrease in density with decreasing distance to the wind farms. The observed densities are plotted on top of the predictions to visualise the agreement between observed and predicted patterns (Figure 6.6).

Based on the model predictions the total number of divers in the study area could also be estimated (Figure 6.6). The highest abundance, 24,100 (± 4,500 model SE), was predicted for April 2016, but the variation between surveys was high and the lowest abundance, 6,300 individuals (± 1,700 model SE) was predicted for May 2017, when many divers most likely already had started migrating towards the breeding grounds. In March 2017 the predicted abundance was 12,600 (± 3,100 model SE) and in early May 2016 the predicted abundance was 19,600 (± 4,000 model SE) individuals.

Diver distributions predicted for hypothetical scenarios with no wind farms indicated high habitat suitability across the areas of current wind farm locations (Figure 6.7). Predicted densities were normalised to range between 0 – 1, because in case of redistribution (i.e. a change in distribution but not abundance), the model without wind farm would over-predict densities.

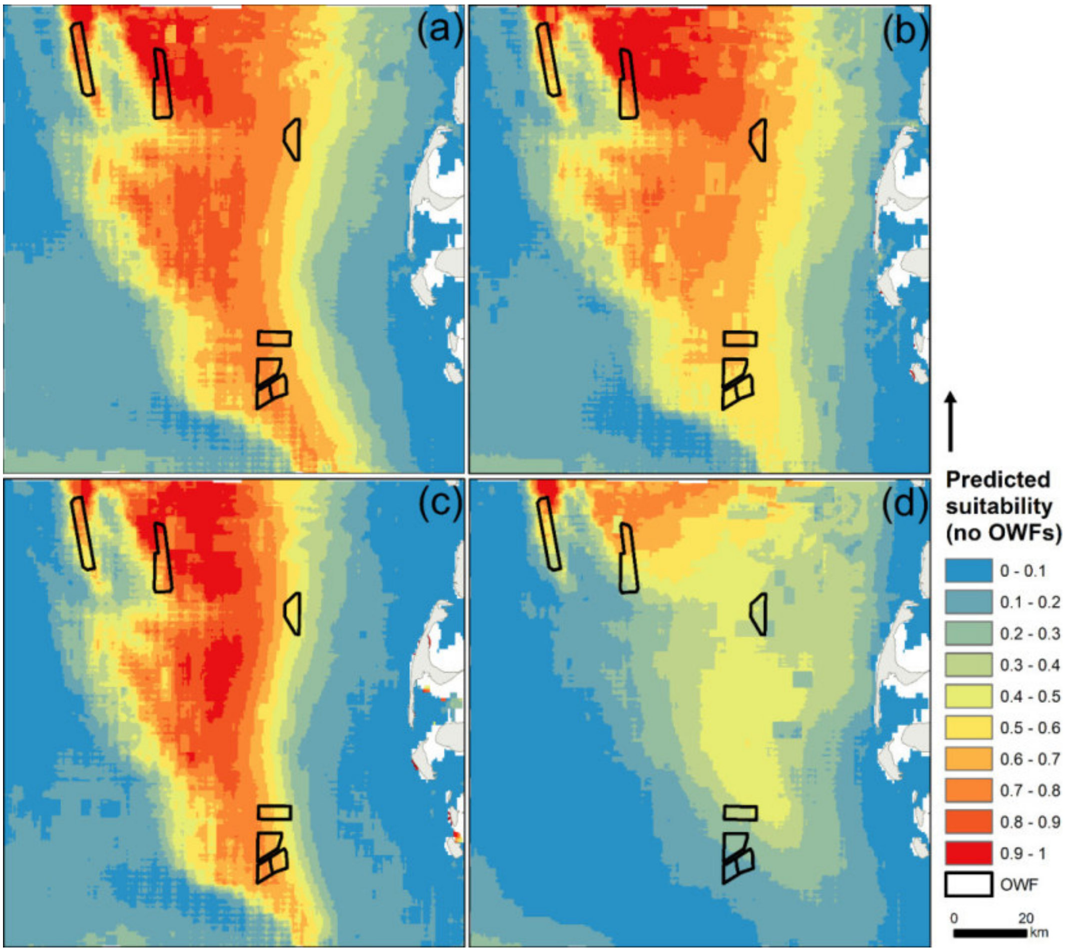


Figure 6.7 Hypothetical predicted mean habitat suitability for red-throated divers based on digital aerial surveys for average conditions on the whole study area for the same days as displayed in Figure 6.6, assuming no wind farms and no shipping in the study area. Important to note that the survey data used for building the model is affected by the wind farms, and therefore the maps should be interpreted carefully and only be considered as indication of suitability in a case without wind farms and shipping, a) 10 April 2016, b) 1 May 2016, c) 25 March 2017 and d) 11 May 2017.

6.4 Discussion

Red-throated divers were found being strongly displaced from offshore wind farms according to the models and the results were highly consistent when comparing models based on the two independent data sets. The effect decreased with distance from the wind farms but was still significant in the distance category 10 – 15 km away from the wind farms (Table 6.1 and Table 6.3). When interpreting the coefficients after combining both model parts based on survey data, the red-throated diver density within the wind farm and 5 km around was more than 90% lower than the reference level (> 20 km away, Table 6.1) keeping all other parameters fixed (Table 6.3). The differences in suitability based on the telemetry data was somewhat weaker, which most likely is due to the overall more coastal distribution of the tagged birds (Table 6.1). Our results were highly similar to those found by Mendel et al. (2019a) based on a more coarse scale analysis, where aggregated data from a large set of pre- and post-construction surveys were interpolated and compared. The displacement distance was similar to what we found. Results from other studies have also found clear displacement effects from the wind farm footprints, however the displacement distance outside the wind farms has often been reported to be only a few kilometres (WELCKER & NEHLS 2016). The reason for this might be that the survey extent of many post-construction studies is small and displacement at larger distances is therefore potentially not detected (or impossible to detect due to the extent of the survey area). Another reason could be that during ship-based surveys divers flush from the approaching ship at very long distance complicating the estimation of the position of divers in relation to the wind farm (BELLEBAUM et al. 2006). However, PETERSEN et al. (2014) showed, based on aerial visual surveys, a similar displacement distance as the present study reaching up to about 14 km at the Horns Rev wind farms north of the present study area in a similar environment (Figure 6.1). We only included post-construction data with the same survey extent in this analysis to avoid biases caused by varying survey extents and survey methods. Often pre-construction data have the shortcoming that they only cover individual projects and are not synchronised, which can result in spatial biases. They are also often too small-scaled (in terms of spatial extent) to describe the full gradient of the disturbance response of divers. The large and consistent survey extent used in this study allowed for a more reliable estimation of environmental relationships, based on broader environmental gradients which enabled a better prediction of suitable habitats. Furthermore, pre-construction data is often not available. The modelling approach demonstrated in this study is a good example of a method that does not require pre-construction data to analyse displacement.

The predicted displacement distance is most likely site- or region-specific due to specific environmental and geographic characteristics of the wind farm location (LYONS et al. 2015). A direct comparison of displacement ranges between different regions can therefore result in different interpretations if environmental, geographic and site-specific variability is not taken into account. A long displacement distance should not by default be assumed to severely impact the birds disturbed (GILL et al. 2001). For example, in an area where suitable habitat is limited outside the wind farm footprint and only available in the vicinity of the wind farm the divers could be forced to use the available habitat close by (in line with “prediction 1.B” by MAY (2015): “the magnitude of displacement depends on the availability of alternative suitable habitat”), yet suffering from decreased food intake or increased competition with conspecifics, despite the shorter displacement range.

The mean total abundance of red-throated divers predicted by this study based on three digital aerial surveys from March, April and early May was 18,800 birds (leaving out the survey in mid-May when many red-throated divers most likely already had left the area). The numbers are, however, not directly comparable to previous surveys as the survey methods, number of surveys and surveyed area(s) are different. Based on this study we can therefore conclude that divers respond strongly to the presence of wind farms, however we do not know what this displacement means in terms of effect on the population size. Continuous monitoring of the population size is therefore important.

Two different, but complementary, data sets confirmed the strong displacement, which can be considered as a sign of robustness of the phenomenon. This is further strengthened by the highly similar findings by MENDEL et al. (2019a) based on a different analytical approach. The data types, telemetry and digital aerial surveys, are complementary in the sense that different aspects of the observed distribution patterns are emphasised by each method (Table 6.4). The survey data describe the distribution pattern based on many individuals within the surveyed area and thereby describe the preference of most of the birds (general patterns). However, the patterns are based on data collected during only four days in good weather conditions. The telemetry data on the other hand describe the preference of 33 individuals over a long time period (several months and for some individuals even for two different years), covering a broad range of environmental conditions and the full diurnal cycle. Due to the rather limited sample size, individual variation may be more influential in the telemetry data set. Some individuals prefer more coastal waters with lower salinity while others prefer offshore areas with higher salinity potentially reflecting individual foraging site fidelity (Wakefield et al. 2015). There might also be a seasonal effect that we have not accounted for in our models.

Table 6.4 Characteristics of digital aerial video survey data vs. satellite telemetry data, highlighting differences and thereby complementarity.

	Digital aerial video survey	**Telemetry**
Characteristics	Count of all birds along a transect	Few individuals
	Restricted to the surveyed area (small scaled)	Area chosen by the tagged birds (large scaled). In this study the same study area is used.
	Density distribution (abundance)	Habitat preference (suitability)
	Snapshot	Long time period
	Common patterns (by the majority of birds)	Individual patterns
	Narrow range of environmental conditions	Complete range of environmental conditions
	Static pattern (snapshot)	Pattern as a result of movement
	Non-invasive	Invasive

In the absence of pre-construction data, it is important to assess whether the wind farms are actually in suitable habitat for divers, which we have tackled by accounting for the dynamic environment. During the non-breeding period bird distribution is mostly driven by food resources (in terms of nutritional content and aggregation), but also by predation/disturbance and inter- and intraspecific competition (Chudzińska et al. 2015). Red-throated divers are generalists and forage on available fish of suitable size. Clupeids belong to their favourite prey providing a high energy food source (Guse et al. 2009; Kleinschmidt et al. 2019). Herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) are common in the study area in spring (ICES-FishMap, www.ices.dk/marineworld/ices-fishmap.asp) and these fish species have been shown to concentrate in frontal zones (Maravelias 1997). The frontal zone has also previously been shown to be important habitat for red-throated divers (Skov & Prins 2001). Demersal fish species are also common in this area and are also reflected in the red-throated diver diet (Kleinschmidt et al. 2019). The frontal zone in the German Bight is most pronounced at depths around 20 – 30 m, which allows divers to catch demersal prey. This frontal zone therefore offers a wide range of potential prey species for divers combined with enhanced food availability. As we hypothesised that diver distribution during the non-breeding season is mostly shaped by prey availability and aggregation, as well as site fidelity, we included predictors describing the frontal zone in the models and these predictors were also influential (significant). Salinity and an index of chlorophyll gradient were included as predictors of the frontal zone and water depth was included as a descriptor of suitable diving depths. Water depth (treated as static in our analyses, i.e. ignoring tidal fluctuations) can also potentially be considered as an indirect predictor of site fidelity (i.e. familiarity to a specific geographic location). Further, as also shown by SCHWEMMER et al. (2011) shipping intensity was influential in the model based on digital survey data (Table 6.3 and Figure 6.5). Mapped model predictions, when excluding the effect of wind farms and shipping, indicated that many of the wind farm areas would have been highly suitable habitats without these pressures (Figure 6.7). These areas have also been shown to be important diver habitats prior to wind farm construction (GARTHE et al. 2015; MENDEL et al. 2019a).

According to the evaluation statistics the predictive ability of the models was moderate with an AUC between 0.7 and 0.8 (FRANKLIN 2009) and a Spearman's correlation of 0.38. These results should be considered as acceptable since there are lots of unoccupied suitable habitat (HEINÄNEN et al. 2017). The mapped patterns also indicate that the model based on survey data was good at replicating the observed patterns based on a visual inspection (Figure 6.6) indicating that the model is accounting for the dynamic environment (see Appendix B, Figure B.1–Figure B.3).

The mechanism behind the diver displacement is not fully clear. A potential and likely reason could be a behavioural response as discussed by MAY (2015) explained by the hypothesis that a wind farm (or other anthropogenic disturbance stimuli) is being perceived by birds in the same way as predation risk (FRID & DILL 2002). If this is the case we could assume that birds are displaced farther away when visibility is good as indicated by our results (Table 6.2). Similarly, the finding that divers show greater distances to the wind farms at night, when the turbines are illuminated with white navigation and red aviation lights point at variable visual stimuli, however, it is not clear whether diver show a stronger response at night because the stimulus of illuminated turbines is stronger or whether diver – which presumably are foraging during daylight – can afford a larger displacement then. We speculate that the response to a stimulus is balanced against its costs so that, for example, displacement would be more pronounced if it has a limited effect on access to food. Another reason could be that habitat quality is reduced within wind farms if prey is also displaced. A decrease in fish abundance has been reported during the wind farm construction phase but not to our knowledge during the operational phase. On the opposite, an increase in many fish species has been observed during the operational phase due to a "reef effect" (BERGSTRÖM et al. 2014; KRÄGEFSKY 2014). A decrease in fish abundance seems therefore less likely to be the reason. The relocation distance (displacement range) can be considered as very long, however lights from the wind farms at night can be seen far away (personal observations). The wind farms might therefore be more visible to the divers during night. During the captures in the middle of the study area, the Butendiek wind farm in the north could be seen at the same time as the Helgoland Cluster wind farms in the south from the small capture boat, the distance to each of the wind farm being about 20 km (Figure 6.1). This might be the reason why the distance between divers and wind farms is lower during the day (Table 6.2). The response to shipping (Figure 6.5) can also be interpreted as a behavioural response in the same way as the response to wind farms.

Beside the strong displacement from offshore wind farms and shipping shown in this study the red-throated diver is also most likely displaced by any other anthropogenic pressures and can therefore be regarded as a particularly sensitive species in accordance with classification by other studies (DIERSCHKE et al. 2016). Diver abundance and distribution should therefore be carefully considered when planning wind farms and other anthropogenic activities in suitable diver habitat, in order to avoid potential cumulative impacts. Cumulative diver displacement can potentially be reduced if fewer larger turbines are built in few locations (i.e. in clusters), preferably in areas of low conservation value, instead of distributing smaller wind farms over several locations, i.e. by that reducing the total exploited area. Nocturnal displacement can likely be mitigated by reducing the lights of a wind farm (aviation lights are already replaced by light-on-demand systems at onshore sites) and disturbance from service vessels might be reduced by coordinating their routes and activity times.

In this study, population impacts were not assessed, only the displacement as a result of a behavioural response. To be able to assess potential impacts further investigations regarding density-dependency and habitat carrying capacity are needed. We need to find out what the carrying capacity is for a suitable habitat and what the consequences for individuals are in terms of, for example, food intake, winter survival and productivity when a carrying capacity threshold is trespassed due to inflow of displaced birds. We now have robust evidence on displacement effect and distance, the next step is to collect data on diving behaviour and fine scale movements and consequently energy budgets. Such information, together with the results already obtained and reported in this study would allow for parameterisation of a detailed individual based model which would allow to assess potential impacts on individuals and further also at the population level (see e.g. WARWICK-EVANS et al. 2018). Until we have better information on potential population impacts, avoiding or reducing anthropogenic pressures in important red-throated diver habitats through sound spatial planning should be the preferred option.

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6.5 Effect of daytime and meteorological factors on diver avoidance of OWFs

6.5.1 Introduction

It has been identified that divers avoid OWFs at large distances (see chapter 6.3), but mechanisms of why birds do that and what triggers the avoidance remain unclear. We therefore aimed to further analyse meteorological factors and diurnal patterns in order to see whether these parameters have an influence on OWF avoidance distance.

The hypothesis is that divers perceive offshore wind farms as visual stimuli, which they do not like and therefore keep the distance from them. If this is true, avoidance distance should be smaller when meteorological conditions reduce visibility in the environment. Similarly, different avoidance distance can be expected during day and night, although it is not clear if diver vision is better suited at depicting wind turbines during the daytime or whether they see red lights on the turbines at night at longer distances.

6.5.2 Methods

Information about meteorological factors was obtained by relating diver tracking locations with a number of parameters characterising environmental conditions that were assumed potentially affecting visibility (Table 6.5). We used the environmental data automated track annotation system that is available on Movebank portal to extract spatially and temporally matching data from European Centre for Medium-Range Weather Forecasts (ECMWF) (DODGE et al. 2013).

Table 6.5 Meteorological parameters that were considered when assessing red-throated diver displacement from OWFs. Data extracted from the European Centre for Medium-Range Weather Forecasts using Movebank's environmental data automated track annotation system.

Parameter	Description	Reason for inclusion
Charnock Parameter	A value used to characterise the surface roughness length over the ocean surface when winds are strong. Unitless.	Visibility is reduced in rough sea conditions due to high waves
Sunshine Duration	Accumulated time that radiation in the direction of the sun is greater than 120 W/m^2. Unit: s	Longer sunshine duration per day may indicate better visibility conditions
Total Cloud Cover	The proportion of the model grid cell covered by clouds. Unit: (0-1)	Higher cloud cover might be characteristic of poorer visibility
Total Precipitation	Accumulated convective and large-scale precipitation, including rain and snow. Does not include fog, dew or the precipitation that evaporates in the atmosphere before it lands at the surface of the earth. Unit: m	Higher precipitation might correspond to poorer visibility
Water Vapor Concentration	Concentration of water vapor in the entire atmospheric column. Sum of water vapor, liquid water, cloud ice, rain and snow. Unit: kg/m^2	Higher concentration of water vapour in the air might correspond to poorer visibility
Total Atmospheric Water	Total water in the entire atmospheric column (water vapor + cloud water + cloud ice). Unit: kg/m^2	Total atmospheric water might correspond to poorer visibility
Mean Sea Level Pressure	Atmospheric pressure at mean sea level. Unit: Pa	Higher pressure may correspond to better visibility conditions
Wind U-Component	Velocity of the east-west component of wind at 10 m above the surface of the	Visibility is reduced in windy conditions due to higher waves

Parameter	Description	Reason for inclusion
	earth. Unit: m/s	
Wind V-Component	Velocity of the north-south component of wind at 10 m above the surface of the earth. Unit: m/s	Visibility is reduced in windy conditions due to higher waves
Wind Speed	Calculated using: sqrt(wind-V^2+wind-U^2). Unit: m/s	Visibility is reduced in windy conditions due to higher waves
Air Temperature	Air temperature 2 m above the ground or water surface. Unit: K	Air temperature in relation to the dew point determines if airborne water vapor condenses or not (thus formation of fog). Higher temperatures more likely lie above the dew point, thus foggy conditions with low visibility are less likely

For day and night assessment, the angle of the Sun in relation to the horizon was calculated using custom-made R function that estimates Sun's position based on geographic location (longitude and latitude) and time of the position. Negative values of the angle indicate that the Sun is below the horizon and positive values that it is above the horizon. As a threshold between day and night we used the angle value of -6 (the Sun is six degrees below the horizon) that refers to the end of civil twilight in the evening and beginning of civil twilight in the morning (see https://en.wikipedia.org/wiki/Twilight).

The assessment was done considering all valid telemetry positions collected in the study area, as defined in chapter 6.2.1. First, generalised additive models (GAMs) were fitted aiming to assess possible influence of each of the considered variables on bird proximity to OWFs. Individual distance to OWF perimeter was used as response variable and meteorological or daytime parameters were used as predictor variables applying them one at a time. Diver distance to OWF showed normal distribution, thus Gaussian family with identity link was used when fitting the models. Initial exploratory analyses revealed that all except one of the considered meteorological variables were significant and shapes of the response curves made good sense when relating them to diver proximity to offshore wind farms and explaining the occurring mechanism (Appendix B.2). However, closer inspection of the model results revealed that autocorrelation was present in the model residuals for up to 10 lags. Thus, there was an uncertainty whether GAM results show actual interactions between the response and predictor variables or whether there was a result of distortion due to autocorrelation in the data (FIEBERG et al. 2010).

In order to deal with autocorrelation and avoid overrepresentation of individuals that collected more positions or environmental conditions on certain days when more data points were logged, we restricted the analysed dataset to a single location per bird per day that were randomly selected from the full dataset. The selected dataset that was used in the analyses consisted of 690 diver telemetry positions representing 33 individuals. Further, the modelling approach was shifted to generalised additive mixed models (GAMMs), where individual bird ID was used as a random factor in order to account for individual effects. GAMs and GAMMs were fitted using *mgcv* package (WOOD 2011) in software R (R CORE TEAM 2018).

6.5.3 Results

Different individuals of red-throated divers were present in the study area during the period lasting from October to May over four winter, moulting and staging seasons starting from March 2015 until May 2018, thus being exposed to a wide range of meteorological conditions.

Several of the considered meteorological parameters were not significant in the models explaining diver distance to OWF. Namely, no statistically significant relationship was found with Charnock Parameter, Sunshine Duration, Total Cloud Cover, Water Vapor Concentration, Total Atmospheric Water, Mean Sea Level Pressure, Wind V-Component, Wind U-Component, and Air Temperature.

Although wind components U and V were not statistically significant when considered separately, overall wind speed, which was calculated using directional component values as input, was significant and revealed that diver distance to OWF was linearly decreasing with increasing wind speed (Table 6.6, Figure 6.8).

Table 6.6 Parameter estimates and significance in the GAMM model relating the overall wind speed to red-throated diver distribution in relation to OWFs.

Parameter coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	23,413	872.4	26.84	<0.001
	edf	**Ref. df**	**F**	**p-value**
Wind speed	1	1	8.862	0.003

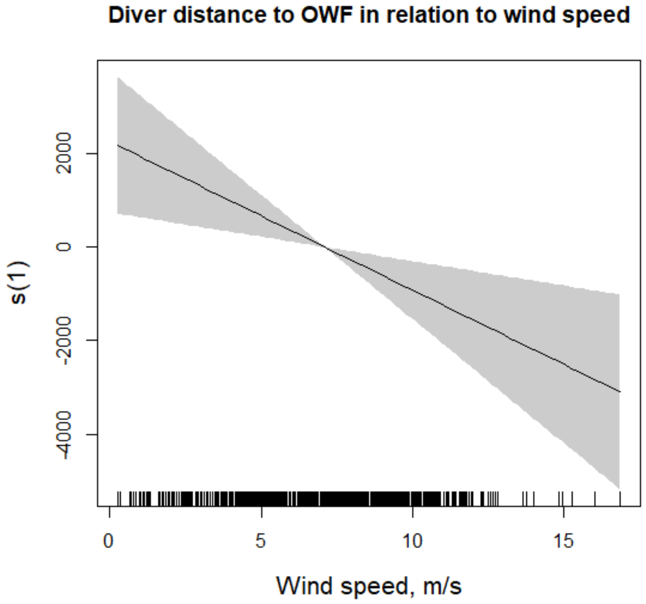

Figure 6.8 GAMM response curve showing that distance between red-throated divers is negatively related to the overall wind speed.

Another meteorological parameter that was statistically significant (at the 5% level) in explaining diver distribution in relation to OWF was total precipitation, suggesting that distance to OWF was decreasing with increasing amount of precipitation (Table 6.7, Figure 6.9).

Table 6.7 Parameter estimates and significance in the GAMM model relating the total precipitation to red-throated diver distribution in relation to OWFs.

Parameter coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	23,407	870	26.9	<0.001
	edf	**Ref. df**	**F**	**p-value**
Total precipitation	1	1	4.093	0.044

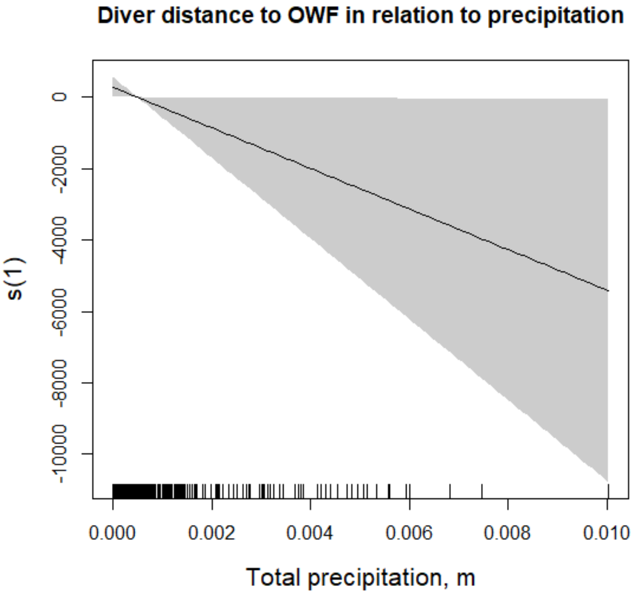

Figure 6.9 GAMM response curve showing that distance between red-throated divers and OWFs is negatively related to the total precipitation.

Other meteorological parameters, which turned out not being statistically significant, often showed expected tendency of diver distance to OWF decreasing as visibility was smaller. E.g. Charnock parameter characterising sea surface roughness was marginally non-significant and showed clear tendency of distance to OWF to be smaller at higher Charnock parameter values (Table 6.8, Figure 6.10).

Table 6.8 *Parameter estimates and significance in the GAMM model relating Charnock parameter to red-throated diver distribution in relation to OWFs.*

Parameter coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	23,427	876.9	26.71	<0.001
	edf	**Ref. df**	**F**	**p-value**
Charnock parameter	1	1	2.976	0.085

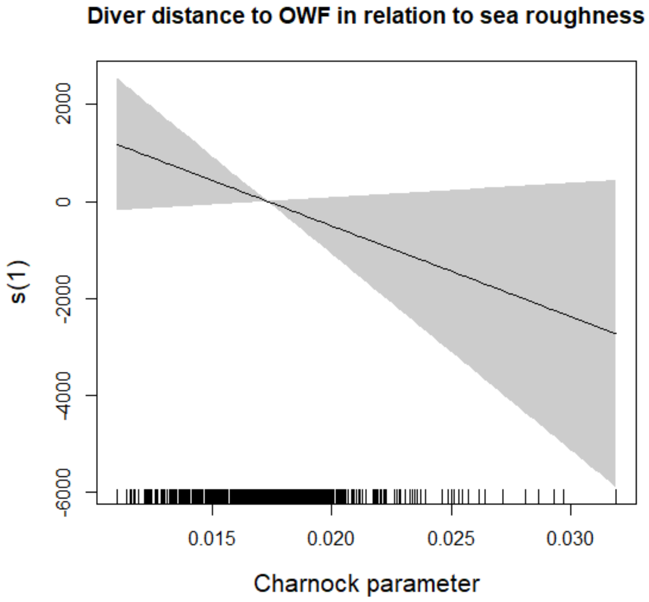

Figure 6.10 *GAMM response curve indicating that distance between red-throated divers and OWF has a tendency to decline at higher Charnock parameter values characterising sea surface roughness. This tendency, however, was not statistically significant.*

Further, assessment of day and night influence on diver proximity to OWF revealed that birds were generally further away from OWF at night and distance was reducing with Sun angle being higher above the horizon (Table 6.9, Figure 6.11). Essentially the same information was obtained when day and night were treated as categorical variable, the breaking point being Sun's angle value of -6 degrees (6 degrees below the horizon, i.e. civil twilight). The model with categorical variable also showed that red-throated divers keep significantly greater distance to OWF at night (Table 6.10, Figure 6.12).

Table 6.9 *Parameter estimates and significance in the GAMM model relating Sun's angle below/above the horizon to red-throated diver distribution in relation to OWF.*

Parameter coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	23483.6	871.2	26.96	<0.001
	edf	**Ref. df**	**F**	**p-value**
Sun's angle	1	1	6.729	0.009

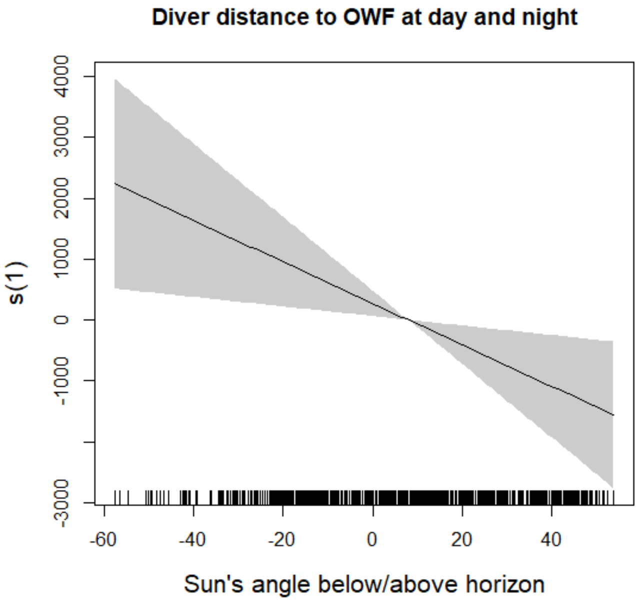

Figure 6.11 GAMM response curve indicating that distance between red-throated divers and OWF declines with Sun's angle increasing above the horizon.

Table 6.10 Parameter estimates and significance in the GAMM model relating proximity of red-throated diver to OWF in relation to day and night.

Parameter coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	23003.7	896.3	25.665	<0.001
Factor "Night"	1378.1	694.2	1.985	0.048

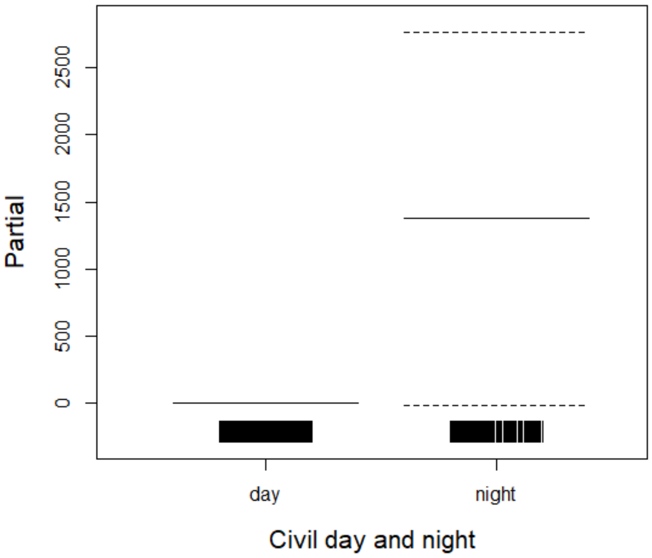

Figure 6.12 Categorical variable defining day and night in the GAMM model reveals that red-throated divers are distributed at significantly larger distances from OWF at night.

6.5.4 Discussion

Some of the considered environmental parameters, namely total precipitation and wind speed, revealed that distances between red-throated divers and OWF are smaller when weather conditions impair visibility. This supports the hypothesis that divers perceive OWF as visual stimuli and occur closer to them when visibility is limited due to meteorological conditions.

Also, considering the day and night effect, it was clear that divers keep longer distances to OWF at night. Exact mechanism explaining that is not known, but we speculate that red and bright warning lights that illuminate the wind turbines at night are visible at longer distances compared to turbine visibility during the daytime, when at some (rather long) distance they start to blend with the background of sea and sky. At least such is human perception of wind turbine visibility at day and night during clear weather conditions (own observations).

6.6 Effect of wind farms on diver relocation distances

6.6.1 Introduction

Red-throated divers were shown to keep long distances to OWFs (see results presented in this chapter above). Within this section the question was addressed whether the disturbance effect of OWFs also results in behavioural changes in terms of an effect on diver relocation distances.

6.6.2 Methods

Analysis on the effect of OWFs on diver relocation distances was done on a subset of the data, comprising 20 individuals that used the eastern German Bight as a staging site during winter and spring seasons between April 2015 and May 2017. For two individuals, two separate years of data could be used.

Package *adehabitat* in R was used to calculate distances and time between relocations. The dataset was reduced to a maximum of one data point per day, selecting the location with the best location quality, and no less than 3 days between subsequent data points of an individual. Only relocations of less than 30 km distance were included, as those were assumed to represent local movements. Longer distances might be related to movements between wintering areas or the onset of migration.

Distances of bird positions to the closest operational wind farm in the area during the study period were calculated. To exclude movements that were potentially influenced by proximity to the coast, a buffer of 5 km was applied around coastal areas. Furthermore, analysis was limited to 30 km around each operational wind farm for the starting position of a movement, as any relocation patterns further away were assumed to be unaffected by OWFs. After applying the described data filtering 377 relocations of 20 individuals were used in the analysis (Figure 6.13).

General additive models (GAM) in R were used to analyse the data. In the model, burst ID (individual ID per year, n = 22) was included as random effect, and water depth as covariate. Model selection was done using backwards elimination of non-significant terms.

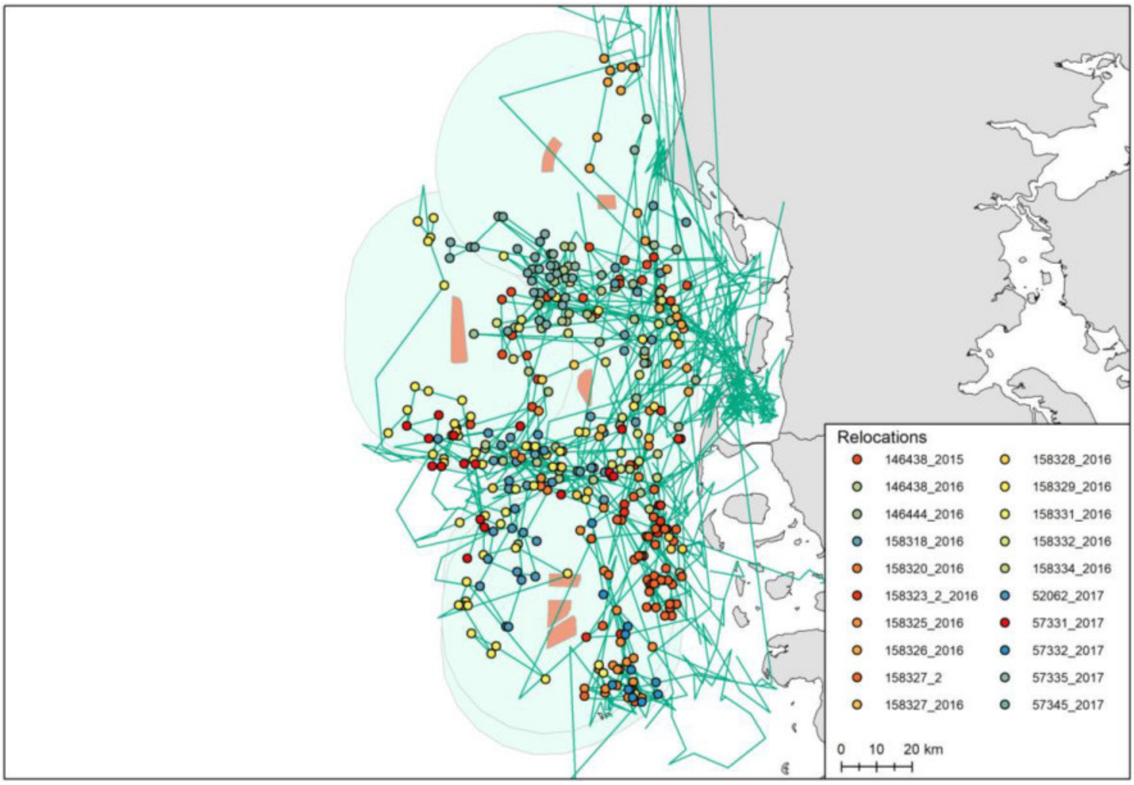

Figure 6.13 *Study area and red-throated diver locations (n = 377) used for the analyses of relocation distances in relation to the distance to OWFs. All relocations of the raw dataset are shown while dots depict only filtered Argos locations.*

6.6.3 Results

The final model contained a smoother of distance to OWF as dependent and burst ID as random effect. Water depth was not significant and was therefore removed from the model. Deviance explained by the model was 18.2%. Analysis showed a significant effect of distance to the closest wind farm: relocation distances were larger when birds were in closer proximity to a wind farm (Table 6.11, Figure 6.14). Between 10 and 15 km, this effect started to level off slightly and reached the lowest values around 25 km. Individual ID also explained a significant part of the variation (Table 6.11).

Table 6.11 Parameter estimates and significance in the GAM model relating distance to OWF and individual ID (burst ID) to red-throated diver relocation distances (n = 377).

Parameter	edf	Ref. df	F	p-value
Distance to OWF	3.518	4.384	8.344	<0.001
Burst ID	7.936	19.000	1.397	<0.001

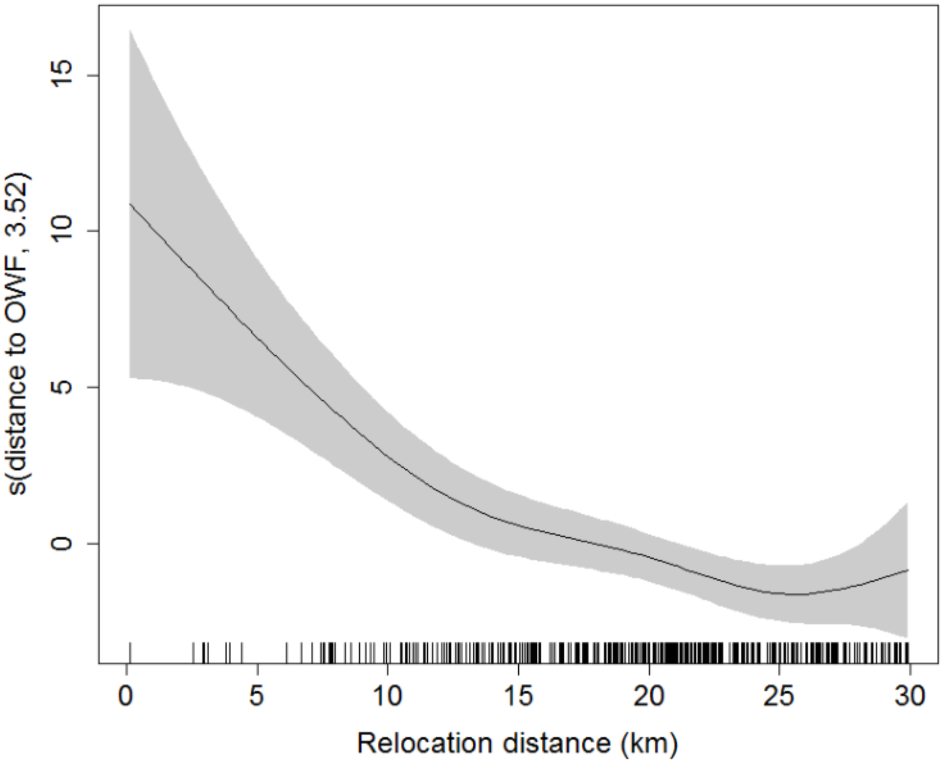

Figure 6.14 GAM response curve showing that relocation distances of divers are negatively related to the distance to OWFs.

6.6.4 Discussion

We found that relocation distances significantly decreased with increasing distance from OWFs. Red-throated divers thus moved longer distances in the proximity of OWFs as compared to further away. This is likely related to disturbance by the wind farms or associated shipping traffic. Raw tracks of individuals show that birds rarely cross wind farms but instead move around them (Figure 6.13). One drawback of our dataset was the rather coarse resolution of the data, hindering more detailed analyses. However, despite the low resolution, we could show that OWFs not only displace birds from the surroundings but also appear to be related to behavioural responses. Greater movements due to disturbance are energetically costly and could thus affect the energy budgets and subsequently body condition of the disturbed individuals.

7 A NOVEL APPROACH FOR ASSESSING EFFECTS OF SHIP TRAFFIC ON DISTRIBUTIONS AND MOVEMENTS OF SEABIRDS

Claudia Burger[1], Alexander Schubert[1], Stefan Heinänen[2,6], Monika Dorsch[1], Birgit Kleinschmidt[1,3], Ramūnas Žydelis[2,4], Julius Morkūnas[5], Petra Quillfeldt[3], Georg Nehls[1]

[1]BioConsult SH, [2]DHI, [3]Justus Liebig University Giessen, [4]Ornitela, [5]Marine Research Institute, Klaipėda University, [6]Novia University of Applied Sciences

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Abstract

Marine habitats are nowadays strongly affected by human activities, while for many species the consequences of these impacts are still unclear. The red-throated diver (Gavia stellata) has been reported to be sensitive to ship traffic and other anthropogenic pressures and is consequently of high conservation concern. We studied red-throated divers in the German Bight (North Sea) using satellite telemetry and digital aerial surveys with the aim of assessing effects of ship traffic on the distribution and movements of this species during the non-breeding season. Data from the automatic identification system of ships (AIS) were intersected with bird data and allowed detailed spatial and temporal analyses. During the study period, ship traffic was present throughout the main distribution area of divers. Depending on impact radius, only small areas existed in which ship traffic was present on less than 20 % of the days. Ship traffic was dominated by fishing vessels and cargo ships, but also wind farm-related ships were frequently recorded. Red-throated divers were more abundant in areas with no or little concurrent ship traffic. Analysis of aerial survey data revealed strong effects of ship speed on divers: in areas with vessels sailing at high speed only a slow resettlement of the area was observed after the disturbance, while in areas with vessels sailing at medium speed the resettlement was more rapid during the observed time period of seven hours. Data from satellite-tracking of divers suggest that large relocation distances of individuals are related to disturbance by ships which often trigger birds to take flight. Effective measures to reduce disturbance could include channeled traffic in sensitive areas, as well as speed limits for ships traveling within the protected marine area.

7.1 Introduction

Marine environments are strongly impacted by various types of anthropogenic activities. Ship traffic is one major anthropogenic activity in coastal and offshore waters of Europe. Impacts of ship traffic on marine life are related to pollution, noise emissions, the risk of collision as well as visual attraction or disturbance (OECD & ITF 2008). For marine mammals, impacts mainly arise from noise emissions or collision risk (CONN & SILBER 2013; MARTIN et al. 2016; PIROTTA et al. 2018b), while for seabirds the visual cue of an approaching ship is the major factor leading to a behavioral or physiological response (BELLEBAUM et al. 2006; KAISER et al. 2006; VELANDO & MUNILLA

2011). The observed responses suggest that ships are perceived similar to a predation risk by sensitive seabird species and thus elicit an evolved avoidance behavior (e.g. flush or dive; Frid & Dill 2002). Consequently, this response can lead to an increase in stress levels and a loss of habitat (VELANDO & MUNILLA 2011; PIROTTA et al. 2018a). One of the main questions in this context is whether the amount of disturbance can be compensated or if it will result in population consequences for these species (PIROTTA et al. 2018a). The assessment of such consequences requires detailed knowledge on the responses towards stressors such as ship traffic. This knowledge is also crucial for the development of efficient mitigation measures.

Our model species, the red-throated diver (*Gavia stellata*) utilizes the North Sea and the Baltic Sea as resting and foraging habitat during the non-breeding season and is thus confronted with their concurrent use for shipping activities. Red-throated divers are among the most sensitive species to anthropogenic disturbances like shipping or offshore wind farms (OWF). Together with the black-throated diver (*Gavia arctica*), the species is ranked highest in sensitivity indices for seabirds (GARTHE & HÜPPOP 2004; FURNESS et al. 2013; BRADBURY et al. 2014). Divers have become a main focus in seabird investigations for OWFs, as strong avoidance of OWFs has been observed (PETERSEN et al. 2014; DIERSCHKE et al. 2016; WELCKER & NEHLS 2016; NEHLS et al. 2018; MENDEL et al. 2019a). In addition to wind farm effects, ship traffic was a strong predictor of diver distribution in a habitat model analyzing displacement effects (HEINÄNEN et al. unpublished data). Also MENDEL et al. (2019a) recently showed that shipping accounts for part of the decline in bird densities in the vicinity of OWFs.

Ship traffic in the North Sea is high (VESPE et al. 2016; ALESSANDRINI et al. 2017) and expected to increase (OSPAR 2010), e.g. due to an increase in trade and the expansion of OWFs. An earlier analysis of ship traffic in the German Bight indicated that the area is strongly used by both fisheries and freight shipping (MENDEL 2012). Moreover, the area in the German EEZ containing commercial shipping lanes and shipping routes (BSH 2018) covers about one third of the main distribution area of divers (DIERSCHKE et al. 2012). Considering OWFs, the potentially disturbed area increases even further (MENDEL & GARTHE 2010; MENDEL et al. 2019a). However, in the past calculations were based on relatively rough estimates of shipping intensity and assumed seabird responses. For a quantitative understanding of the consequences of this disturbance, detailed data on ship traffic is needed.

Most studies investigating the effects of ship traffic on seabirds in offshore waters have focused on behavioral responses of scavenging seabird species towards fishing vessels (VOTIER et al. 2010; TEW KAI et al. 2013; BODEY et al. 2014; SOMMERFELD et al. 2016; LE BOT et al. 2018). With respect to disturbance by ships, only few studies exist, mainly due to the difficulty of studying these interactions. Using research vessels as observation platforms, high response distances from approaching vessels were recorded for common scoters (*Melanitta nigra)* and divers (BELLEBAUM et al. 2006; SCHWEMMER et al. 2011; FLIESSBACH et al. 2019). A recent study by Mendel et al. (2019a) found the strongest impact of ships on red-throated divers for a radius of 5 km and within 5 min of the passage of a ship. However, long-term effects over several hours could not be investigated. To estimate the duration of the displacement effect which could indicate the resilience of species to the disturbance, SCHWEMMER et al. (2011) used an experimental set-up. In that study, no divers were observed after 3 h since the disturbance, suggesting a strong fleeing response to the ship and slow resettlement. Shorter resettlement durations were found for some other species like long-tailed duck (*Clangula hyemalis*) and red-breasted merganser *Mergus serrator* (PETTERSSON 2005). The different responses are likely related to the ecology of the species: for example, while seaducks depend on local shellfish-beds for foraging, species like divers and grebes mainly forage on fish which represent a mobile food source (MENDEL et al. 2008). Also different shipping activities, such as variation in ship speed, have been shown to affect the behavior of seabirds (GARTHE & HÜPPOP 1999). However, for red-throated divers no such data has been published so far.

Here, we used a novel approach to investigate red-throated diver distribution and movements in relation to ship traffic. Data on bird distribution were obtained from digital aerial surveys which provide a snapshot of bird distribution in an area, while disturbance by the observation platform is avoided due to the high flight altitude (WEIß et al. 2016; ŽYDELIS et al. 2019). Data on individual movements of birds in the area were available from satellite-tracking of red-throated divers (www.divertracking.com). Simultaneous information on ship traffic spanning a time period of more than two months in total and covering a large part of the south-eastern German Bight was obtained by utilizing data from the automatic identification system of ships (AIS). AIS is a system that transmits information on vessel identity, position and speed (among other attributes) to receivers on other ships or land-based receiving stations (NATALE et al. 2015; SHELMERDINE 2015; ROBARDS et al. 2016). It is now a mandatory system under provisions of the International Maritime Organization (INTERNATIONAL MARITIME ORGANIZATION 2002). Not only large commercial vessels carry AIS transponders but also many small seagoing vessels like fishing vessels and pleasure crafts are nowadays equipped with this system. Since 2014, all EU fishing vessels > 15 m in length have to be equipped with an AIS Class A transmitter (EUROPEAN COMMISSION 2014).

Using this unique and detailed dataset, our aim was to quantify the responses of red-throated divers to ship traffic. We used data from digital aerial surveys to investigate (1) the effects of the presence of ships on the small-scale distribution of red-throated divers, and (2) the effects of vessel size and speed on diver abundance. This dataset also allowed us to estimate the resettlement time after disturbance by a ship. Data from satellite-tracking were used to investigate the movements of birds, and whether ship encounters are related to longer relocation distances. This is, to our knowledge, the first published analysis that explores detailed effects of different types and activities of ship traffic on the distribution and behavior of a highly sensitive seabird, the red-throated diver. This study can be a basis for informed conservation actions through the development of effective mitigation measures.

7.2 Methods

7.2.1 Study species and area

The red-throated diver is a circumpolar species, breeding on lakes from the boreal zone to the high Arctic. During the non-breeding season this species is found widely in coastal areas in the Northern Hemisphere. Birds are usually scattered individually or in small groups across suitable habitat. They forage on a wide range of fish species, most commonly herring and sprat (GUSE et al. 2009; KLEINSCHMIDT et al. 2019) which they catch while diving. Red-throated diver is listed in Annex I of the EU Birds Directive, in Annex II of the Bern Convention, in the African Eurasian Waterbird

Agreement and is further listed by the HELCOM convention as a critically endangered species in the Baltic Sea. The Northwest-European winter population was estimated at 216,000 to 429,000 birds (Wetlands International 2019).

The study was carried out in the German Bight of the North Sea (Figure 7.1), in the area west of the islands of Sylt and Amrum, which harbors the highest densities of red-throated divers in the German Bight during spring (Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit 2009; Garthe et al. 2015; Mendel et al. 2019a). Birds from a wide range of breeding origins, from Greenland to Siberia, stage in this area during spring (Dorsch et al. 2016; www.divertracking.com) which emphasizes the importance as pre-breeding staging site for this species. The special protection area "Eastern German Bight" with a size of 3,135 km^2 has been established here in 2005 (Figure 7.1) and a diver main distribution area has been identified (Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit 2009). Ship traffic in this area is widespread and mainly consists of fishing vessels which occur locally in high numbers (mainly shrimp fishery, Sommerfeld et al. 2016), cargo ships which usually cross the area on more or less straight path, and offshore service vessels.

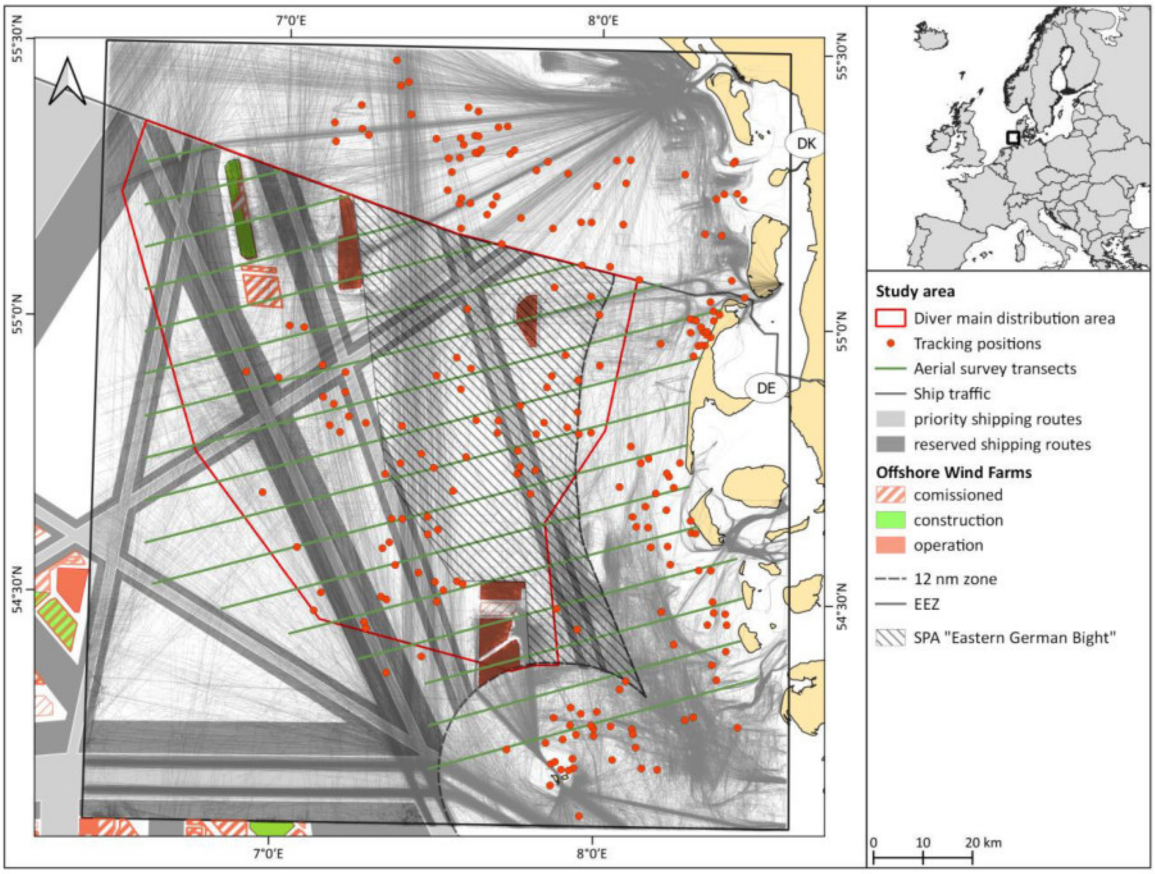

Figure 7.1 *Overview of study area: Diver main distribution area (Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit 2009), aerial survey transects, bird tracking positions and ship traffic, during the study period in 2016 and 2017 (80 days of data). Shipping routes were adapted from BSH (2018).*

7.2.1.1. Digital aerial surveys

Data on bird distribution were obtained from four digital aerial surveys using the HiDef high definition aerial video technique (WEIß et al. 2016; ŽYDELIS et al. 2019) at a flight height of 549 m. The airplane was equipped with a rig of four digital cameras which covered a strip of 544 m. Surveys were carried out within the study area during the following dates: 10th April 2016, 1st May 2016, 25th March 2017 and 11th May 2017. The dates in March and April fall within the main spring/migration period for this species (GARTHE et al. 2007), the dates in early May can be regarded as late spring staging/migration period with still high bird numbers in the area. A transect design consisting of 17 parallel transect lines was used with a total length of roughly 1,300 km and with a transect spacing of about 8 km (Figure 7.1). During the species identification process, 97% of all divers could be identified to species level. Only 0.1% were identified as black-throated divers and were included in the dataset, together with all unidentified divers which presumably mainly consisted of red-throated divers as well. Bird numbers along transects were calculated per survey, separate for transect segments with a defined length of 1 km and equal survey effort. The number of birds per segment was used for all further analyses.

7.2.1.2. Tracking data

Between 2015 and 2017, 45 red-throated divers were equipped with Argos satellite transmitters (platform transmitter terminals PTTs) as part of the project DIVER (www.divertracking.com). Birds were captured in the German North Sea, about 20 – 30 km west of the island of Amrum. Birds were captured using the night-lighting technique and transmitters were implanted by an experienced wildlife veterinarian (SPIEGEL et al. 2017; www.divertracking.com). We used implantable Argos satellite PTTs manufactured by Telonics, Inc. (40 units) and Sirtrack, Ltd (5 units). Transmitters were programmed using varying duty cycles with 3 or 4 transmission hours and 12 – 24 h intervals between them when birds were expected to be on wintering grounds and longer 60 – 68 h intervals during the breeding season. These varying duty cycles were chosen to answer questions related to the larger framework of the DIVER project and not particularly for this study. Surgeries and all fieldwork (animal capture, sampling and tagging) were conducted under appropriate ethics and approvals; approved by BfN (Federal Agency for Nature Conservation, Germany, 05.08.2014; and Ministry of Environment and Food Denmark, Danish Veterinary and Food Administration, permit no. 2014-15-0201-00239, issued 18.12.2014).

Prior to the analysis, tracking data were filtered using Freitas filter (FREITAS et al. 2008; R CORE TEAM 2018) to reduce noise produced by location fixes with low or unknown accuracy (for details see also chapter 6). The filtered dataset was further inspected visually and several obvious outlier positions were flagged and eliminated from the dataset. Finally, positions recorded during the first two weeks after the release were excluded from any analyses due to possible unnatural behavior during that period. In a second filtering step, we only selected locations with the highest location quality (1, 2 or 3). Estimated location error of these positions ranges between less than 1.5 km for class 1 and less than 250 m for positions of class 3. After filtering, data from 20 birds could be used for the analyses (17 for statistical analyses).

7.2.1.3. Ship data

Terrestrial AIS data (i.e. AIS data from receiver stations based on land or on offshore structures, no satellite AIS data were used) from ships for the study area within the German Bight were obtained through www.marinetraffic.com. The dataset included all ships (with AIS transponders) present within the study area. AIS data were obtained to match the main time period when data on red-throated diver abundance was available. This comprised all data from 1st April to 3rd May in 2016 and from 25th March to 12th May in 2017.

For analysis of digital aerial surveys, AIS data were available within a maximum timestamp from 7 h before an aerial survey up to the time when the video footage was taken. Initial data analysis using shorter time frames showed that resettlement of disturbed areas was still incomplete and thus the maximum available time frame was chosen for further analyses. This enabled us to investigate any long-lasting effects of ship traffic on the spatial distribution of red-throated divers.

Processing of raw AIS data was done in ArcGIS 10.7 (ESRI 2019) to obtain the relevant covariates for analysis. Individual ship signals within the study area were used to calculate tracks by interpolation, applying a custom developed script. For interpolation, successive AIS-signals of each ship were connected to ship tracks and timestamps at points of interest, i.e. intersections of ship tracks with buffers around bird tracking data or transect segements, were calculated depending on track distance and ship speed. AIS signals are sent by ships at varying intervals (from 2 s to several minutes depending on transmitter type and ship activity). Gaps due to missing signals in the AIS dataset occurred frequently and were filled by interpolation. However, more than 99.5 % of all gaps were shorter than 2 h. The raw AIS dataset showed several unrealistic values for ship speed and thus speed was calculated from timestamps and distance between ship positions. It has to be noted that some small ships (e.g. pleasure crafts, small fishing vessels) do not use AIS transponders. Thus, the presence of small ships is likely underestimated. Our study area reached from the coast far offshore into the German Exclusive Economic Zone (EEZ), and it can be assumed that only few small ships without the AIS system are missed for the analysis of ship traffic. Even in coastal waters, hardly any leisure traffic is occurring during this time of year. Spatial coverage of land-based receiver stations in the study area was high (VESPE et al. 2016). Data from the vessel monitoring system (VMS) were not used, as only AIS-data provided sufficient detail for the intended analyses. It is thus likely that a few small ships equipped with only VMS-transmitters were missed.

For visual representation, maps were created depicting tracks of all ship traffic within the available time window (representing about 5 weeks of each spring season sampled: 2016 and 2017) for the study area (Figure 7.1). These tracks were overlaid with the designated and reserved shipping routes which were established by the Federal Maritime and Hydrographic Agency (BSH 2018) and are based on existing shipping routes and on information about areas of increasing usage by ship traffic (MENDEL & GARTHE 2010). These routes are established to ensure the safety of ship traffic and within those areas ship traffic is prioritized before other types of usages (NORTHSEE 2019). There is however no obligation for ship traffic in German waters to utilize these designated and reserved shipping routes and some clear discrepancies between shipping routes and ship traffic have been identified in the North Sea (NORTHSEE 2019).

7.2.2 Data analysis

7.2.2.1. Digital aerial survey data

The digital aerial survey data and AIS data were spatially and temporarily aligned in ArcGIS. The following covariates within a radius of 1.5 km and 3 km (to assess two different scales) were extracted for transect segments of 1 km: number of ships, time since last ship passage, speed of the last ship, length of the last ship, water depth and the interaction between latitude and longitude to account for additional geographical variation. As water depth and the interaction between latitude and longitude were correlated, it was decided to only keep the interaction between latitude and longitude in the initial models, in order to capture geographical variation. The data were analyzed using generalized additive models (GAM) in R (R CORE TEAM 2018) using the *mgcv* package (WOOD 2015) and function *gam()*. For the analyses, all areas within 10 km of OWFs were removed, to separate the effect of ship traffic from wind farm effects, which were shown to negatively affect the abundance of divers (NEHLS et al. 2018; MENDEL et al. 2019a).

Two different models were constructed, and these were applied separately for a radius of 1.5 km and 3 km. The first model (model 1) was constructed to describe changes in abundance of divers (number of birds) in relation to the number of ships present in a 1.5 or 3 km radius. First, an initial model was built with the number of ships present as smooth terms (thin plate spline smoother) and the interaction between latitude and longitude to account for geographical variation. To account for possible non-independence of data, models with different structures regarding survey date were compared: 1. a model with survey date as a factor 2. survey date as a random intercept, using a smoother of date with argument *bs* = *"re"* 3. a grouped spline for each level of survey date, using the *"by"* argument and including date as factor 4. a model without survey date. The concurvity estimates (WOOD 2006) were regarded acceptable (all < 0.5). Plots of the model residuals with function *acf* and *pacf* (stats package; R CORE TEAM 2018) revealed no problems with autocorrelation. A negative binomial family distribution was used for fitting the model. Family distribution was chosen with the help of package *fitdistrplus* in R. QQ-plots and histograms were used to assess normality, and residuals versus fitted values were used to assess homogeneity (ZUUR et al. 2009). The models were compared using Akaike information criterion (AIC) and the best fitting model was selected. A list of models is presented in the supplementary material (Appendix C).

The second model (model 2) was constructed to describe changes in abundance of divers when a ship was present within a 3 km radius depending on the time period before the survey (max. 7 h before) and on certain characteristics of these ships. The initial model contained a smoother (thin plate spline smoother) of number of ships and, as tensor product smoother, interactions between covariates 'ship length' and 'time since last ship'; as well as 'ship speed' and 'time since last ship'. The tensor product smoother was used in order to model the interaction of two covariates that are on different scales (different units). A smoother (thin plate spline smoother) of latitude and longitude of each segment was included as interaction as well to account for geographical variation. To account for possible non-independence of data, models with different structures regarding survey date were compared: 1. a model with survey date as a factor 2. survey date as a random intercept, using a smoother of date with argument *bs* = *"re"* 3. a grouped spline for each level of survey date, using the *"by"* argument, for each covariate and their interactions and including date as factor 4. a model without survey date. Non-independence of data could also occur between survey years, but ‘survey date’ was assumed to best control for non-independence, as e.g. weather conditions might vary between surveys. A negative binomial family distribution was used for fitting the model. A similar model validation procedure as described for model 1 was applied. The concurvity estimates (WOOD 2006) of initial models were regarded acceptable (all < 0.75). Further model selection was done by rerunning the model using method “ML” and removing non-significant terms in a step-wise procedure (WOOD n.d.). Initial and final models are presented in the supplementary material (Appendix C). Results of the final models were visualised for every significant parameter of interest as plots of the fitted GAM (using function *fvisgam* from package *itsadug*; VAN RIJ et al. 2017).

7.2.2.2. Tracking data

For analyses of ship-bird interactions, all filtered bird tracking positions were used to calculate the distance of each position to the closest ship in the area, within a time frame of ± 1 h of the recorded position time. When several positions of the same individual were available less than 1 h apart in time and at the same time within a radius of 1 km, only the first position was used, in order to avoid overrepresentation of concurrent bird tracking positions and autocorrelation between positions in the dataset (AARTS et al. 2008). Bird relocation distances were calculated between subsequent bird positions, but were only used in the analysis when below 30 km and when positions were recorded less than 30 h apart, as movements further away probably did not represent local movements but were rather related to movements between wintering or stop-over sites. Similar to the analysis of aerial survey data, all points within 10 km of OWFs were removed for statistical analysis.

A general additive model using the mgcv package (WOOD 2015) was applied to the data, with bird relocation distance as dependent variable and a thin plate spline smoother of number of ships within a radius of 3 km around a tracking position as covariate (see Supplementary material, Appendix C). To account for geographical variation, the interaction between latitude and longitude was included as smoother as well. Including this interaction also resolved problems with autocorrelation. Individual ID was included as random intercept to account for nonindependence of the data, using a smoother of ID with argument *bs = ”re”.* Although concurvity estimate of individual ID was high (> 0.8), it was retained in the model as no problems in the estimation of the smooths were found. A normal family distribution was used for fitting the model. Similar model diagnostics as described in section 7.2.2.1. were applied (ZUUR et al. 2009). No further model selection was performed. The temporal resolution of the bird tracking data was coarse and variable (see Supplementary Material, Appendix C) and thus no re-discretising of the trajectory in time was applied, as this is only advised for filling in a small number of relocations (CALENGE 2016). Nevertheless, the current analysis gives a good indication of whether birds change their behavior in the presence of ships (e.g. travel longer distances), although true relocation distances are probably underestimated.

7.3 Results

7.3.1 Ship traffic within the study area

Ship traffic in the south-eastern German Bight showed clear patterns for the two spring periods in 2016 and 2017: The eastern, coastal parts were dominated by fishing vessels, showing erratic movement patterns due to fishing activities (Figure 7.1). Further offshore, most vessels were crossing the area on a relatively straight path (mainly cargo ships). Several designated shipping routes have been defined by German authorities within the study area, however, these only partly match with actual ship traffic crossing the area. Little channeling of traffic traversing the area can be seen, as opposed to ship traffic within the traffic separation scheme in the southern part of the study area (“German Bight Western Approach”; BSH 2018). High ship traffic occurs on the routes to OWFs and within (Figure 7.1). Shipping intensity within the main diver distribution area showed rather small areas of low intensity (ships crossing on less than 20% of days), even when assuming only a buffer of 1 km around the ship track (Figure 7.2). Per day (n = 80), between 14.6% and 66.0% (mean = 47.4%) of the area was potentially disturbed by ships using the 1 km buffer, and between 35.2 % and 92.9% (mean = 77.3%) of the area was disturbed using the 3 km buffer.

When looking at ship types in relation to speed during four days with digital surveys (excluding a 10 km buffer around OWFs), it was found that ships sailing at speeds > 40 km/h mainly comprise crew vessels and other ships termed ‘high speed crafts’ (Figure 7.3) which often resemble crew vessels (usually catamaran-type), but exact task could not be determined from AIS-data. Slow-sailing ships (< 20 km/h) were dominated by fishing vessels. Fishing vessels were also the most abundant ship type in the dataset. Ships sailing at medium speed (between 20 and 40 km/h) were dominated by cargo ships (Figure 7.3).

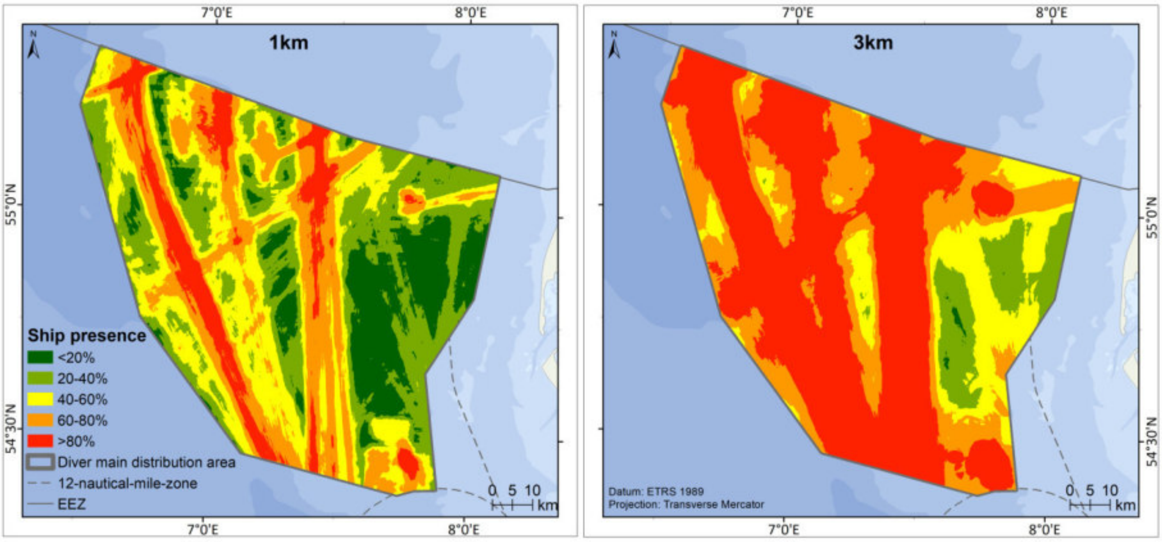

*Figure 7.2 Ship presence per day (in %) within the diver main distribution area in Germany, as defined by German authorities (*Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit *2009). Left panel shows ship presence per day during the study period in 2016 and 2017 (80 days of data) for a 1-km buffer around each ship track, right panel shows data for a 3-km buffer.*

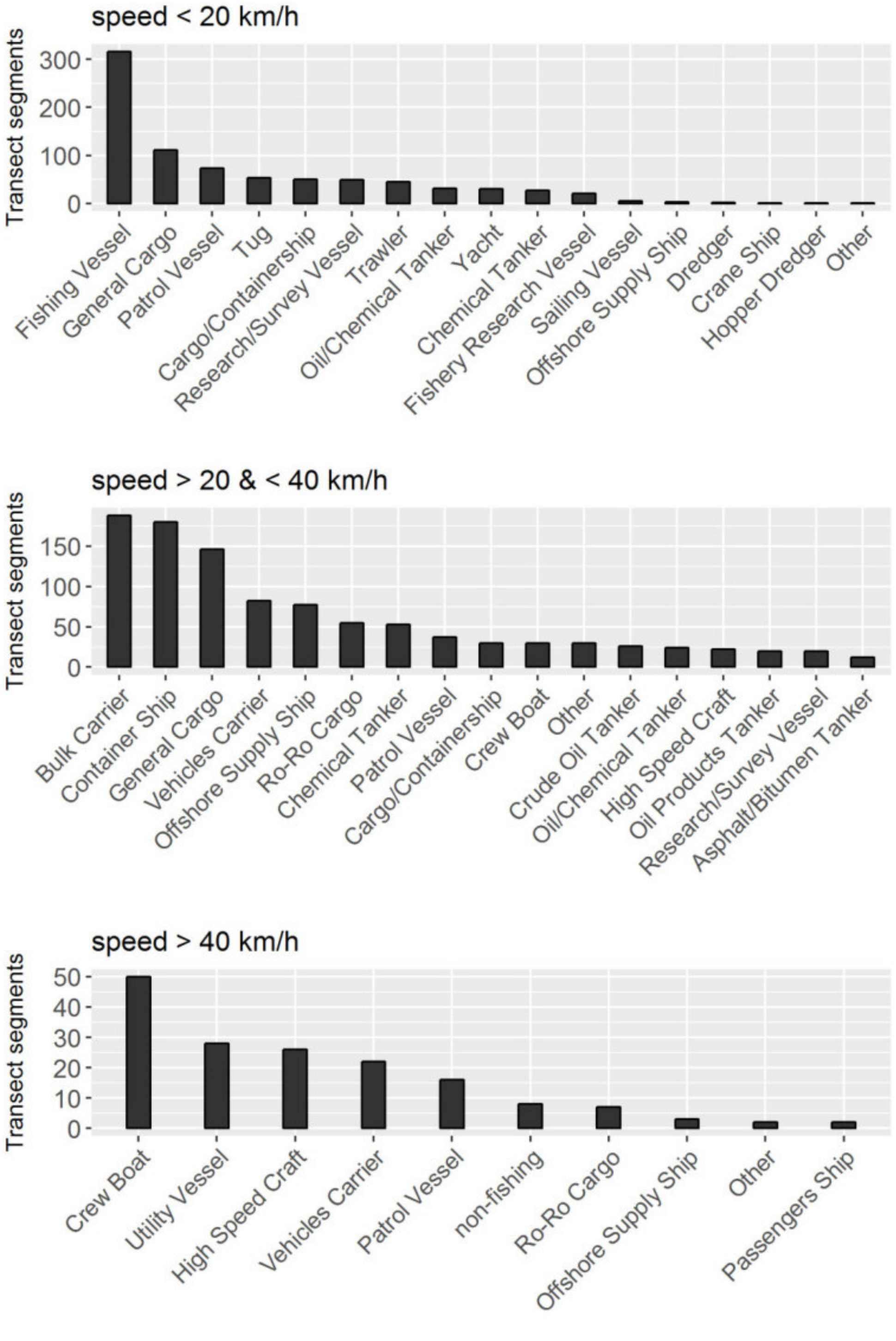

Figure 7.3 Ship types recorded within the study area (excluding a 10 km buffer around OWF) during four days with digital aerial surveys in spring 2016 and 2017. Panels depict ship composition for three categories of ship speed. 'Other' includes various other types of ships. The y-axis indicates the number of transect segments (from digital aerial surveys) which contained the respective ship types.

7.3.2 Digital aerial surveys

During digital aerial surveys, the highest numbers of red-throated divers (~1,400 birds) were observed during the survey conducted during 10th April 2016 and slightly fewer during 1st May 2016 (~1,100 birds). In 2017, notably fewer birds were counted during 25th March (~570 birds) and during 11th May (~330 birds). During all surveys only 0.9 % of birds were observed flying.

Initial data analysis using model 1 to describe changes in abundance of divers (number of birds) in relation to the number of ships present indicated that diver abundance was not only reduced when ships were present at distances up to 1.5 km, but also in distances between 1.5 km and 3 km. Therefore, model results for 1.5 km distance are only given in the supplementary material, while results for 3 km are presented in the main text (Table 7.1). This first model indicated a significant negative effect of ships on the number of birds present, for a radius of 3 km. The effect varied between dates (Table 7.1). Deviance explained by the model was 42.2%. Between 0 and 6 ships were present within a radius of 3 km around segments that contained one or more diver sightings, but 57.7% of segments with diver sightings contained no ships within this radius and the time frame from 7 h before the sighting. For segments that contained no birds, up to 15 individual ships were observed within 7 h before the surveys and in a 3 km radius. The highest ship densities (> 10 ships per 3 km radius) in our dataset were located approximately 8 km northwest of the island of Helgoland (Figure 7.1).

The final model 2 contained the tensor product smoother for the interaction between 'ship speed' and 'time since last ship' and the interaction between latitude and longitude. For the best fitting 1.5 km model, 'survey date' was included as factor. For the best fitting 3 km model, 'survey date' was included as random effect (Supplementary material, Appendix C). Results of model 2 (Table 7.2) showed that diver numbers significantly increased with increasing time since the last ship passage, but this effect was dependent on ship speed (Figure 7.4). For ships sailing at speeds between 10 and 40 km/h, diver numbers steadily increased during the 7 h observed, while for fast-moving ships (> 40 km/ h), diver abundance showed only a weak or no increase over time (only 6.4% of segments contained divers as compared to 17.6% when speed was < 40 km/h, Figure 7.4). However, most data for ships sailing at high speed only cover the time period up to 4 h before the aerial survey and gaps in the data occur for the time period between 4 and 7 h, probably due to the reason that these vessels only sail at certain times of the day (e.g. OWF-related crew vessels usually sail during morning and evening hours). For ships sailing at very low speed (< 2 km/h) no change in diver abundance over time was detected, presumably because these ships were still present in the vicinity just outside of the 3 km radius and thus there was little change in the extent of disturbance over time. Deviance explained by the model was 45.8%, indicating that model covariates explained a considerable part of the variation in the data. Ship length and the interaction between time and length were not significant in the final model and were therefore removed. Additional figures for the different models can be found in the supplementary material (Appendix C).

Table 7.1 Aerial survey data: Results of the best fitting GAM (model 1) for data with 3 km radius and 7 h time frame (n = 3,388).

Parametric coefficients	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-0.938	0.092	-10.158	<0.001
Date [10 Apr 2016]	0.370	0.114	3.238	0.001
Date [11 May 2017]	-1.957	0.593	-3.297	0.001
Date [25 Mar 2017]	-0.357	0.125	-2.850	0.004
Smooth terms	**edf**	**Ref.df**	**Chi-sq.**	**p-value**
s(N_{Ships}) [01 May 2016]	1.354	1.636	22.305	<0.001
s(N_{Ships}) [10 Apr 2016]	1.945	2.445	1.219	0.628
s(N_{Ships}) [11 May 2017]	2.800	3.054	81.245	<0.001
s(N_{Ships}) [25 Mar 2017]	2.547	3.158	22.513	<0.001
s(Longitude, Latitude)	24.664	27.814	715.771	<0.001

Table 7.2 Aerial survey data: Results of the best fitting GAM (model 2) for data with 3 km radius and 7 h time frame (n = 1,891).

Parametric coefficients	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-1.115	0.115	-9.669	<0.001
Date [10 Apr 2016]	0.476	0.154	3.097	0.002
Date [11 May 2017]	-2.312	0.242	-9.550	<0.001
Date [25 Mar 2017]	-0.487	0.157	-3.105	0.002
Smooth terms	**edf**	**Ref.df**	**Chi-sq.**	**p-value**
te(Time, Speed)	7.545	9.703	49.27	<0.001
s(Longitude, Latitude)	21.898	26.089	287.42	<0.001

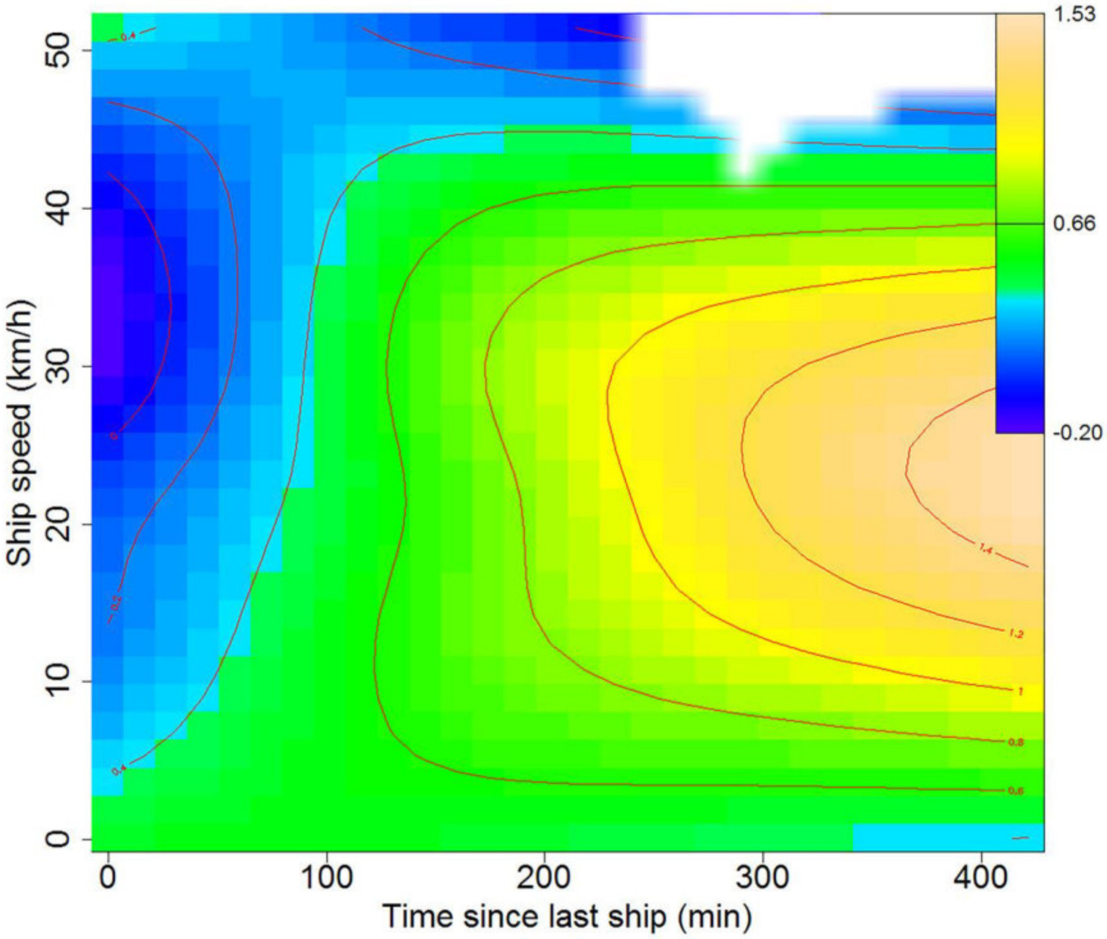

Figure 7.4 *Predicted diver abundance. Red-throated diver abundance for the interaction between time since last ship (in minutes) and ship speed (in km/h). Fitted values are shown for one survey date, 25 March 2017. Transparent areas indicate a lack of data (argument too.far set to 0.1).*

7.3.3 Tracking data

The analysis on 17 individuals using a general additive model showed a highly significant effect of numbers of ships (within 3 km and ± 1 h of the tracking position) on the relocation distance of birds ($p < 0.001$, $n = 170$, Figure 7.5, Appendix C, Table C 5). Relocation distance of red-throated divers was shorter when no ships were present as compared to when one or more ships were present within the 3 km radius. From the raw dataset, the average relocation distance was 4,261 m (per day) when ships were absent, while it was 10,849 m when ships were present. An additional calculation within a time frame of ± 15 min from every bird position (20 individuals) showed that the closest ship was more than 10 km away for 69% of all bird tracking positions. On 14 occasions (out of 402) and for nine different individuals, ships were recorded within 1 km of the bird position. Out of these, six ships were fishing vessels, sailing at low speed (4 – 8 km/h) and three ships were offshore supply or crew vessels, with one vessel passing at high speed (> 40 km/h). For 24% of all bird tracking positions, ships were present within a 5 km radius. Also within this 5 km radius, fishing vessels were most common (35.7%).

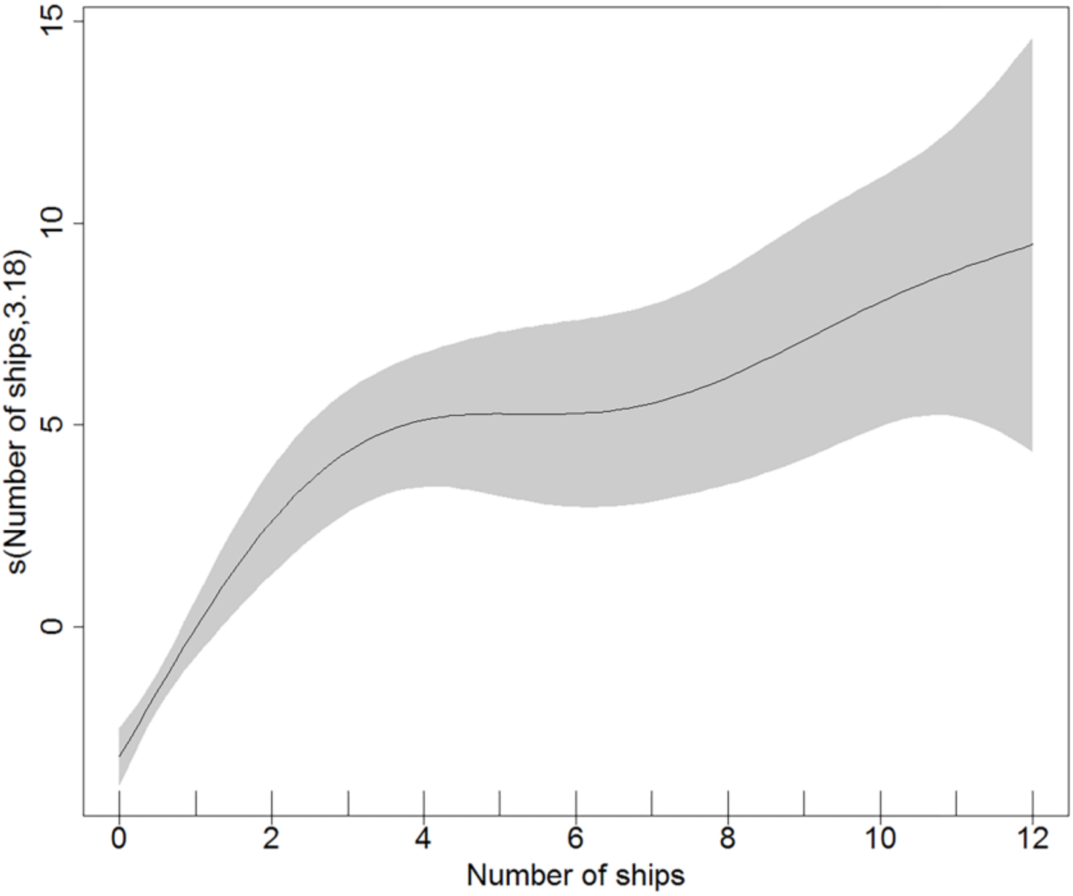

Figure 7.5 Relocation distance of divers relative to the number of ships encountered within a 3 km radius. Smooth curve from fitted GAM with 95% confidence interval (shaded area).

7.4 Discussion

The analysis of digital aerial survey data as well as satellite tracking data showed changes in the distribution as well as behavioral responses of red-throated divers towards ships. Divers were significantly more abundant in areas with low-frequency ship traffic. With our dataset we were able to investigate effects for a wide range of vessels present in the study area. Aerial survey data showed that within the maximum observed time period of 7 h after the passage of the ship, observations of red-throated divers increased over time and approached a plateau, but only for segments where the last ship passed at medium speed. In areas where high-speed vessels (> 40 km/h) passed, very few divers were subsequently observed, and no or little increase in diver numbers was found. These effects were investigated for ships within a radius of 3 km around each transect segment, but patterns for a radius of 1.5 km were also similar. One explanation for the lack of resettlement within time could be that high-speed vessels displace birds within a much larger radius than investigated in this study, and thus it takes longer before these areas are used again. A recent study by MENDEL ET AL. (2019a) suggests an effect of ships on red-throated divers up to 5 km distance. However, some uncertainty about the disturbance radius remains, as a rather coarse grid of bird data was used in that analysis. Alternatively, the repeated use of the same routes by high-speed vessels could lead to a permanent displacement of birds (SCHWEMMER et al. 2011). Vessels sailing at high speed were mainly present on the routes towards OWFs, but also scattered throughout the study area in small numbers (Appendix C, Figure C 7). From an analysis of habitat suitability (chapter 6) it seems likely that large parts of these areas used for shipping are suitable for divers and were not avoided for other reasons. We could also demonstrate that areas of designated shipping routes (NOLTE 2010) do not show a good match with actual ship traffic. Therefore, estimating habitat loss merely on the basis of shipping areas alone would substantially underestimate the amount of potential diver habitat that is impacted. Rather, the use of detailed historical AIS-data is encouraged for future studies.

7.4.1 Resettlement of disturbed areas

The overall long resettlement time might be related to the low abundance of divers of a few individuals per km², even in suitable habitat (MENDEL et al. 2008; GARTHE et al. 2015). During digital aerial surveys, less than 1 % of divers were recorded in flight. As birds mainly move and distribute themselves by drifting or swimming, it can be hypothesised that any gaps that occur due to a temporal disturbance will only be filled gradually when new birds slowly move into the area again. The fastest recovery of diver abundance was found for ships sailing at medium speed. These ships mainly comprise of cargo ships which usually sail on a straight path. It remains unclear, whether this pattern is also an indicator of habituation towards these types of shipping activity. Habituation effects have been described but such effects are often difficult to interpret (BEJDER et al. 2009). SCHWEMMER ET AL. (2011) found indications for habituation towards shipping lanes for long-tailed ducks and eiders, but not for common scoters. For red-throated divers however, habituation towards ships or OWFs has not been detected in any previous study (e.g. PERCIVAL 2014). With this study we could demonstrate that for a proper estimation of the amount of habitat loss on a temporal scale, it is crucial to include information on ship traffic covering several hours before the survey.

7.4.2 Individual movements

The analysis of satellite-tracking data showed that the majority of ship signals within the vicinity of bird tracking positions stemmed from fishing vessels. Furthermore, the statistical analysis of tracking data revealed subsequent greater relocation distances when ships were present in a 3 km radius around the tracking position. The results thus suggest a behavioral response of birds when ships are encountered close by. Red-throated divers might fly more often when encountering ships, while they swim and drift with (tidal) currents otherwise, covering smaller distances. Such fleeing behavior is commonly observed from research vessels (own unpublished data). In previous studies, flight distances of red-throated divers and other species were recorded from typical research vessels sailing at low to intermediate speed (usually 18.5 km/h, < 50 m ship length) and former fishing vessels are often used for these tasks (BELLEBAUM et al. 2006; SCHWEMMER et al. 2011; FLIESSBACH et al. 2019). In such cases, only the immediate response is recorded, while divers likely respond already at larger distances with other behavioral changes (e.g. swimming away). Such responses have been frequently described for other species (RONCONI & CLAIR 2002; STOLEN

2003; MERKEL et al. 2009; MARCELLA et al. 2017). One drawback of our dataset was, however, the rather coarse resolution of tracking data. We thus do not know the exact bird movements between positions being up to 30 h apart. Nevertheless, even with this low accuracy, also the raw data shows clear effects of ship encounters on relocation distances (Appendix C, Figure C 9), supporting our analyses and suggesting that individual daily movements are indeed related to disturbance by ships.

7.4.3 Habitat suitability

Habitat characteristics of large parts of our study area in the German Bight seem suitable for red-throated divers, with water depth and salinity being important habitat parameters (chapter 6; SKOV & PRINS 2001). These habitat parameters are likely related to prey abundance, as fish species have been shown to concentrate in frontal zones (MARAVELIAS 1997). Red-throated divers are opportunistic foragers and prey on a wide range of fish species (DURINCK et al. 1994a; KLEINSCHMIDT et al. 2019). Pelagic fish like herring, sprat and mackerel were most commonly found in their diet when sampled from an offshore location within the main diver distribution area (KLEINSCHMIDT et al. 2019). Habitat suitability is however limited due to several OWFs within the study area. Red-throated divers have been found to shift their main wintering areas in the German Bight away from operating OWFs and show large displacement radii of more than 10 km (GARTHE et al. 2015; NEHLS et al. 2018; MENDEL et al. 2019a). As part of the ship traffic is associated with OWFs (e.g. for maintenance), displacement effects by OWFs are not only related to the OWF structures, but also to the regular service vessels and other wind farm-related traffic which concentrates in and around OWFs (MENDEL et al. 2019a).

7.4.4 Population consequences

We have identified disturbance effects by shipping which manifest in temporal habitat loss and behavioral changes. These patterns were found for areas with little direct disturbance by OWFs (more than 10 km away). Ship traffic thus represents another source of disturbance which is present throughout the main distribution area of red-throated divers. Given the strong responses found, it is unclear whether the different anthropogenic disturbances allow birds to still track areas of high food abundance within their wintering and staging sites. No data exists so far whether these responses also lead to a reduction in fitness and whether this could even potentially lead to population declines (PIROTTA et al. 2018a). GILL ET AL. (2001) investigated the notion that animals which show the strongest responses to human disturbances are also those that suffer the most in terms of fitness costs. They suggest that strong displacement need not necessarily lead to population-level consequences but rather could be interpreted as having the capacity to respond. For red-throated divers, foraging ecology and especially density effects in the species are so far poorly understood, and population effects are difficult to judge until better knowledge is available. A previous study using long-term data (2002-2013) on red-throated divers in the German Bight did not detect a population decline (GARTHE et al. 2015), despite ship traffic being present and increasing also in the past. It is unknown whether the population size is determined by conditions in the wintering or in the breeding areas. Overall, the impact of ship traffic on population size might turn out to be rather low if a more complex picture of red-throated diver ecology is available.

7.4.5 Conclusions

This study yielded much needed information on red-throated diver response patterns towards ship traffic which are essential to inform conservation and management of this sensitive species. As ship traffic is the dominating anthropogenic activity in this important seabird staging area, it is crucial to include this sector for marine spatial planning (METCALFE et al. 2018). It is now apparent that also the disturbance by OWFs is caused by a combination of OWF structures and associated ship traffic (MENDEL et al. 2019a). High ship traffic in the area could make it difficult for birds to find an undisturbed location. Due to the predicted future increase in ship traffic (KAPLAN & SOLOMON 2016) and additional anthropogenic disturbances such as the construction of OWFs, possible mitigation measures need to be discussed. Channeled ship traffic on certain routes crossing important seabird habitats could render traffic more predictable for sensitive seabird species and reduce disturbance in adjacent areas. Our study area is mostly located in a newly created nature conservation area under German law (and is for some years a Natura 2000 area), and thus management measures (e.g. bundled ship traffic) might be considered in order to minimize disturbance of divers. As shown in this study, ship speed is an important determinant of the duration and range of disturbance. Speed limits within the protected marine area could thus further reduce the spatial extent of disturbance. Ultimately, models of the population consequences of human stressors need to be applied for sensitive species using existing frameworks (PIROTTA et al. 2018a), in order to estimate the impact of human activities, and to develop effective mitigation measures.

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8 THE DIET OF RED-THROATED DIVERS (*GAVIA STELLATA*) OVERWINTERING IN THE GERMAN BIGHT (NORTH SEA) ANALYSED USING MOLECULAR DIAGNOSTICS

Birgit Kleinschmidt[1,2]*, Claudia Burger[2], Monika Dorsch[2], Georg Nehls[2], Stefan Heinänen[3,8], Julius Morkūnas[4], Ramūnas Žydelis[3,7], Rosemary J. Moorhouse-Gann[5], Helen Hipperson[6], William O.C. Symondson[5] & Petra Quillfeldt[1]

[1]Department of Animal Ecology and Systematics, Justus Liebig University Giessen, [2]BioConsult SH, [3]DHI, [4] Marine Research Institute, Klaipėda University, [5]Cardiff School of Biosciences, Cardiff University, [6]NERC Biomolecular Analysis Facility, Department of Animal and Plant Sciences, University of Sheffield, [7]Ornitela, [8]Novia University of Applied Sciences

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Abstract

In Europe, the German Bight is one of the most important non-breeding areas for protected red-throated divers (*Gavia stellata*). It is unclear what attracts the birds to this area, especially as the food composition of seabirds outside the breeding season is notoriously difficult to study. To obtain information on prey species composition of red-throated divers in this area, faecal samples from 34 birds caught alive were analysed using DNA metabarcoding. Prey DNA was detected in 85% of the samples with a mean number of 4.2 ± 0.7 taxa per sample (n = 29). Altogether we found a broad prey spectrum with 19 fish taxa from 13 families dominated by five groups: clupeids, mackerels, gadoids, flatfish and sand lances with clupeids being the most frequently detected prey.

Our results indicate that red-throated divers are generalist opportunistic feeders in the German Bight, but pelagic schooling fish that aggregate at frontal zones and have a high energetic value might be favoured. Atlantic mackerel appears to be a more important prey for red-throated divers in this area than previously thought.

The precision achievable using metabarcoding has revealed a number of prey species that are consumed by red-throated divers in the German Bight, which helps to explain the selection of this area by divers in winter and spring.

Keywords: Diet composition, DNA Metabarcoding, Next Generation Sequencing, North Sea, Red-throated diver/loon, Site selection

8.1 Introduction

Understanding resource utilisation is fundamental for managing wildlife populations. Data on diet composition and feeding strategies are essential for understanding habitat selection and for predicting the ecological consequences of habitat change (Davoren et al. 2003). Predator abundance is often regulated by bottom-up effects of prey abundance (ENGELHARD et al. 2013). Thus, the availability of prey may affect not only predator distribution and abundance but also foraging strategies (FAUCHALD et al. 2011; LYNAM et al. 2017).

Diet composition of seabirds outside the breeding season, when they remain at sea, is notoriously difficult to study. This is especially true for protected species where only non-invasive methods are applicable. In the past, various techniques have been developed to analyse seabird diet. These include visual observations, morphological identification of regurgitates or gut contents, or biochemical methods such as the analysis of fatty acid and stable isotope concentrations (BARRETT et al. 2007; MEIER et al. 2017; QUILLFELDT et al. 2017; QUINN et al. 2017). A highly efficient alternative approach is to use DNA metabarcoding (DEAGLE et al. 2005, 2007; POMPANON et al. 2012; VESTERINEN et al. 2013; ALONSO et al. 2014). This involves amplification of DNA from faecal material and assignment of taxonomical information using Next Generation Sequencing (NGS) and DNA barcode databases.

Our study focused on the prey spectrum of the red-throated diver (*Gavia stellata*), a protected marine bird species, in its wintering and spring staging areas in the German Bight (eastern part of the North Sea). During the non-breeding season about 84,200–186,000 individuals stay in the Baltic Sea, the North Sea and the NE-Atlantic (DIERSCHKE et al. 2012; BIRDLIFE INTERNATIONAL 2019). Around 20% of the NW-European wintering population occurs in the German Bight (GARTHE et al. 2007; MENDEL et al. 2008; DIERSCHKE et al. 2012) classifying it as an internationally important staging area for these birds, especially in spring before migration starts (GARTHE et al. 2012, 2015). To date three studies have been published on the prey composition of non-breeding red-throated divers in the North Sea and the Baltic Sea, which analysed gut contents using morphological tools (Table 8.1). However, information is not available from the German Bight (Figure 8.1). Red-throated divers feed on a wide range of fish species and, given that the energy content of prey fish varies with size and season, they appear to choose prey of high energetic value (PEDERSEN & HISLOP 2001) like gadoids (MADSEN 1957) or clupeids (DURINCK et al. 1994a; GUSE et al. 2009). Additionally cephalopods were found in one of these studies (DURINCK et al. 1994a) in four of eight birds. Small specimens of polychaetes, crustaceans, copepods, bivalves and gastropods were reported in all studies although these were considered to be secondary prey (i.e. prey in the guts of the fish eaten by the divers). The German Bight is characterised by an estuarine frontal system, created by the Jutland costal current (JCC) that is primarily driven by discharges from the Elbe river and other rivers further south (SKOV & PRINS 2001). Red-throated divers have been shown to concentrate at the productive frontal zone, where prey fish aggregate (SKOV & PRINS 2001). The area is also suitable for the development of offshore wind farms as it has extensive areas of shallow waters (< 40 m). To date, 17 wind farms have been installed in German North Sea waters. Thus, there is potential overlap between offshore wind farm sites and the preferred habitat of non-breeding red-throated divers (chapter 6; GARTHE et al. 2015). Red-throated divers have been shown to strongly avoid both shipping traffic and wind farms (GARTHE & HÜPPOP 2004; BELLEBAUM et al. 2006; DIERSCHKE et al. 2006, 2012; PETERSEN et al. 2006; MENDEL et al. 2019a; BURGER et al. 2019; see also chapter 6). To understand the environmental importance of the German Bight for red-throated divers, to assess the possible impacts arising from displacing divers from substantial parts of their staging areas, and to analyse whether alternative staging areas might be available, it is crucial to understand what resources these birds rely on.

Figure 8.1 Study site where red-throated divers were captured and sampled in the German North Sea. The German Economical Exclusive Zone (EEZ) and 12 nautical miles are indicated (grey line). Red-throated diver capture positions for both sampling years are summarised as a black dot. Large symbols indicate the locations of previous dietary studies on red-throated diver in adjacent waters, star presents DURINCK *et al. (1994a), triangle presents* MADSEN *(1957), square presents* GUSE *et al. (2009).*

In this study we had the unique opportunity to collect a small number of faecal samples from red-throated divers captured in the German North Sea in 2015 and 2016 in both winter and spring. We applied DNA metabarcoding as a non-invasive technique to analyse diet composition, and thus to provide a detailed overview of recent meals of these birds in the German Bight. Specifically, we aimed to document the diversity of prey species eaten by the birds in this particular staging area when red-throated diver abundance is highest. Additionally, we aimed to compare data for two consecutive sampling years to determine if the prey species consumed is consistent between years. By comparing dietary data with published data on local fish distribution, we aimed to determine whether the abundance and distribution of prey fish correlate with red-throated diver diet and how this may help to explain red-throated diver distribution.

Table 8.1 Main fish prey species of red-throated divers detected in previously published studies using morphological methods (Madsen 1957; Durinck et al. 1994a; Guse et al. 2009) and this study using molecular tools listed as FO for the corresponding areas where birds were examined.

Prey item (Group)	**Prey item (Family)**	**Prey taxa (Genus/species)**	**Madsen 1957 (North Sea/Inner Danish Waters) n = 173**	**Durinck et al. 1994 (North Sea) n = 8**	**Guse et al. 2009 (Baltic Sea) n = 82**	**This study**
Gadiformes	Gadidae	Common cod (*Gadus callarias*)	54%	-	-	-
Gadiformes	Gadidae	Whiting (*Merlangius merlangus*)	-	25%	-	6.9%
Gadiformes	Gadidae	Blue whiting (*Micromesistius poutassou*)	-	37.5%	-	-
Gadiformes	Gadidae	Gadoids indet.	-	50%	-	31%
Perciformes	Gobiidae	Common goby (*Pomatoschistus microps*)	-	-	winter 38.2% / spring 10.4%	-
Perciformes	Gobiidae	Gobies (*Gobius sp.*)	14%	-	winter 41.2% / spring 20.8%	13.8%
Clupeiformes	Clupeidae	Atlantic herring (*Clupea harengus*)	12%	87.5%	winter 23.5% / spring 95.8%	55.2%
Clupeiformes	Clupeidae	European sprat (*Sprattus sprattus*)	-	75%	winter 14.7% / spring 27.1%	58.6%
Clupeiformes	Clupeidae	(*Clupea sp./Sprattus sp.*)	-	37.5%	winter 14.7% / spring 22.9%	-
Gasterosteiformes	Gasterosteidae	Sticklebacks (*Gasterosteus sp.*)	11%	62.5%	winter 52.9% / spring 39.6%	10.3%
Osmeriformes	Osmeridae	Smelt (*Osmerus eperlanus*)	-	-	winter 44.1% / spring 4.2%	-
Perciformes	Percidae	Zander (*Sander lucioperca*)	-	-	winter 91.2% / spring 10.4%	-
Perciformes	Percidae	European perch (*Perca fluviatillis*)	-	-	winter 17.6% / spring 2.1%	-
Perciformes	Percidae	Ruffe (*Gymnocephalus cernus*)	-	-	winter 38.2% / spring 20.8%	-
Perciformes	Ammodytidae	Lesser sandeel (*Ammodytes tobianus*)	< 1%	12.5%	winter 8.8% / spring 12.5%	31%
Perciformes	Scombridae	Atlantic mackerel (*Scomber scombrus*)	< 1%	-	-	55.2%
Pleuronectiformes	Pleuronectidae	Flatfish indet.	5%	37.5%	winter - /spring 2.1%	51.7%

8.2 Methods

8.2.1 Sample collection and study site

This dietary study was part of a satellite telemetry project on red-throated divers. A total of 36 red-throated divers were captured in March and April 2015 and in February and March 2016 in the German Bight (Figure 8.1). Sampling was focused on late winter and spring when red-throated diver abundance is highest in the German Bight (MENDEL et al. 2008; DIERSCHKE et al. 2012; GARTHE et al. 2015). The capture area was approximately 30 km offshore in water depths of around 20 m, which is approximately in the centre of the staging area for red-throated divers (Figure 8.1). Birds were captured from a rigid inflatable boat using a hand net and the "night lighting technique", where the sea is searched for resting divers with a spot light. If a bird is sighted, it often becomes disoriented by the bright light and can be captured with a net (WHITWORTH et al. 1997; RONCONI et al. 2010). In 2015 captured birds were kept in boxes for an average time of 18.3 h (min 6.3 h, max 27 h) and in 2016 for an average time of 9.2 h (min 7 h, max 13 h). After release the boxes were searched for scat. The boxes were cleaned and disinfected after every use with bleach (1% hypochlorite solution), water and ethanol (70%) to prevent cross contamination. During the two field seasons a total of 34 faecal samples were collected (2015 n = 15; 2016 n = 19, Table 8.2). Samples were preserved in absolute ethanol and stored at -20 °C until further analysis.

Table 8.2 Timing and sample size of analysed faecal samples of red-throated divers from the German Bight. One sample per bird was taken for analysis.

Sampling year	**2015**	**2015**	**2016**	**2016**
Time period	March	April	February	March
Sample size (captured birds)	10	6	8	12
Sample size (faecal samples)	10	5	8	11
Positive samples	9	4	8	8
Total of positive samples	13		16	

8.2.2 DNA extraction

Faecal DNA was isolated using the QIAamp DNA Stool Mini Kit (Qiagen) following the manufacturers protocol with the following modifications: (i) the samples were resuspended in the storage ethanol by vortexing before moving 200 µL of the ethanol-scat slurry to a new clean 2 ml Eppendorf tube and centrifuging for 30 s at 4000 x g (DEAGLE et al. 2005); (ii) the lysis step was extended by adding 1.4 mL Buffer ASL instead of 1.6 mL to each sample and incubating at 70 °C for 10 min and then for 1.5 h at room temperature to improve lysis output; (iii) the digestion step was extended by adding 20 µl instead of 25 µl proteinase K and incubating samples at 70 °C for 30 minutes prior to an increased incubation time at a lower temperature (56 °C for 1.5 h). All remaining steps followed the manufacturer's instructions except that buffer volumes were cut down to reduce risk of cross contamination by minimising the number of pipetting steps and by reducing the volume of liquid loaded into spin columns and tubes (DEAGLE et al. 2005). The final elution step used a total elution volume of 100 µl (as recommended by the manufacturer`s protocol), but was divided into two steps with each elution using 50 µL Buffer AE.

8.2.3 Primer design and preparation for sequencing

Three separate PCR primer pairs were used to comprehensively target all the major potential prey species of red-throated divers in this area (Table 8.3). These prey species are widespread in the North Sea and were informed by previous diet studies on red-throated divers (Table 8.1; Madsen 1957; Durinck et al. 1994b; Guse et al. 2009).

Table 8.3 Sequences of primers used to amplify red-throated diver faecal samples for Next Generation Sequencing. Modifications from original primers (Waap et al. 2015) in bold.

Target amplification	Gene	Primer name	Sequence (5'–3')	Approximate product size incl. primer sequence (bp)	Annealing temperature (°C)
Fish (Chordata)	mtDNA 16S	FISH2_16S_F	CGAGAAGACCCTDTGRAG**CT** (20)	~264	58
Fish (Chordata)	mtDNA 16S	modifiedChord_16S_R1	GCTGTTATCCCTRGRGTAA (19)		
Cephalopod (Molluscs)	mtDNA 16S	Ceph_16S_R	AGGGACGA**R**AAGACCCTANTGAGC (24)	~244	56
Cephalopod (Molluscs)	mtDNA 16S	Ceph_16S_F	**A**C**S**CTGTTAYCCCTATG (17)		
Crustacean (Invertebrate)	mtDNA COI	mICO1int_F	GGWACWGGWTGAACWGTWTAYCCYCC (26)	~332	50
Crustacean (Invertebrate)	mtDNA COI	Nancy_R	CCCGGTAAAATTAAAATATAAACTTC (26)		
Blocking probe	-	-	GTGGA ACTTAAAAATCAGCAGCCACCA[SpcC3]	-	-

Primers for each prey group were tested in silico, using ClustalX 2 (Larkin et al. 2007) and MEGA7 (Kumar et al. 2016). Conserved primer binding sites were tested against a DNA barcode database of barcode-sequences extracted from GenBank. Sequences of 16S DNA of 28 representative fish species from 7 orders and 15 families as well as 12 cephalopod species from 5 families were aligned for these tests. For crustaceans COI barcode sequences of potential prey species from 6 orders and 8 families of shrimp and krill were aligned and tested. Furthermore primers for each prey group were tested in vitro on DNA from tissue samples of corresponding potential prey species occurring in the German Bight (clupeids, perciformes, gadoids, flatfish, octopus, squid, cuttlefish and shrimp) to optimise PCR conditions. Multiplex identifier (MID) tags were added to the primer sequences and used to assign DNA sequences to their respective samples (n = 34). MID tags were added to each of the three tested primer sets (fish, cephalopods and crustaceans). For each of the three primer sets we used 24 forward primers/MID and 2 reverse primer/MID combinations, and all in vitro testing was performed using primer pairs first without and then with the MID tags to ensure amplification was not affected.

To amplify DNA from fish and cephalopods, we used primers targeting the 16S region originally published by WAAP (2015) and modified from Chord_16S_F/Chord_16S_R (DEAGLE et al. 2009). We further modified the primer sequence to comprehensively match the range of potential prey species (Table 8.3). To amplify fish DNA, the forward primer has additional CT bases at the 3´end for NGS sequencing to improve the blocking probes (see below), so that the mismatch was not located at the last base pair (WAAP, pers comm.). To amplify cephalopod DNA, we modified the forward primer by one base and the 5´end of the reverse primer. Both primer pairs tested positive in silico and in vitro for potential prey of red-throated divers.

To amplify crustacean DNA, a primer combination targeting the Cytochrome oxidase I region (COI) was used that was likely to amplify crustaceans and molluscs (STOCKDALE 2018; Table 8.3). The forward primer (LERAY et al. 2013) was designed to amplify arthropod DNA, including crustaceans and molluscs. The reverse primer (SIMON et al. 1994) was also designed to amplify arthropods including crustaceans. The primers tested positive in silico and in vitro for potential prey of red-throated divers and provided a good coverage of our target species and a good coverage with reference sequences available in public databases. This primer set amplified a product size of 332 bp and thus represents a good compromise as it is long enough to provide good taxonomic information and short enough to survive digestion.

8.2.4 Blocking primer

The primers chosen to amplify fish prey were universal chordate primers that could also amplify other chordates, including predator DNA. To prevent the amplification of predator DNA, we developed a blocking probe using a C3 spacer (Table 8.3; VESTHEIM & JARMAN 2008). However, the blocking probe reduced amplification success and a second amplification of samples was performed excluding the blocking probe. Gel electrophoresis (see below) was used to visually monitor the amplification of predator and prey DNA, assisted by the inclusion of red-throated diver (300 bp) and fish (264 bp) reference samples. This differential in PCR product size allowed for predator amplicons to be easily identified (Figure 8.2).

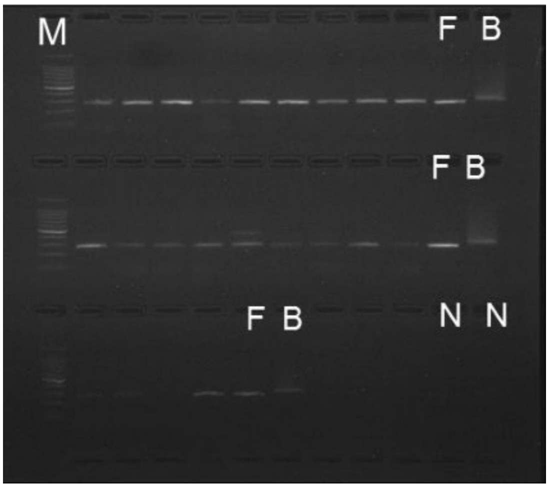

Figure 8.2 Agarose gel electrophoresis of 16S mtDNA fragments amplified from faecal samples with fish (chordate) primers. M = 1000bp ladder, F = fish DNA control, B = red-throated diver DNA control and N = negative control.

8.2.5 PCR amplification of fish and cephalopod prey DNA from faeces

PCR amplifications were performed in single reactions using Multiplex PCR Kits (Qiagen) and a 20 µL PCR reaction volume. Thermal cycling conditions for fish and cephalopod prey were 95 °C for 15 min followed by 45 cycles of: 94 °C for 30 s, a primer specific annealing temperature (Table 8.3) for 90 s, and 72 °C for 45 s, followed by a final extension at 72 °C for 5 min. Thermal cycling conditions for crustaceans were 95 °C for 15 min followed by 45 cycles of: 94 °C for 30 s, a primer specific annealing temperature (Table 8.3) for 90 s, and 72 °C for 90 s, followed by a final extension at 72 °C for 15 min.

All PCR products were visualised by gel electrophoresis on 2% agarose gels stained with SYBR®Safe (ThermoFisher Scientific, Paisley, UK) and compared to a standardised 1000 bp ladder. The PCR product concentration in successful reactions was quantified with a Qubit fluorometer (Thermofischer) and subsequently pooled into two equimolar libraries of individually tagged amplicons (PoolA using a blocking probe and PoolB without a blocking probe). To remove primer dimer we ran a magnetic clean up (AMPure). Concentrations of DNA and primer dimer were measured on a tape station (D1000 Screen Tape; Tape Station Analysis Software A.01.05 SR1, Agilent technologies) and a Qubit before and after the magnetic clean up.

8.2.6 Next Generation Sequencing

NGS library preparations were performed at the NERC Biomolecular Analysis Facility – Sheffield (NBAF-S), Sheffield, UK using the NEBNext Ultra DNA Library Prep Kit for Illumina (New England Biolabs, Ipswich, MA). To characterise the diet content of the individually tagged amplicons the libraries (PoolA and PoolB) were sequenced at the Sheffield Diagnostics Genetics Service (Children's Hospital, Sheffield, UK) using 250 bp paired-end reads on a MiSeq desktop sequencer (Illumina, San Diego, CA).

8.2.7 Bioinformatics

We performed eight steps to transform the raw Illumina sequence data into a list of molecular operational taxonomic units (MOTUs) with assigned taxonomy. These steps included assessing sequence quality, trimming sequences (BOLGER et al. 2014), aligning paired reads (MAGOC & SALZBERG 2011), matching sequences to MID tags and amplicon primers (SCHLOSS et al. 2009), and demultiplexing sequences into files for each amplicon. We used USEARCH (EDGAR 2010) to dereplicate the sequence file, to detect and to remove chimeric sequences and to cluster into MOTUs based on 97% identity. Clustering is an important step in metabarcoding analysis to group similar sequences into distinct taxonomic units, but remains one of the central challenges. If the clustering threshold is too conservative, e.g. 5% sequence divergence, the dietary richness could be underestimated due to a high mean overlap of MOTUs. Conversely, a less conservative decreased threshold, e.g. 2% sequence divergence, could overestimate species richness (CLARE et al. 2016). Here we applied the established clustering threshold of 97% similarity (EDGAR 2010, 2016) using the 'cluster_fast' function in USEARCH (EDGAR 2010). We applied the BLASTn algorithm (ALTSCHUL et al. 1990) to match MOTU sequences to reference sequences in the NCBI GenBank nucleotide database, using a cut-off of 90% minimum sequence identity and a maximum e-value of 0.00001. For detailed information about options, parameters and values please see Table D.11.2 in Appendix D.

We subsequently manually performed further filtering steps to produce robust taxonomic assignments. We discarded MOTUs (sequence clusters 97%) that corresponded to contaminants that can occur regularly in faecal samples, such as bacterial, human or predator DNA. MOTUs were retained in a sample only if they contained a minimum of 5 sequences. Taxonomic assignment was based on the percentage similarity of the query and the reference sequences. Since short fragments are less likely to contain reliable taxonomic information we only retained sequences with a minimum length of 190 bp and a BLASTn assignment match greater than 98%, following DEAGLE et al. (2009) and VESTERINEN et al. (2013).

Finally, we combined both pools (PoolA with a blocking probe and PoolB without a blocking probe) together for final analyses. To avoid overrepresentation we excluded prey species of samples from PoolB that were also present in PoolA.

8.2.8 Analysing the Blast output

We used MEGAN Community Edition version 6.8.8 to visualise the accession number identifiers on the NCBI taxonomy (HUSON et al. 2016). We imported the blast output and used the default LCA parameters to assign a taxon name to each MOTU (HUSON et al. 2007). If all retained hits of a MOTU with the same quality criteria (sequence identity, sequence length, e-value) matched the same species then we have a species-level assignment, otherwise the MOTU was assigned to the lowest shared taxonomic level, e.g. genus or family.

8.2.9 Statistical analysis

We analysed prey range by determining the presence of prey items, their frequency of occurrence (FO) (BARRETT et al. 2007; TOLLIT et al. 2009), and species richness. FO was calculated as: FO = (n/t) X100 where n was the number of samples in which the specific prey item appeared and t was total number of samples containing prey. FO reveals the percentage of sample units in which each prey item occurred (Barrett et al. 2007). The number of MOTUs (defined by 97% clustering threshold, n = 169) assigned for each prey taxa were additionally presented as percent occurrence in faecal samples (n = 29) to visualise the sequencing output (Figure 8.4). No further quantitative analyses were done with these data due to a range of possible biases and as interpretation of sequence proportions generated via high-throughput sequencing requires careful data analysis (DEAGLE & TOLLIT 2007; POMPANON et al. 2012; DEAGLE et al. 2013, 2019).

Whether or not there is consistency in prey consumption by red-throated divers over time informs our understanding of prey selection in this particular area. We tested this by comparing FO of prey items in 13 samples from 2015 with FO of prey items in 16 samples from 2016. Statistical tests suitable for small sample sizes were performed in Rcmdr (FOX & BOUCHET-VALAT 2018). We used Pearson’s chi squared-test to compare the frequency of occurrence between years for each prey group when sample sizes fulfilled the minimum requirements for this test (n > 5). When sample sizes were small (n < 5), we implemented the Fisher's Exact Test for Count

Data. To compare the number of prey detections per sample between sampling years the T-Test for independence was used. Small sample sizes precluded further analyses (e.g. comparing seasons) or to use other statistical tests. Considering the sample size and the temporal scope of faecal DNA sampling only marked differences were expected to be identified.

8.3 Results

8.3.1 Overview of sample quality and prey species found

Neither cephalopods nor crustaceans were detected in the diet, despite successful in vitro PCR amplification using reference tissue samples from potential prey items from the German Bight (octopus, squid, cuttlefish and shrimp samples).

The fish primer set produced more than 800,000 sequences from both pools combined, for specific information on number of sequences during bioinformatics analysis, see supplementary material. Of 34 screened samples 29 samples gave positive PCR amplifications (PoolA: n = 21; PoolB n = 29). Both pools had ~ 50% of MOTUs assigned to prey fish (PoolA = 56%; PoolB = 48%), plus with other MOTUs being from the predator DNA (red-throated diver) and contaminants such as bacteria and human DNA (Figure 8.3). Using the blocking probe, we still amplified predator DNA but the amount of MOTUs assigned to the predator was slightly lower in PoolA (9%) than in PoolB (17%).

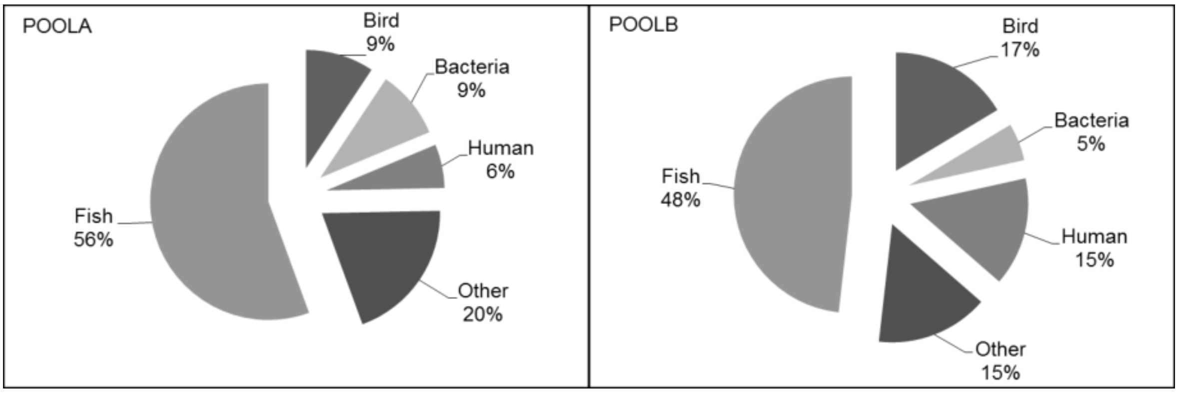

Figure 8.3 Proportions of MOTUs in per cent for fish, contamination (bacteria, human and others) and for bird assignments amplified with the fish primer set. On the left with the blocking probe (PoolA) and on the right without the blocking probe (PoolB) for both sampling years (2015 and 2016) combined.

After filtering for contaminants, sequence length and mapping to reference sequences, 20 and 24 faecal samples remained for PoolA and B respectively. After merging both pools, the final sample set consisted of 29 samples (PoolA n = 20, PoolB n = 9) which corresponds to 85% of all samples collected (Table 2). Four samples were discarded (PoolB) as they contained only contaminants and predator DNA, and two samples were discarded as the amplicon length criteria were not met (1x PoolB, 1x PoolA).

Clustering the sequences by 97% similarity to each other and subsequent filtering resulted in 169 MOTUs that were used for further analyses. A list of a representative query sequences of each

MOTU and its quality criteria is listed for each prey assignment in Appendix D (Table D.11.2) and for all MOTUS in Table D.11.5 (Appendix D.2). For the two sampling periods 19 taxa from 13 families were identified in 29 faecal samples (Figure 8.4, Table 8.4). In 2015 we detected a slightly higher number of taxa in comparison to 2016 (18 and 13 taxa assigned to species, respectively; Table 8.4). The prey species spectrum was similar between the two years with 12 matching taxa and no significant differences ($\chi^2 = 1.004$, $p = 0.316$). European anchovy (*Engraulis encrasicolus*), turbot (*Scophthalmus maximus*), European pollock (*Pollachius pollachius*), cod (*Gadus* sp.), European bass (*Dicentrarchus labrax*) and sand lances of the genus *Ammodytes* were detected only in 2015, and whiting (*Merlangius merlangus*) only in 2016 (Table 8.4).

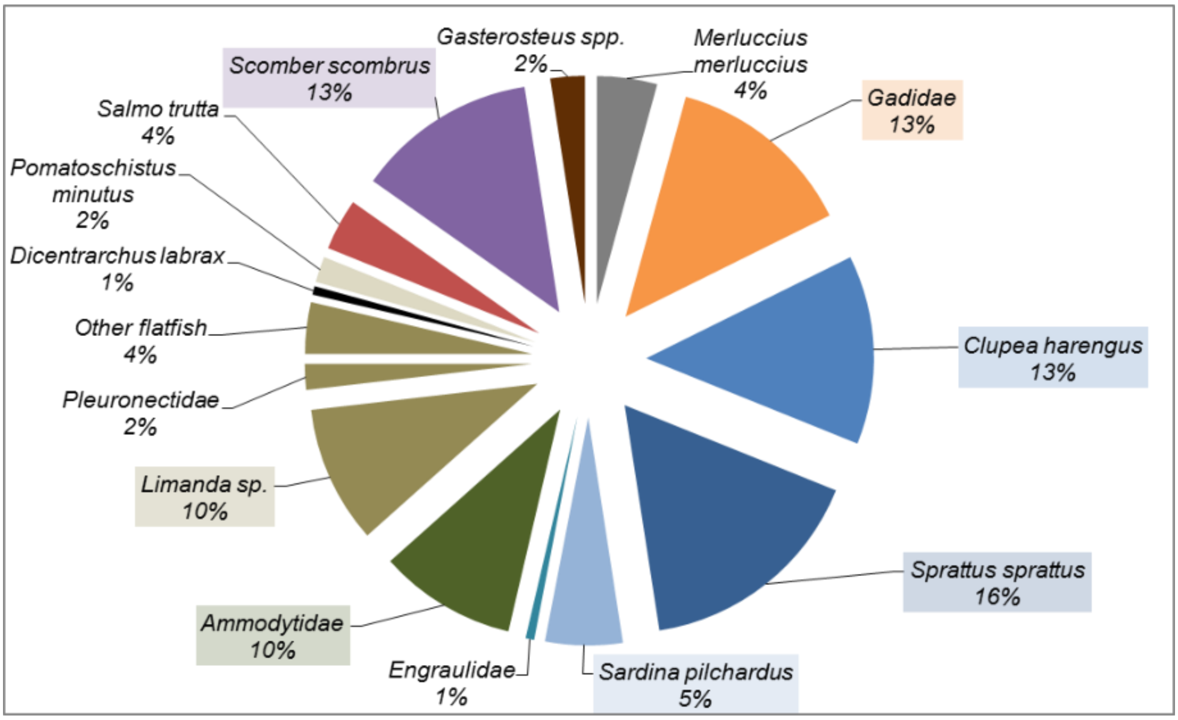

Figure 8.4 Percent occurrence of MOTUs (n = 169) in all faecal samples (n = 29) assigned for fish prey: blue – clupeids, orange – gadoids, grey – hake, brown – sticklebacks, violet – mackerels, red – salmonids, beige – sand gobies, black – seabass, grey – light-brown flatfish and green – sand lances. Captions of prey groups with highest proportions (> 5%) are highlighted.

Table 8.4 Detected prey species of red-throated divers with regard to presence (MOTUs) and frequency of occurrence (FO) for each sampling year and the full dataset.

				2015			**2016**			**2015 & 2016**		
				MOTUs found in x samples (n=13)	**FO (%, n=13)**	**No of MOTUs (n=101)**	**MOTUs found in x samples (n=16)**	**FO (%, n=16)**	**No of MOTUs (n=68)**	**MOTUs found in x samples (n=29)**	**FO (%, n=29)**	**No of MOTUs (n=169)**
Clupeiformes	Clupeidae	*Clupea harengus*	Atlantic herring	7	53.8	10	9	56.3	15	16	55.2	25
Clupeiformes	Clupeidae	*Sprattus sprattus*	European sprat	9	69.2	15	8	50.0	12	17	58.6	27
Clupeiformes	Clupeidae	*Sardina pilchardus*	European pilchard	3	23.1	6	3	18.8	4	6	20.7	10
Clupeiformes	Engraulidae	*Engraulis encrasicolus*	European anchovy	1	7.7	1	0	0.0	0	1	3.4	1
			Clupeids	9	69.2	32	10	62.5	31	19	65.5	63
Pleuronectiformes	Pleuronectidae	*Limanda sp.*	Common dab	8	61.5	8	5	31.3	7	13	44.8	15
Pleuronectiformes	Scophthalmidae	*Scophthalmus maximus*	Turbot	1	7.7	2	0	0.0	0	1	3.4	2
Pleuronectiformes	Soleidae	*Solea solea*	Common sole	1	7.7	2	1	6.3	1	2	6.9	3
Pleuronectiformes	Pleuronectidae		Right eye flounders	2	15.4	3	1	6.3	1	3	10.3	4
			Flatfish	8	61.5	15	7	43.8	10	15	51.7	25
Salmoniformes	Salmonidae	*Salmo trutta*	Sea/Brown trout	4	30.8	5	1	6.3	1	5	17.2	6
Gadiformes	Merlucciidae	*Merluccius merluccius*	European hake	3	23.1	5	1	6.3	2	4	13.8	7
Gadiformes	Gadidae	*Pollachius pollachius*	European pollock	2	15.4	2	0	0.0	0	2	6.9	2
Gadiformes	Gadidae	*Melanogrammus aeglefinus*	Haddock	2	15.4	4	1	6.3	1	3	10.3	5
Gadiformes	Gadidae	*Merlangius merlangus*	Whiting	0	0.0	0	1	12.5	1	1	6.9	1
Gadiformes	Gadidae	*Gadus sp.*	Cod	1	7.7	1	0	0.0	0	1	3.4	1
Gadiformes	Gadidae		Codfishes	5	38.5	6	5	31.3	7	10	31.0	13
			Gadoids	5	38.5	13	6	37.5	9	11	37.9	22
Gasterosteiformes	Gasterosteidae	*Gasterosteus sp.*	Sticklebacks	2	15.4	3	1	6.3	1	3	10.3	4
Perciformes	Moronidae	*Dicentrarchus labrax*	European bass	1	7.7	1	0	0.0	0	1	3.4	1
Perciformes	Ammodytidae	*Hyperoplus lanceolatus*	Greater sand eel	3	23.1	3	1	6.3	1	4	13.8	4
Perciformes	Ammodytidae	*Ammodytes sp.*	Sand eel	6	46.2	8	0	0.0	0	6	20.7	8
Perciformes	Ammodytidae		Sand lance	2	15.4	3	1	6.3	1	3	10.3	4
			Ammdytidae	8	61.5	14	1	6.3	2	9	31.0	16
Perciformes	Gobiidae	*Pomatoschistus minutus*	Sand goby	2	15.4	2	2	12.5	2	4	13.8	4
Perciformes	Scombridae	*Scomber sombrus*	Atlantic mackerel	7	53.8	11	9	56.3	10	16	55.2	21

8.3.2 Prey detection

Of the samples where prey were detected, the mean number of taxa found was 4.2 ± 0.7 per sample (n = 29) with minimum and maximum values of 1 and 16 respectively. There was no significant difference (t = 1.58, p = 0.135) between the number of prey items detected in 2015 (mean = 5.3) and 2016 (mean = 3.1).

Clupeids were the most frequently detected prey group (FO of 65.5%, Table 4). Within this group, Atlantic herring (*Clupea harengus*) and European sprat (*Sprattus sprattus*) occurred most frequently (FO of 55.2% and 58.6%, respectively). No significant differences were found between years for clupeids (χ^2 = 0.030, p = 0.863), European sprat (χ^2 = 0.283, p = 0.595), or for Atlantic herring (χ^2 = 0.005, p = 0.945).

The Atlantic mackerel (Scomber scombrus) was the only species of mackerel detected (Table 8.4), with a total FO of 55.2% and no significant differences between the two sampling years (FO 53.8% in 2015, FO 56.3% in 2016; χ^2 = 0.005, p = 0.945).

Flatfish were recorded with a total FO of 51.7% (Table 8.4) and no significant difference between the two sampling years (61.5% in 2015, 43.8% in 2016; χ^2 = 0.287, p = 0.592). Most taxonomic assignments were at the family or genus levels. Righteye flounders (Pleuronectidae) were dominant and where MOTUs were assigned at the species level the common dab (*Limanda limanda*) was the most frequent species detected.

Gadoids (Gadidae) were recorded with a total FO of 37.9% and high similarity between sampling years (38.5% in 2015, 37.5% in 2016; χ^2 = 0.001, p = 0.972, Fishers exact test p = 0.976). Most MOTUs could only be assigned to the family level, but of those assigned to species cod (*Gadus* sp.), European pollock (*Pollachius pollachius*), whiting (*Merlangius merlangus*) and haddock (Melanogrammus aeglefinus) were detected at least once. Detections of these species varied between years but sample sizes were too small for statistical tests.

Sand lances had a total FO of 31%, with a similar proportion of greater sand eel (*Hyperoplus lanceolatus*; FO of 13.7%) and sand lances of the genus *Ammodytes* (FO of 20.7%). There were significantly more sand lances detected in 2015 (61.5%) in comparison to 2016 (6.3%; χ^2 = 5.394, p = 0.020; Fishers exact test p = 0.026).

Other prey species infrequently occurred and are detailed in Table 8.4 and Figure 8.4.

8.4 Discussion

The aim of this study was to analyse prey species composition in faecal samples from red-throated divers caught in the German Bight, using high throughput sequencing. In our data set we found an exclusively piscivorous diet, with no evidence of cephalopod or crustacean consumption and a similar prey spectrum between two consecutive sampling years.

8.4.1 Application of high throughput sequencing to study diver diets

The DNA metabarcoding methodologies utilised in this study have previously been applied in diet studies on other marine predators (DEAGLE et al. 2005, 2007; POMPANON et al. 2012). However, this study is the first application of this approach to analyse the diet of red-throated divers in the German Bight or elsewhere. Using reference sequences, we found high taxonomic coverage for both the COI and 16S barcode primers. Because of their commercial importance in the German Bight many fish species (e.g. Atlantic herring), alongside some cephalopod species, are well studied and the majority of these species appear in the Genbank database (DICKEY-COLLAS et al. 2010; ENGELHARD et al. 2013).

Sequences were clustered at 97% identity and represented consistent taxonomical units (MOTUs). Some prey species were represented by multiple MOTUs, suggesting that the clustering threshold could have been lower. However, a lower threshold would have increased the risk of clustering two closely related species into a single MOTU and thus reduced taxonomic discrimination. In practice, it is difficult to apply an 'average' threshold when diet is diverse and the prey are likely to have differing evolutionary rates. On balance, we deem the clustering threshold applied as appropriate and this method provided a good estimate of species richness with distinct taxonomic units.

We obtained sufficient sequencing data from 85% of the analysed faecal samples using universal primers. The species richness was higher in 2015 but individual variances may be due to sampling conditions, sample quality and amplification success. The use of a blocking probe proved to be of little advantage, with sufficient prey DNA amplified using both approaches (Figure 8.3). The use of a blocking probe reduced the amplification of predator DNA but also amplification success in general since the output of prey-positive samples was higher when the blocking probe was omitted.

The detection rate of prey species can be biased by the method applied. For example, Tollit et al. (2009) found some prey (Ammodytidae, Cottidae and Gadidae) were more reliably detected with morphological tools, whereas other prey (Salmonidae, Pleuronectidae, Elasmobranchii and cephalopods) were only detected with molecular tools. However, the overall results did not dramatically differ. In general molecular methods have been shown to identify more trophic links (number of taxa identified) with higher rates of taxonomic discrimination in comparison to morphology (e.g. SOININEN et al. 2009; ALONSO et al. 2014; BERRY et al. 2015; WAAP et al. 2017). Using molecular methods, we found a similar prey composition to conventional morphological methods applied in previous studies on red-throated diver diet. Using faecal samples coupled with DNA metabarcoding is now an established non-invasive approach for dietary studies. However, it is debatable whether or not this method can provide quantitative (read number) in addition to qualitative (presence and absence) estimates of diet (DEAGLE & TOLLIT 2007; POMPANON et al. 2012; DEAGLE et al. 2013, 2019). In this study we applied a conservative approach of using only qualitative data. However, if quantitative data are required we recommend combining DNA metabarcoding and morphological methodologies, where the latter can provide quantitative information as in ALONSO et al. (2014) and WAAP et al. (2017).

A faecal sample, for most species, will represent an individual's most recent meals. Other methods, including fatty acid composition and stable isotope analyses, can provide information over a longer time frame (MEIER et al. 2017). Although our sample size is small, samples were collected from birds caught in two consecutive years at dispersed intervals encompassing late winter and spring (February – April); when red-throated diver abundance is highest in the German Bight. Thus, this dataset provides dietary information from a time period when this area is particularly attractive to these birds. Wintering home ranges of red-throated divers can cover several connected sites, including sites outside the German Bight, such as the Baltic Sea (see chapter 3). The German Bight also represents an important staging area in spring when some birds have already started migration (GARTHE et al. 2015) and the availability of suitable prey types is probably one of the main determinants of habitat quality for these birds. In this context the time frame over which a faecal sample provides dietary information helps to reflect the situation in the particular area of interest for this study.

8.4.2 Fish availability in the German Bight, red-throated diver diet and comparison to previous studies

Potential prey availability is an important factor affecting habitat choice and diet selection. We searched the species factsheets (ICES 2006a; b), reports and publications (ICES & ADVISORY COMMITTEE 2008; ICES 2011; DFS 2016; ICES 2016, 2017a; b, 2018a) to compare fish distribution (a proxy for potential prey availability) with the diet of red-throated divers in our study in addition to previous studies. In our dataset red-throated divers consumed a wide range of fish prey species consisting of both a pelagic and a benthic component. We found mainly clupeids, mackerels, flatfish, gadoids and sand lances in the diet of red-throated divers but no clear dominance of a single species or species group could be identified. A similarly wide, although slightly different range of prey species was found in previous studies on red-throated diver diet. For example, MADSEN (1957) found a broad prey spectrum but the majority of analysed birds (82%) fed exclusively on cod, gobies, sticklebacks and herring with varying intensities. GUSE et al. (2009) found 11 species from 9 families with clupeids, zander, European smelt, ruffe, lesser sandeel, three spined stickleback and common goby being dominant species. Similarly, DURINCK et al. (1994a) identified clupeids and gadoids as the most frequent prey items.

Clupeids, specifically sprat and herring occurred most frequently in both sampling years of our study. These species are typically high in lipid content and energy density (PEDERSEN & HISLOP 2001; BALL et al. 2007). Sprat and juvenile herring are also two of the most abundant pelagic species in the German Bight in spring (ICES 2006a; b), which coincides with our sampling period. The size of available prey fish is also important for prey selection. In general, herring occurs in the North Sea with a size of 20-30 cm but in our sampling period smaller (juvenile) herring with a size < 20 cm are the most abundant and widely distributed in the German Bight and the Kattegat (ICES 2006a; TRUEMAN et al. 2017). Sprat is a pelagic species abundant in frontal areas of the North Sea with a size of < 16 cm (KANSTINGER & PECK 2009). We also found European sardine (*Sardina pilchardus*) and European anchovy (*Engraulis encrasicolus*) in the diver diet but less frequently, which is consistent with the distribution of both these clupeid species. They originate from the Mediterranean Sea (MOTOS et al. 1996) and since 2003 are expanding into the North Sea (KANSTINGER & PECK 2009). Like sprat, sardine occurs in frontal areas whereas anchovy is primarily found in near-shore areas. The distribution of clupeids is in good agreement with red-throated diver distribution, which appear to be attracted by frontal zones (SKOV & PRINS 2001; GOYERT et al.

2016; HEINÄNEN et al. unpublished data). Hence these areas provide a source of energetically valuable species for red-throated divers. The high detection rate of clupeids is in line with two earlier studies on red-throated diver diet and reinforces their importance as red-throated diver prey (DURINCK et al. 1994a; GUSE et al. 2009).

Atlantic mackerel is widespread throughout the North Sea and is one of the most commonly exploited species (ICES 2011, 2016, 2017b). Due to its high energetic value, mackerel is an attractive fish for seabirds (MONTEVECCHI et al. 1984, 1988; GARTHE et al. 2014). Overfishing triggered a population collapse in the North Sea in the 1970s but since 2000 the stock has increasing again (ICES 2011; JANSEN et al. 2012b; a, 2015; JANSEN & GISLASON 2013; JANSEN 2014). These changes in mackerel availability may explain why both MADSEN (1957) and the current study detected mackerel in the diet, while DURINCK et al. (1994a) did not. Mackerel appeared in our samples in considerable numbers indicating that it may now be a more important prey than previously thought.

Most flatfish were identified to family level, but of those identified to species level, common dab was the most common in both years. Flatfish have been recorded in low numbers in red-throated diver diet (MADSEN 1957; DURINCK et al. 1994a; GUSE et al. 2009), possibly due to their wide-bodied shape making adult flatfish an unfavourable prey item (REIMCHEN & DOUGLAS 1984; GUSE et al. 2009). Dietary studies in the adjacent Wadden Sea have shown that juvenile flatfish are selected as important food items by other water birds such as benthic feeding cormorants (NEHLS & GIENAPP 1997). The Wadden Sea and adjacent waters are an important nursery ground for several flatfish species (DFS 2016) and juvenile common dab is highly abundant in spring within the German Bight over a wide depth range (BEEK et al. 1989; BOLLE et al. 1994; CAMPOS et al. 1994; HUFNAGL et al. 2013; DFS 2016; ICES 2017a; b). Prey size cannot be deduced from metabarcoding but red-throated divers may be preying on juvenile flatfish. Although flatfish are considered to have a low energy content (BALL et al. 2007), the probable high encounter rate may explain the high detection rate in our samples.

Gadoids, particularly cod, were described by MADSEN (1957) as the most important prey group for red-throated divers in the Kattegat and Belt Sea. In the current study, gadoids were infrequently present in the diet. This is in line with findings of DURINCK et al. (1994a) from the south-western part of the Skagerrak. Juvenile gadoids (< 20 cm) are more likely than adults to be prey for red-throated divers. Recordings of this size class of gadoids are mostly restricted to the eastern inshore water of the Skagerrak and Kattegat, with low abundances in the German Bight (MUNK et al. 1999; MUNK 2014; ANDRÉ et al. 2016). Thus, gadoids may be a favoured prey item but low availability at the study site limits feeding on these species.

Sand lances are an important prey for seabirds in general, particularly in the North Sea (HARRIS & WANLESS 1991; MENDEL et al. 2008; ICES 2011, 2016; ENGELHARD et al. 2013). Sand lances appeared at a high frequency in 2015 but were less common in 2016 in our data set. This pattern is reflected in commercial catch rates for sand lances in the central and south-eastern North Sea ecoregion (Division 4b-c): average catch rates and a low recruitment in 2015 and low catch rates and high recruitment in 2016 (ICES 2018b; c). Previously, sand lances have been recorded at both high (GUSE et al. 2009) and low (MADSEN 1957; DURINCK et al. 1994a) frequencies in red-throated diver diet. These patterns suggest that the frequency of sand lances in the diet is determined by their availability.

Smelt (*Osmerus eperlanus*) was not detected in this study but has been highlighted as an important prey species for red-throated divers in the Baltic Sea (ŽYDELIS 2002; GUSE et al. 2009). Smelt occurs in parts of the Wadden Sea with low salinity and close to the coast. Here it forms dense spawning aggregations in estuaries and anadromous migrations in late winter and early spring (DFS 2016). The German Bight is further away from river mouths, the lack of smelt in our dataset could probably be explained by the low abundance of this species here.

Sea trout (*Salmo trutta*), European hake (*Merluccius merluccius*), sticklebacks (*Gasterosteus* sp.), European bass (*Dicentrarchus labrax*) and sand goby (*Pomatoschistus minutus*) were recorded in our dataset at low frequencies. These species are widely distributed in the North Sea with varying densities. Some, such as gobies, are known to be important prey items for other marine predators (HAELTERS et al. 2012; MÉHEUST et al. 2015; ANDREASEN et al. 2017) and were previously recorded as prey items of red-throated divers (MADSEN 1957; DURINCK et al. 1994a; GUSE et al. 2009). Sticklebacks were frequently found in all previous studies. However, the current study suggests that these species are of low importance for red-throated divers in the German Bight.

In contrast to our study, GUSE et al. (2009) found zander as one of the most important prey items of red-throated divers wintering in the Baltic Sea. This fish species prefers freshwater or brackish habitats, and therefore is almost absent in the saline waters of the German Bight.

Non-fish prey such as insects, polychaetes, molluscs or crustaceans were detected in small amounts in all previous studies. Cephalopods were detected in a single previous study (DURINCK et al. 1994a). We found no evidence that non-fish prey were consumed by red-throated divers in the German Bight and thus our results reinforce previous conclusions that these taxa are not an important part of the diet.

In summary, prey species of red-throated divers identified in this study occur in the study area as both adult (e.g., clupeids, sand lances) and juvenile fish (e.g., gadoids, flatfish, mackerels). Thus the area seems to be a good foraging ground for red-throated divers. There is an overlap between the prey fish of red-throated divers and commercial fish species, like herring and mackerel (ICES 2011, 2016, 2017a). This overlap increases the risk of gill-net mortality, which is a conservation issue in other regions such as the Baltic Sea. In the German Bight, there is a lower potential for such conflicts because trawls are more commonly used to fish as opposed to gill-nets. The oceanographic conditions (sea surface temperature (SST), salinity and chlorophyll a, NAO) were similar between the two sampling years and no important changes in prey community can be expected within such short timeframe, with the exception of the observed fluctuations in sand lance abundance. For this prey group, detections in the diet and reported catch rates (ICES 2018b; c) showed a similar trend. Reasons for this are unclear but sand lance productivity in the North Sea is known to fluctuate. Such fluctuations depend on a combination of several regulating factors including fishing, climate effects, density dependence and food availability (WRIGHT et al. 2017; LINDEGREN et al. 2018). Although we present data from only two sampling years, the consistent pattern of prey species suggests a relatively stable diet that is likely to reflect the availability of these fish species in the study area. There are long-term increases in sea temperature and species usually associated with warmer waters are expanding their range to include the North Sea. Such species include European sardine and European anchovy (KANSTINGER & PECK 2009). The diet of red-throated divers in the German Bight includes these expanding species and also recovering species like mackerel, indicating that the dietary data may reflect changes in the fish community and some flexibility in prey consumption. However, a larger sample size across a broader temporal scale is required to fully support this conclusion.

The samples analysed here were collected in late winter and early spring, shortly before the migration to the breeding grounds. For non-breeding red-throated divers little is known about energy expenditure, resource partitioning and energy requirements during wintering, staging and migration. SCHMUTZ (2014) suggested that marine conditions could affect adult survival of red-throated divers with indications of a higher risk of mortality during the non-breeding season. Red-throated divers are medium sized birds with weight varying between 1400 g–2000 g (own observations), and with high wing loading (STORER 1958; LOVVORN & JONES 1994). Despite this, these birds often need to cover long distances to their breeding grounds (www.divertracking.com; MCCLOSKEY et al. 2018), with some individuals travelling as far as 850 km or 1300 km in a single flight (see chapter 3). WEBER & HOUSTON (1997) showed the importance of resting sites for refuelling. Consequently, migration represents periods of high energetic demand and adequate energy reserves seem to be essential. If prey of rich calorific value becomes unavailable due to displacement effects, red-throated divers may fail to balance their energy budgets. In general, these birds winter in temperate marine waters with low ambient temperatures, consequently reliable and sufficient energy intake is likely to be a necessity and influences prey consumption.

Conclusion

Overall, our results demonstrate that the use of faecal samples coupled with DNA metabarcoding and NGS is a valid and appropriate approach to non-invasively study the diet composition of red-throated divers.

Our results provide important dietary data for red-throated divers in the German Bight, which is needed for a good understanding of their habitat preferences during wintering and spring staging. This baseline information can be used to evaluate changes associated with human developments in the offshore environment, changes in oceanography, or population declines. The results for the German Bight complement other dietary studies on red-throated divers that show a somewhat different composition of fish species, reflecting regional differences in fish fauna. Among a generalised prey spectrum, bentho-pelagic schooling fish seem to dominate the diet of red-throated divers (CRAMP & SIMMONS 2004; GUSE et al. 2009). In our study five species groups are concluded to be major dietary components for red-throated divers in the German Bight. We found clupeids, mackerels, flatfish, and gadoids occurring in substantial proportions in both sampling years, and the frequency of sand lances varied between the two sampling years. Hence the diet consistently includes some common species with a high nutritional value (HISLOP et al. 1991; BALL et al. 2007), indicating the importance of these fish groups as prey items for red-throated divers in the German Bight. Red-throated divers stage in a specific habitat, mostly influenced by frontal zones in coastal areas in the German Bight (SKOV & PRINS 2001; HEINÄNEN et al. unpublished data). The preferred feeding at frontal zones may also explain the higher abundance of pelagic fish among the red-throated diver prey, where these species aggregate, while demersal species depend mainly on suitable sediments. Considering the effects of disturbance, displacement or barrier effects arising from anthropogenic activities such as ship traffic and offshore wind farms (MENDEL et al. 2019a), the broad prey spectrum that we found could indicate resilience of red-throated divers against changes in community composition of available fish or resilience against displacement from suitable habitat. However, if alternative sites of high-quality habitat are not sufficiently available, displacement may result in a decreased energy intake and subsequently poorer body condition. Thus, altered food accessibility as a result of disturbance or displacement could have severe effects on red-throated divers. In general, the availability of some prey species may explain, at least to some extent, the preference of this area as wintering and staging habitat. Further studies could aim to discern whether the birds use this area because of a high abundance of suitable and energy rich prey or if they simply feed on the most abundant prey.

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9 BLOOD PARASITES OF RED-THROATED DIVERS WINTERING IN THE GERMAN BIGHT

9.1 Introduction

This section contains additional analyses from red-throated diver blood samples testing for infection with blood parasites. Infection with blood parasites can be considered as an additional pressure for wintering divers and add to any disturbance effect from offshore wind farms or shipping traffic.

Although birds in general are frequently infected with a number of intracellular blood parasites, including Haemosporidia of the genera *Plasmodium*, *Haemoproteus* and *Leucocytozoon*, seabirds mostly have low levels of blood parasite infections, with only one third of the species showing infections by hematozoa (Quillfeldt et al. 2011). The most common hematozoa found in seabirds were avian malaria of the genera *Haemoproteus* and *Plasmodium*, each showing infections for 13% of the species studied (Quillfeldt et al. 2011). *Plasmodium*, *Haemoproteus* and *Leucocytozoon* are vector-borne blood parasites that cause malaria-like disease in birds (Scheuerlein & Ricklefs 2004; Wood et al. 2007; Jenkins & Owens 2011).

Parasitic infections can have a negative impact on the body condition of their hosts and lead to reduced expression of sexual ornaments (Barbosa & Palacios 2009) and decreased reproductive success (Allander & Bennett 1994; Martínez-Abraín et al. 2004; Dunning 2008). Blood parasites can exert important selection pressure on their hosts through direct or indirect effects on survival (Sorci & Møller 1997; Hõrak et al. 2001; Sol et al. 2003; Møller & Nielsen 2007; del Cerro et al. 2010). Many hypotheses exist about why these blood parasites are not that common in seabirds but one hypothesis proposed to explain differences in blood parasite prevalence is the vector-density hypothesis (Bennett et al. 1992; Tella et al. 1996; Piersma 1997; Sol et al. 2000; Jovani et al. 2001; Martínez-Abraín & Urios 2002; Fokidis et al. 2008). This hypothesis suggests that bird species associated with inland environments are more exposed to the malaria-like parasites as land habitats provide more suitable breeding areas for vectors (Piersma 1997; Sol et al. 2000; Mendes et al. 2005) whereas marine and coastal habitats are typically relatively free of parasite vectors (Piersma 1997; Mendes et al. 2005). In Antarctic and Arctic regions blood parasites were absent from seabirds tested so far (Quillfeldt et al. 2011) though the vectors are present as *Plasmodium* is transferred by mosquitos and sand flies and *Hemoproteus* by louse flies and biting midges and some of vectors are quite common at least in Arctic regions.

So far infections of *Plasmodium* as well as *Leucocytozoon* were found in two individuals of the family Gavidae (*Gavia immer*) in the United States (Lindsay unpublished data; Martinsen et al. 2017; MalAvi database) but nothing is known about infections with blood parasites in red-throated divers or divers in general in Europe. The eastern German Bight presents an internationally important habitat for red-throated divers in winter and spring but is also characterised by an increasing offshore wind farm development (Dierschke et al. 2012; Garthe et al. 2015; Schwemmer et al. 2019). Red-throated divers are known to show a negative behavioural response towards offshore wind farms (see chapter 6). Functional habitat loss and displacement into less suitable foraging habitats might result in an increased stress level or poorer nutritional condition. An infection with parasites in general and blood parasites in particular could cause a downturn or deterioration of the physical condition of a host. These effects might also be relevant for red-throated divers in the German Bight. In this part of the project we aim to test an appropriate sample size of blood samples taken from red-throated divers in the German Bight to reveal presence/absence of the blood parasites *Plasmodium*, *Haemoproteus* and *Leucocytozoon* in these birds. A high infection rate of red-throated divers could mean an increased risk to suffer from an increased stress level and a potential higher mortality rate. The results thus contribute to a comprehensive overview of potential threats for red-throated divers and hence to assess the impacts of different pressures to that species.

9.2 Methods

We used blood samples from 33 individual red-throated divers to test for a *Haemoproteus, Plasmodium* or *Leucocytozoon* infection.

We used molecular methods to test blood samples taken from red-throated divers captured in the German Bight and stored on FTA cards. In the laboratory, a 2 x 2 mm piece of the dried blood sample was cut out of the FTA card and the DNA was isolated using an ammonium acetate protocol (adapted from Martinez et al.(2015)). The final DNA concentration of the sample was determined with a NanoDrop2000c UV-Vis spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA). We stored the extracted DNA frozen until further analysis. We applied polymerase chain reaction (PCR) methods to screen the samples for presence/absence of blood parasites. We used a nested PCR (HELLGREN et al. 2004) which is a two-step PCR and enables simultaneous typing of species from the three most common avian blood parasite genera (*Haemoproteus*, *Plasmodium*, and *Leucocytozoon*). In a first step the primers HaemNFI and HaemNR3 were used to generally amplify DNA from all three blood parasites. In a second step the PCR products from the first step were used as a template,the primers HaemF–HaemR2 were used to specifically amplify DNA from the blood parasites *Haemoproteus/Plasmodium* and HaemFL-HaemR2L were used to amplify DNA from the blood parasite *Leucocytozoon*.

We followed HELLGREN et al. (2004) and used for the three PCR reactions each a 25 µl reaction volume that contained 1 x Dream Taq PCR Master Mix ready to use solution (Thermo Fisher Scientific, Germany), 4 µl of template (extracted DNA in the initial step and PCR product in the parasite specific step), 0.6 µM of each primer and sterile water. Cycling conditions included an incubation step at 94°C for 3 min, a final extension at 72 °C for 10 min and a thermal profile of 30 sec at 94 °C, 30 sec at 50 °C, and 45 sec at 72 °C for 20 cycles in the initial PCR and for 35 cycles in the parasite specific PCR. A negative and a positive control were included into each PCR.

Table 9.1 Primer sequences applied to amplify DNA of blood parasites Haemoproteus/Plasmodium/Leucocytozoon.

Primer	Primer sequence	Target DNA
HaemNFI	5´-CATATATTAAGAGAAITATGGAG-3´	*Haemoproteus/Plasmodium/Leucocytozoon*
HaemNR3	5´--ATAGAAAGATAAGAAATACCATTC-3´	*Haemoproteus/Plasmodium/Leucocytozoon*
HaemF	5´-ATGGTGCTTTCGATATATGCATG-3´	*Haemoproteus/Plasmodium*
HaemR2	5´-GCATTATCTGGATGTGATAATGGT-3´	*Haemoproteus/Plasmodium*
HaemFL	5´-ATGGTGTTTTAGATACTTACATT-3´	*Leucocytozoon*
HaemR2L	5´CATTATCTGGATGAGATAATGGIGC-3´	*Leucocytozoon*

PCR amplicons were visualised using QIAxcel Advanced (Qiagen, Switzerland) high-resolution capillary gel electrophoresis. Samples rendering a clear peak during gel electrophoresis were bi-directional Sanger sequenced by Microsynth-Seqlab (Sequence Laboratories Goettingen GmbH, Germany). Sequencing results were matched with existing data available in the avian haemosporidian parasite database (MalAvi).

Sequences were aligned to sequences deposited in the MalAvi (http://mbio-serv2.mbioekol.lu.se/Malavi/blast.html) and GenBank nucleotide databases using Blast (https://blast.ncbi.nlm.nih.gov). The best MalAvi lineage and the GenBank hit with the highest similarity (99–100%) were downloaded. The downloaded sequences, the consensus sequences from our own samples, and a sequence from Babesia (GenBank accession no. KC754965, QUILLFELDT et al. 2014) as the outgroup were aligned in BIOEDIT using the ClustalW multiple alignment tool. A phylogenetic tree was inferred with the reference sequences and outgroup. The final alignment included 10 nucleotide sequences (one outgroup, four sequences from this study and five reference sequences). The best suitable nucleotide substitution model (HKY) for our alignment was determined with jModelTest 2.1.10 using Bayesian Information Criterion scores. A Bayesian phylogenetic tree was generated with BEAST v1.8.4. Model parameters for this analysis were selected in BEAUTi v1.8.4 with the HKY substitution model, strict clock as clock type and a Yule speciation process as tree prior. The chain length for the Metropolis coupled Markov Chain (MCMC) was set to 25 Mio generations (burn-in 10%), and one tree was recorded every 1000 generations. Using Tracer v1.6, we verified the trace for convergence. We used TreeAnnotator in BEAST v1.8.4 to generate a maximum clade credibility tree (MCCT). Finally, FigTree v1.4.3 (RAMBAUT 2016) was used to visualise the final phylogenetic tree. Similarities between sample sequences were calculated in BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi).

9.3 Results

Three red-throated divers were tested positively for blood parasites of the genera *Leucocytozoon* (9.1%) and one for blood parasites of the genera *Plasmodium* (3.0%) and this individual showed a double infection for blood parasites of the genera *Plasmodium* and *Leucocytozoon* (Table 9.2).

Table 9.2 *List of positively tested red-throated divers for blood parasite infections, with ID (ARGOS-ID), parasite genera and identity match.*

ID (ARGOS ID)	Blood Parasite Genus	Closest Lineage	Similarity
146441	*Leucocytozoon*	CIAE02	100%
146445	*Leucocytozoon*	GAVIM01	99%
146449	*Leucocytozoon*	GAVIM01	99%
146441	*Plasmodium*	TURDUS1	99%

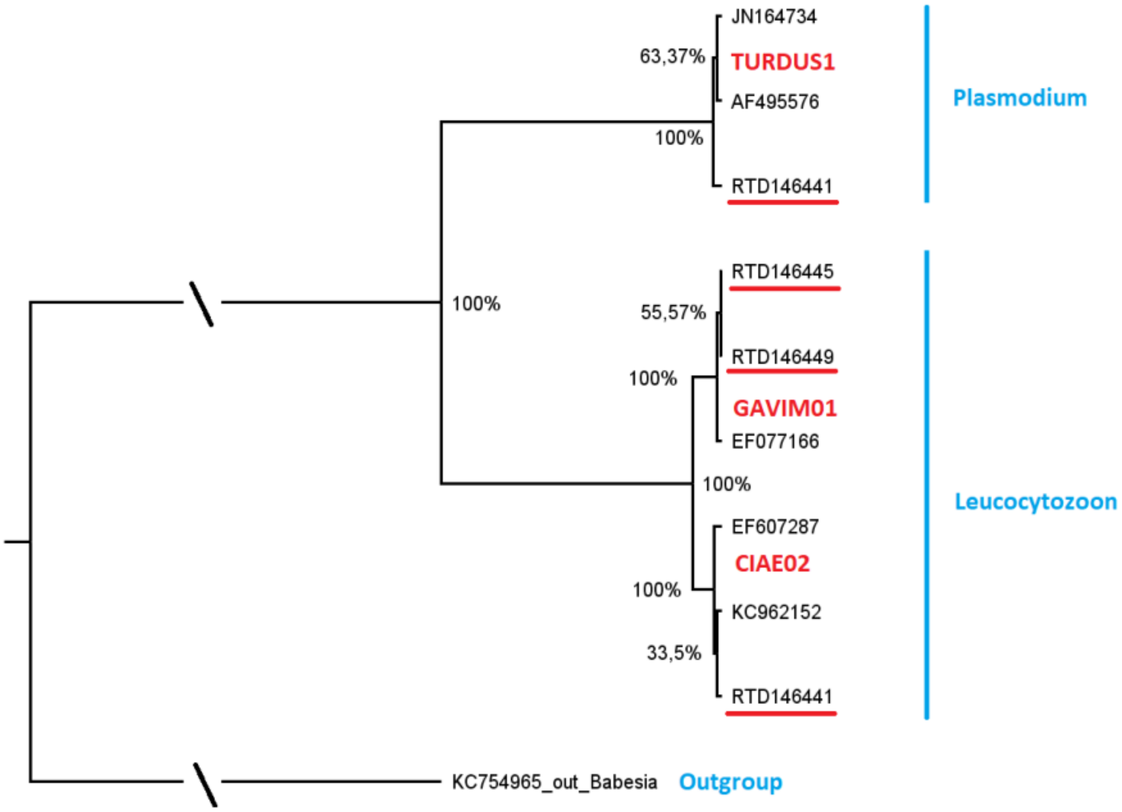

Figure 9.1 *Molecular phylogenetic analysis by Maximum Likelihood Bayesian analysis based on parasite DNA sequences. Posterior probabilities of the nodes are shown. Parasites from red-throated diver samples are given with bird IDs, and underlined red. Details of the reference sequences (not underlined), including blood parasite and host species identity and code and location, are given in Table 9.3. MalAvi lineage names are included in red letters, and genus names in cyan.*

Table 9.3 Reference sequences included in the molecular phylogenetic analysis.

Reference	Blood Parasite	MalAvi Lineage	Host and country
JN164734	*Plasmodium circumflexum*	TURDUS1	*Sylvia atricapilla* (Spain)
AF495576	*Plasmodium circumflexum*	TURDUS1	*Turdus philomelos* (Sweden)
KC962152	*Leucocytozoon sp.*	CIAE02	*Buteo buteo* (Turkey)
EF607287	*Leucocytozoon sp.*	CIAE02	*Circus aeruginosus* (Germany)
EF077166	*Leucocytozoon sp.*	GAVIM01	*Gavia immer* (North America)

9.4 Discussion

We found a positive blood parasite infection rate in tested red-throated divers for *Leucocyozoon* and *Plasmodium* with more individuals infected by *Leucocytozoon* (Table 9.2, Figure 9.1). These birds were captured in the eastern German Bight and can be assigned to the European breeding population including individuals from Greenland (BirdLife International 2019) and the NW European wintering population (Wetlands International 2018). According to the tracking data collected in this project (see chapter 3), breeding location of one of the infected divers was Norway (ARGOS-ID 146449). Breeding locations of the other two infected red-throated divers could not be identified due to early mortalities (ARGOS-ID 146441, ARGOS-ID 146445).

Infections with these avian malaria parasites are expected to have negative effects on host fitness as they occur intracellular and affect host metabolism (Marzal et al. 2008). We tested presence-absence but did not examine the degree of prevalence (i.e. the number of infected blood cells), due to the absence of blood smears. High prevalence of infected blood cells in particular have been shown to have long-term effects on reproductive success, condition and survival (Marzal et al. 2008).

Most studies on avian malaria were performed on songbirds so far and comparing these results the percentage of infected birds (9.1%) seems to be relatively low. However, when comparing the proportion of infected birds with results of other seabird studies on avian malaria, the infection rate is close to the mean value as described in Quillfeldt et al. (2011). Although we cannot determine the individual physical condition, we could show that red-throated divers can be infected by avian malaria. Five mortalities of 45 tagged red-throated divers occurred within two weeks and are likely related to bird handling (stress factor) and/or surgery and transmitter implantation. Of these five mortalities two birds were infected with blood parasites and two of the three infected red-throated divers died within two weeks after transmitter implantation. However, it remains unclear if these early mortalities are related to the infection with blood parasites as dead birds could not be recovered to analyse blood smears or organs for an increased prevalence.

The rate of infection in general presents important information when assessing the impacts and behavioural responses to environmental changes that are assumed to increase the stress level of a species. Red-throated divers wintering and staging in the eastern German Bight are exposed to several pressures, such as intense shipping (see chapter 6.6) or offshore wind farms (see chapter 6), which result in behavioural changes of impaired birds and potentially increase their stress level. When assessing the combined impacts of different pressures on red-throated divers, the potential risk of an infection with blood parasites and thus a potential lower ability to physically cope with environmental changes should be taken into account.

10 SYNTHESIS

10.1 Introduction and background

The red-throated diver (*Gavia stellata*) is a Holarctic breeding bird which spends the non-breeding period in marine coastal habitats of the Northern Hemisphere. The eastern part of the North Sea serves as an internationally important wintering and staging area of this strictly protected species in winter and also in spring with an abundance estimate of 48,000 individuals (SKOV et al. 1995). In the waters west of the Jutland peninsula from the island of Helgoland in the south to northern Denmark, highest numbers are reached in spring (March to May). A recent estimate for the German North Sea reached 22,000 individuals (SCHWEMMER et al. 2019). Here, especially the area west of the islands of Sylt and Amrum in the northeast of the German North Sea holds high diver densities in late winter and spring and has been classified as a main diver distribution area by German authorities (BUNDESMINISTERIUM FÜR UMWELT, NATURSCHUTZ UND REAKTORSICHERHEIT 2009). The area lies within a shallow shelf sea with the 40 m depth contour extending up to 200 km into the North Sea, and is strongly influenced by tidal motion (OTTO et al. 1990). It is characterised by a dynamic frontal zone between two main water masses, the North Sea water mass and the continental water mass which is influenced by discharges from the river Elbe (BECKER et al. 1992). Red-throated divers have been found to prefer the frontal zone between these two water masses (SKOV & PRINS 2001) and the overall distribution of divers in the North Sea indicates some prevalence for coastal and tidal mixing zones. While compared to other parts of the North Sea, the numbers of other fish-eating seabirds in the German Bight is rather low, but it is the most important part of the North Sea for red-throated divers.

The development of offshore wind farms (OWFs) is an important element towards expanding the share of renewable energy in Germany and elsewhere. However, this development aims not only to provide clean energy but needs to safeguard protected species and protected areas. Generally, the expansion of offshore wind energy shall aim to prevent and minimise possible impacts on the marine ecosystem. From the beginning of the offshore wind planning in Germany it has been clear that divers are one of the key species when it comes to assessing the potential impacts on the environment. From the European Seabirds at Sea (ESAS) boat surveys it was known that divers exhibit strong fleeing reactions from the approaching ship (BELLEBAUM et al. 2006). SCHWEMMER et al. (2011) later confirmed divers being among the most sensitive seabird species with regard to disturbance from shipping (2011).

The main wintering and staging areas of red-throated divers are located in relatively shallow coastal waters, which are also used for anthropogenic activities, especially shipping and fishing and recently also OWFs. In the north-eastern part of the German North Sea, today six OWFs are located, three single OWFs west of Sylt and a cluster of three OWFs north of Helgoland. Further OWFs are installed or are under construction in adjacent Danish waters which hold similar high diver densities. However, there are no recent survey data from this area available. In order to explore the responses of red-throated diver to OWFs in a core wintering and staging area, the German Bight was chosen for the DIVER project, where birds were tagged with satellite transmitters and additional digital aerial surveys were carried out (Figure 4.1).

When assessing the possible impacts of OWFs on divers prior to the installation of the first OWFs, the impacts could only be estimated from existing knowledge on diver sensitivity to other anthropogenic pressures. Based on observed diver fleeing distances from approaching ships, for EIA studies mostly conducted in the early 2000's, a complete displacement of divers from the OWF footprint plus a 2 km buffer had been taken as basic value for impact assessments and wind farm permitting. Outside this buffer zone no further reduction of diver numbers was assumed. This approach had initially been regarded as being precautionary, likely overestimating the numbers of displaced divers.

Studies published already prior to the start of the DIVER project confirmed that divers are very sensitive to disturbance and described a significant avoidance reaction to OWFs (e.g. PETERSEN et al. 2006, 2014; DEWAR 2011; DIERSCHKE et al. 2012). However, operational monitoring studies showed differing displacement effects, thus the wind farm effect (and its detectability) seemed to vary with the study area (WELCKER & NEHLS 2016) pointing at some site- or region-specific variation (LYONS et al. 2015). The reported avoidance distances ranged from statistically not detectable or little effects for the Dutch OWFs 'Princess Amalia' and 'Egmond aan Zee' (IMARES 2011, 2013) and no statistically detectable effects at 'Kentish Flats' OWF (REXSTAD & BUCKLAND 2012) to effects ranging beyond 5 km distance from OWFs for the Danish OWF 'Horns Rev 2' (PETERSEN et al. 2014). Little or no effects found in the mentioned studies are predominantly believed to be due to low diver abundances in the respective areas and therefore small sample size for statistical analyses (as true for the Netherlands) or due to the limited geographical range of monitoring undertaken by using ship-based surveys, as for 'Kentish Flats' OWF. Operational monitoring studies based on boat surveys generally indicated much smaller displacement ranges for red-throated divers and partly even suggested habituation effects (e.g. PERCIVAL 2013), which indicates that the spatial extent of boat survey data are not capable to detect the full effect of OWFs on red-throated divers. This might also be due to the large fleeing distance of divers from the approaching survey vessel which affects the accuracy of diver localisations from boat surveys. In case of the first study describing significant effects of reduced densities up to more than 10 km distance to the OWF (PETERSEN et al. 2014), it could not completely be disentangled if the described significant changes in diver distribution were solely an effect of the OWFs or if other reasons interfered with the wind farm effect. Effects found in distances up to 5-6 km from the OWF in this study were regarded as displacement effect from the OWF (PETERSEN et al. 2014).

The range of effects described by different monitoring studies at operational OWFs differed markedly and some studies indicated that the assumed 2 km buffer range of complete displacement of divers from OWFs as applied in EIA studies likely underestimates the actual number of birds being displaced (e.g. PETERSEN et al. 2014). These uncertainties regarding the magnitude of the displacement effect, and relevant knowledge gaps regarding diver ecology hindered a profound assessment of the cumulative effects of several OWFs in the German North Sea to red-throated divers.

10.2 The DIVER project – questions raised and study approach

The DIVER project was initiated to fill relevant knowledge gaps and to evaluate the impacts of OWFs to red-throated divers by studying the seasonal movements and habitat use of birds tagged with implantable satellite transmitters in the main diver distribution area in the German North

Sea. Within the three late winter/spring seasons 2015, 2016 and 2017 in total 45 red-throated divers were captured in the German EEZ in the main diver distribution area north of Helgoland and west of the islands of Sylt and Amrum (Figure 4.1). Transmitters were programmed aiming to last long enough to cover a full annual cycle and second winter season to gain a high sample size to answer questions related to diver wintering and spring staging areas. The analysis of tracking data in the core study area was supplemented by analyses of digital aerial survey data (in total four aerial surveys in spring seasons of 2016 and 2017) and studying diver winter diet from faecal samples by using state of the art genetic methods.

The following questions were in focus of the DIVER study:

- How do red-throated divers move within their wintering area? How big are the areas used? Do divers use one or more distinct core wintering areas? How long do they stay in the different areas?
- How are different known resting areas linked to each other through bird movements?
- What are the breeding areas of red-throated divers using the core study area in the German North Sea in late winter and spring?
- How faithful are red-throated divers in using different areas during their annual cycle? Do birds stick to the same places year after year or do birds show flexibility in the use of areas?
- How can the habitat use of red-throated divers in the core study area be characterised? What is the effect of OWFs on diver distribution in that area? What avoidance distances can be described from tracking and aerial survey data? How do results of two different and independent methods – satellite tracking data and digital aerial survey data – compare when answering these questions?
- Does the avoidance distance to OWFs change with weather (i.e. visibility) conditions or with day- or night-time?
- Are there any other pressures identified which significantly add to the impacts of OWFs to red-throated divers in the core study area, e.g. ship traffic?
- What are the prey fish species of red-throated divers wintering in the core study area? Are the birds relying on specific fish species or are they more generalist foragers? Can habitat restrictions be deduced from prey species found in red-throated diver diet?

10.3 Main results of the DIVER study

The study approach and chosen sample size of the DIVER study were suitable for answering the key questions raised at the start of the project. In the following, the main results of the DIVER study are summarised:

Movements and origin of red-throated divers captured in the German North Sea

- The origin of red-throated divers captured in the eastern German Bight in late winter and spring spans from Western Greenland to Taimyr Peninsula in Siberia. The eastern German Bight serves as wintering and staging area for divers from at least four different breeding regions: Greenland (West- and East-Greenland), Scandinavia (Norway), Svalbard, and Northern Russia (European and Siberian part).

- Diver annual movement patterns show a high variability among individuals regarding both small- and large-scale movements, as well as on timing of migration and number of staging areas.
- Movements during winter varied between individuals, ranging from birds staying within a relatively small area for the entire wintering period, others almost continuously moving between different wintering sites. Home range analysis using dynamic Brownian bridge model approach provided home range sizes for 95% UD (utilisation distribution) ranging from 3,033 km² to 20,783 km² and 50% UD ranging from 218 km² to 3,828 km² for the entire range of winter distribution covered by tracking data.
- Individual winter home ranges included different areas in the eastern German Bight, but also areas in the Baltic Sea (Kiel Bight), the Kattegat, the southern German Bight (east Frisian coast), the Southern Bight including the English Channel (Dutch, Belgium and French coast, the British east coast with the Thames Estuary and the greater Wash area), and Liverpool Bay in the Irish Sea.
- Tagged red-throated divers showed a high fidelity to breeding locations. With regard to migration routes and the use of staging and wintering areas the fidelity in using those areas in two consecutive years was scale-dependent. At large scale red-throated divers were found being very faithful to their general migration routes, moulting, staging and wintering areas. At smaller scale, however, birds were less faithful and e.g. core winter home ranges (50% UD areas) often differed between wintering seasons.
- Red-throated divers were found initiating migration (spring and autumn) under no wind or tail wind conditions and avoiding headwinds. Other meteorological parameters than those related to wind conditions (speed and direction), such as precipitation, atmospheric pressure or cloud cover showed no significant relationship to spring and autumn migration.

Red-throated diver habitat use and effects of OWFs on diver distribution

- Aerial survey data showed red-throated diver densities peaking at about 25 m water depth and in areas of higher salinity. Based on the model predictions the total number of divers in the study area covered by aerial surveys has been estimated between 6,300 (May 2017 survey) and 24,100 individuals (April 2016 survey).
- Divers were found in strongly reduced numbers around the OWFs and were almost absent within OWF areas and 5 km around. The displacement effect gradually decreased with distance from OWFs, but a significant effect could be detected up to 10–15 km away. Telemetry and aerial surveys provided similar results.
- Suitable red-throated diver habitat could partly be described by salinity, water depth and chlorophyll (the latter for survey data only), although overall, environmental parameters explained relatively little variation in the data.
- Diver core winter home range areas (50% UD) often were located in between OWF areas reflecting the strong avoidance response.
- Diver relocation distances significantly decreased with increasing distance from OWFs. Red-throated divers thus moved longer distances in the proximity of OWFs as compared to further away.
- Weather conditions in terms of visibility and day-/night-time affected distances of tracking positions to OWFs. During weather conditions indicating poor visibility (e.g. high wind speeds and high precipitation) red-throated divers were located closer to OWFs than during good

visibility. Divers kept longer distances to OWFs at night, when wind turbines are illuminated with bright red aviation lights and white navigation lights.

Effects of shipping traffic on red-throated diver distribution and movements

- Data from the automatic identification system of ships (AIS) were intersected with red-throated diver satellite tracking and digital aerial survey data and allowed detailed spatial and temporal analyses. During the study period, shipping traffic was present throughout the main distribution area of divers and only in small areas shipping traffic was present on less than 20% of the days. Shipping traffic was dominated by fishing vessels and cargo ships, but also wind farm-related ships were frequently recorded.
- Red-throated divers were more abundant in areas with no or little concurrent shipping traffic.
- Analysis of aerial survey data revealed strong effects of ship speed on divers: after disturbance with high-speed vessels resettlement of the disturbed area was slow, after disturbance with slow- or medium-speed vessels faster resettlement has been observed.
- Data from satellite tracking suggest that large relocation distances of red-throated divers are related to disturbance by ships which often trigger birds to take flight.

Diet of red-throated divers captured at their wintering area in the German North Sea

- Prey species composition of red-throated divers wintering in the north-eastern German North Sea was studied by analysing faecal samples from 34 birds caught for transmitter deployment by using state of the art genetic method, DNA metabarcoding.
- We found a broad prey spectrum with 19 fish taxa from 13 families dominated by five groups: clupeids, mackerels, gadoids, flatfish and sand lances with clupeids being the most frequently detected prey.
- Our results characterise red-throated divers as generalist opportunistic feeders in the eastern German Bight, but pelagic schooling fish which aggregate at frontal zones and have a high energetic value seem to be favoured.
- While diver distribution is restricted to coastal mixing waters, the main fish species consumed by divers are widely distributed in the North Sea. However, most of the main prey species found in red-throated diver diet use the Wadden Sea or coastal mixing waters as nursery areas.

Blood parasites of red-throated captured at their wintering area in the German North Sea

- Blood samples of captured red-throated divers indicated an infection rate of 9.1% (three out of 33 individuals) with the Malaria-like blood parasites *Leucocytozoon* (three individuals, 9.1%) and *Plasmodium* (one individual double infected, 3.0%). Two of the three infected birds died within the first two weeks after transmitter deployment indicating infected birds possibly being less resistant to additional stressors, in this case capture and surgery.

10.4 Discussion

The DIVER study shows that the eastern German Bight is visited by birds from a wide breeding range. The variety of different breeding areas goes along with a variety of different migration patterns found, different use of staging areas and differences in timing between tagged individuals. The eastern German Bight serves different functions for red-throated divers. Some individuals were observed spending the entire wintering period in the area; others used the area as one wintering area among others in the course of one winter, indicating a patchy habitat use in space and time. Again others used the area only as short stop-over while on migration between other staging areas, and others used the area also for moult in autumn. The origin of divers caught in the eastern German Bight was mostly of arctic breeding grounds from Greenland, Svalbard and Siberia, from closer distances only birds from Norway were recorded, leaving breeding grounds from Iceland, Scotland, Sweden and Finland without a record. The migration patterns of red-throated diver thus resembles a classic leap-frog migration where birds from arctic breeding origins winter further south than those from temperate origins (ALERSTAM & HÖGSTEDT 1980). While this might be the case for Icelandic and Scottish birds, it seems to be unlikely for Scandinavian birds, because their more northern wintering areas would be located in the Baltic Sea, which at least until recent times is subject to regular freezing in the winter likely forcing birds at least partly to move to the North Sea.

The high mobility of birds, the wide range of breeding areas identified, the different movement patterns and timing found between individuals in this study suggest that a large sample size is needed to adequately cover the behavioural variation expressed by this species. The time of bird captures in late winter and spring may have played an important role in what breeding populations and annual movement patterns were mostly sampled. Other well-known breeding areas, such as Finland, were not represented in the dataset. The data suggest that there is a high turn-over rate of divers using the eastern German Bight, suggesting that the published abundance estimates for different sub-areas only reflect numbers being concurrently present in the area. The actual number of individuals using the area between autumn and spring, and therefore being exposed to pressures in the area, is expected to be considerably higher.

Winter home ranges of red-throated divers captured in the eastern German Bight generally were large, but differed markedly between individuals. Some individual home ranges overlapped almost completely with the wintering area as described from the distribution obtained from aerial surveys. Core utilisation areas showed almost no overlap with OWF footprints, reflecting the almost complete absence of tracking data points within OWF footprints. The high mobility of divers could be interpreted as continuous search for better habitats as a consequence of birds being displaced into suboptimal habitats due to wind drift, water currents and different anthropogenic pressures (DIERSCHKE et al. 2017).

Red-throated divers were found being highly faithful to their general wintering areas, but showing flexibility at small scale as core home ranges often showed only little or no overlap between different wintering seasons. This indicates that the species shows some flexibility when choosing specific wintering sites. This can be explained by diver reliance on mobile prey in dynamic marine habitats which require continuous adaption of birds to the given environmental conditions. As long as sufficient suitable habitats are available in an area, red-throated divers should be able to find and exploit those.

The diet analysis of red-throated divers wintering in the eastern German Bight (see chapter 8 of this report) indicates that red-throated divers are generalist opportunistic piscivores with no indication of reliance on a specific prey species in the area. However, the species appears to prefer pelagic schooling fish, namely clupeids, which aggregate at frontal zones and have a high energetic value. The clupeids sprat and (young) herring are among the most abundant and widely distributed pelagic fish species in the German Bight in spring, the time of red-throated diver main abundance in the area. However, it has to be noted that the distribution of the main prey species greatly extends the diver distribution area (KNIJN et al. 1993; ICES 2006a; b) while nursery grounds of main prey species are mainly related to coastal waters and mixing zones (PETITGAS 2010).

From distribution and food choice it is thus concluded that divers are generally adapted for coastal frontal zones habitats as compared to other seabirds with similar foraging behaviour such as auks, which predominantly occur in the high sea. As divers wintering areas extend up to 100 km offshore the environmental conditions are similar to those in the high sea and a coastal occurrence does not mean more benign conditions. The obvious difference between the coastal frontal zones and the high seas is a higher turbidity in coastal areas and it might be that divers are better adapted to turbid conditions due their foraging behaviour, but little is known about this so far. For a better understanding of the distribution of divers it would thus be useful to use advanced GPS- and activity-logging techniques to relate their foraging behaviour to specific hydrographic conditions. Our study revealed a high sensitivity of red-throated divers to OWFs. Both datasets analysed, digital aerial survey data and tracking data, show the species clearly avoiding OWF areas and the adjacent marine areas. The effects of OWFs were significant up to a distance of more than 10 km which exceeds by far most effect ranges described in literature on divers published prior to this study. Other recent studies come up with similar effects found for the OWF Lincs (UK) and the same general study area in the eastern German Bight (WEBB et al. 2017; MENDEL et al. 2019a). Analyses of tracking data showed that weather conditions describing visibility and day- or night-time have an effect on the distance red-throated divers kept to OWFs. Distances between red-throated divers and OWF are smaller when weather conditions reduce visibility. This supports the hypothesis that divers perceive OWFs as visual stimuli and occur closer to them when visibility is limited due to meteorological conditions. Longer distances to OWFs kept at night may indicate that the bright red warning and navigational lights that illuminate the wind turbines at night are visible for red-throated divers at longer distances compared to turbine visibility during daytime.

Analysis of red-throated diver relocation distances in relation to the distance to OWFs revealed the relocation distances significantly decreasing with increasing distance from OWFs, indicating that disturbance from OWFs (and related shipping) does not only result in displacement but additionally in changes in bird behaviour. Increasing relocation distances in close vicinity to OWF may be partly explained by divers avoiding to cross the OWF footprints by detouring that area.

Some studies on different bird species suggest that the displacement effect following disturbance from onshore wind farms are smaller for breeding birds as compared to staging birds (e.g. STEINBORN et al. 2011) and thus disturbance effect is dependent on the stage within a bird's annual cycle. For red-throated divers to our knowledge there is no indication that the species is less susceptible to disturbance from wind farms during the breeding season (HALLEY & HOPSHAUG 2007; BLACK et al. 2015, pers. comm. A. Webb), indicating a general high sensitivity of the species to the pressure which is not dependent on the bird's status within the annual cycle.

Shipping traffic also results in strong displacement effects to divers. Here our study revealed that high speed vessels as often used for maintenance and crew change tasks at OWF sites have the largest effect on red-throated divers, with regard to the duration of the effect. The analysis of AIS shipping data in the eastern German Bight visualises the intensity of shipping occurring in that area, which affects major parts of the area, also outside defined shipping routes, leaving only little undisturbed habitats for sensitive species. The intense shipping traffic within diver areas significantly adds to the effects of OWFs and needs to get more attention in spatial management of marine areas. Displacement effects from OWFs likely describe a combined effect of the wind farm structures itself and the related high intensity of service shipping traffic as also suggested by MENDEL et al. (2019a). The high mobility of red-throated divers, as observed during the DIVER study, may partly be explained by the frequent, for the birds unpredictably occurring disturbances in their wintering and staging areas.

It is unclear why divers show such an exceptional avoidance response to OWFs and shipping which goes well beyond those recorded for other species. GILL et al. (2001) described in their study that the simple magnitude of the displacement does not necessarily reflect population-level consequences for a species. This hypothesis was further elaborated in the study by MAY (2015). Similar to animal behavioural reactions to predation risk, which depends on the availability and quality of other sites (e.g. YDENBERG & DILL 1986), a species with suitable habitat nearby may avoid disturbance simply because it has alternative sites to go (GILL et al. 2001). Following this hypothesis, a large displacement effect, as observed for red-throated divers from OWF areas, does not necessarily result in a significant impact on the species if individuals find enough food and suitable habitats outside the disturbance range.

Therefore it can be expected that anthropogenic pressures and related species reactions have different consequences to individual divers as these are impaired during different stages of their annual cycle. A diver exhibiting only a few day stop-over in the area may be less affected by possible consequences of impairments than an individual spending its complete wintering season in that area. Also, divers conducting only short migration distances to breeding areas (e.g. Norway) are likely less susceptible to constraints which limit the build-up of energy reserves compared to the birds preparing themselves for long-distance migration of several thousand kilometres to Greenland and Siberia with single non-stop flights of up to 1,400 km.

Displacement of birds from impaired areas to other habitats may result in inter- and/or intra-specific competition between displaced individuals and other members of the same ecologic guild. Red-throated divers usually occur in low densities in their wintering areas. Densities in areas of main winter abundance rarely exceed values of 5 ind./km² (GARTHE et al. 2015; IRWIN et al. 2019). Intra-specific interactions and competition for resources therefore are rather unlikely to occur for red-throated divers in their wintering areas. Other piscivorous seabirds, such as auks, occur only in low densities in the areas of main diver abundance due to different habitat requirements. Harbour porpoises (*Phocoena phocoena*) use similar habitats as red-throated divers and may partly forage on similar small size prey concentrating at estuarine fronts (SKOV & THOMSEN 2008). Little is known about such inter- and intraspecific interactions, however, it is unlikely that harbour porpoises – themselves occurring in even lower densities in the area in winter and spring – significantly interfere with red-throated divers foraging in the same general habitats.

Changes in foraging behaviour of piscivorous seabirds are typically explained by bottom-up ecosystem processes (e.g. ÖSTERBLOM et al. 2001; DAVOREN & MONTEVECCHI 2003; MILLER & SYDEMAN 2004; WANLESS et al. 2005; DURANT et al. 2009; HUGHES et al. 2015), thus there is no indication that top-down driven depletion of fish by piscivorous seabirds would play an important role in marine systems. Due to this and regarding the absolutely low numbers of piscivores using the main diver distribution areas, it is very unlikely that red-throated divers or other piscivores could deplete their food resource in the area. Thus, the local increase in red-throated diver densities through displacement from other areas is neither expected to result in any intra- and inter-specific competition nor to have any effect on the available food resources. Together with the presumed flexibility of red-throated divers to switch between different prey species and the wide distribution of the main prey, prey depletion by inter- and intra-specifics is not expected to limit the prey intake of red-throated divers, which was also suggested by DIERSCHKE et al. (2017). Interaction with commercial fisheries has not been analysed in this study.

When assessing the impacts of offshore wind farm development to individual movements and species-specific conditions, it needs to be considered that for species with low reproductive capacity and slow maturation rate, as this is true for divers, small changes in adult survival can result in significant population declines (JOHNSGARD 1987; MITRO et al. 2008). Displacement caused by offshore wind farm development can potentially lead to effects in wintering areas such as increased energy expenditure. For answering if the recorded displacement of red-throated divers from large parts of their main distribution area results in a significant impact on the species at population level, more information on diver foraging behaviour in their wintering areas and their annual energy budgets and thus body condition are needed. This information would allow assessing if the species has the capacity to buffer for additional energetic expenses of avoidance reactions due to OWFs and other anthropogenic pressures. When such information is lacking, analysis of long-term trends of red-throated diver abundance in main distribution areas at larger scale is the first approach in assessing whether an impact on the red-throated diver wintering population is apparent through a decline in bird numbers. Due to the high mobility of the species local red-throated diver numbers can fluctuate substantially between years (e.g. WEBB et al. 2009). Operational monitoring studies of individual OWFs can describe the displacement effect for the particular area, but are not capable to assess whether displaced birds were able to successfully redistribute into other suitable habitats further away. Also, on national level trend figures are not fully conclusive as there are different trends observed when looking at different subsets of the dataset. Results by SCHWEMMER et al. (2019) indicate different trend patterns of red-throated diver abundance, dependent on the considered spatial and temporal scale. For the diver main distribution area in the German North Sea (BUNDESMINISTERIUM FÜR UMWELT, NATURSCHUTZ UND REAKTORSICHERHEIT 2009) red-throated diver numbers were relatively constant over the past years (SCHWEMMER et al. 2019), however, with a shift in the distribution. Recent British studies on diver concentration areas in relation to OWFs give no indication for a decline in diver numbers. Long-term monitoring data from the Outer Thames Estuary SPA (IRWIN et al. 2019) indicate increasing red-throated diver numbers for the SPA area as a whole, though the construction and operation of several OWFs within the SPA resulted in marked displacements from the OWF areas. While large numbers of displaced red-throated divers were calculated for the Lincs OWF (WEBB et al. 2017), the abundance of divers increased in the Greater Wash study area by a factor of two to over five times the amount displaced, indicating no decline in overall diver numbers in the area. For Liverpool Bay the pattern is similar where red-throated diver numbers do not suggest any decline (pers. comm. A. WEBB). Available different national and regional data from main diver distribution area do not indicate a general decline in overall red-throated diver numbers over the past years. However, data from large-scale operational monitoring would be needed including relevant areas which are not monitored at the moment (e.g. Horns Rev 3 OWF) in order to assess the large-scale impact of OWFs to the red-throated diver wintering population.

10.5 Conclusion and recommendations from project results

The DIVER study revealed novel knowledge on red-throated diver ecology and behaviour by using different state of the art methods to study bird movements, habitat use and bird diet. The different analyses complement each other and increase our understanding about red-throated divers using the eastern German Bight during the period of the species maximum abundance in the area in late winter and spring, allowing for a more comprehensive assessment of displacement effects from OWFs and marine traffic in the area.

Red-throated divers occurring in the eastern German Bight originate from different breeding regions and show a variety of different individual movement patterns and timing. The species is very mobile in wintering areas and individuals likely encounter OWFs frequently during migration and wintering. Red-throated divers wintering in European marine waters are amongst the most sensitive species to anthropogenic disturbances and show strong avoidance of OWFs. Analyses of the displacement effect by using two different and independent datasets – digital aerial survey data and telemetry tracking data – identified a large-scale displacement response of red-throated divers following a gradient of reduced densities extending to more than 10 km. Further, shipping traffic was identified being an important pressure resulting in diver displacement, with high-speed vessels causing the longest time periods until resettlement of disturbed areas. Results of site fidelity and diet analyses suggest some flexibility of red-throated divers in using different areas and switching between different available prey species. There is indication that red-throated divers have some capacity to cope with being displaced from OWF areas as for different core diver staging areas red-throated diver numbers seem to be stable or even increasing. However, large-scale monitoring data covering the German Bight, including Danish diver high distribution area west of Jutland, would be required to analyse the cumulative impacts of OWFs and the resulting displacement effect and changes in diver distributions to conclusively being able to answer the question whether the observed displacement effects of different OWFs have an impact on red-throated diver population level.

A number of recommendations were made with regard of improving marine spatial planning in order to avoid or reduce the adverse effects of OWFs and shipping in red-throated diver wintering areas and with regard to future research needed.

The following recommendations were derived from the project results:

- Regarding the large displacement effect ranging beyond 10 km from OWFs, OWF planning should carefully consider the occurrence of the species and seek to minimise impacts on important wintering and staging areas.

- The impact of OWFs can be reduced by clustering projects as the total disturbed area then is reduced markedly.
- Tracking data suggest the displacement effect from OWFs being even larger during night. A demand-driven lighting of OWFs, as also suggested with regard to reducing bird collisions, is therefore highly recommended aiming to reduce the disturbance of sensitive seabird species resting in the area.
- Besides OWFs, ship traffic has also been identified as a pressure resulting in a strong displacement effect for divers leaving only small undisturbed areas of low shipping intensity for sensitive species. Managing shipping, for example by channelling shipping activities to defined shipping routes whenever possible, might reduce the impaired area and should be developed as a mitigation measure to reduce impacts on red-throated divers.
- The speed of ships has a large effect on red-throated diver resettlement time of disturbed areas with high-speed vessels having the greatest negative impact on divers. Shipping speed should be limited in areas with high diver abundance to reduce the impact on the species.
- The results of the DIVER project and other recent studies show that the effect of OWFs on red-throated diver distribution is much greater than anticipated from earlier investigations. A large-scale and international operational monitoring is needed for assessing the large-scale and cumulative impacts of OWFs on red-throated divers wintering in the German Bight to be able to disentangle if large-scale changes in red-throated diver distribution represent only a redistribution of birds to other sufficiently available suitable habitats or if the displacement effects have an impact on the red-throated diver wintering population.
- For assessing if the displacement of red-throated divers from their primary habitats to other areas has an impact on the species population, more information on the species foraging behaviour and energy budgets is needed as the bird’s body condition may have implications for individual birds’ fitness in terms of survival and breeding success.

10.6 Discussion of used methods and outlook

The methods used in this study meet the latest scientific standards and are appropriate to answer the raised questions.

State of the art genetic methods of DNA metabarcoding have been applied successfully for the first time in red-throated divers and added novel knowledge on red-throated diver diet in their wintering area.

The used implantable Argos PTT satellite transmitters were to date of bird captures the only suitable device type which could be used for studying the movements of diving seabirds over the period of at least one year. The resolution of Argos locations has its known shortcomings of being less accurate than GPS locations. Also number of location fixes is limited due to limited battery capacity of implantable transmitters. However, by using statistical methods these shortcomings could be dealt with in data analyses and were recognised already in the project planning. The satellite telemetry data added plenty of novel information on red-throated diver movement patterns, which were used to answer several questions with regard to diver ecology and for studying the effects of OWFs and shipping to the species in a core wintering area of the species.

Newly available implantable combined GPS/dive loggers would allow for more fine-scale resolution movement data allowing for small-scale analyses of diver movements and foraging behaviour in their wintering area. Such data would allow answering different questions such as analysing red-throated diver foraging behaviour and energy budgets which currently remains an open question. Such information, together with the results already obtained and reported in this study would enable the parameterisation of a detailed individual based model which would allow to assess potential impacts at the population level (see e.g. WARWICK-EVANS et al. 2018)

11 LITERATURE

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A APPENDIX TO CHAPTER 5

A.1 Satellite tracks of individual red-throated divers

This appendix contains all tracks from red-throated divers equipped with satellite transmitters within the DIVER project. Tracks include all data after filtering to reduce noise produced by location fixes, manual removal of obvious outliers and first two weeks data sampling after release of the birds. Tracks cover the full time period the particular transmitter was active ranging from few weeks to 23 months.

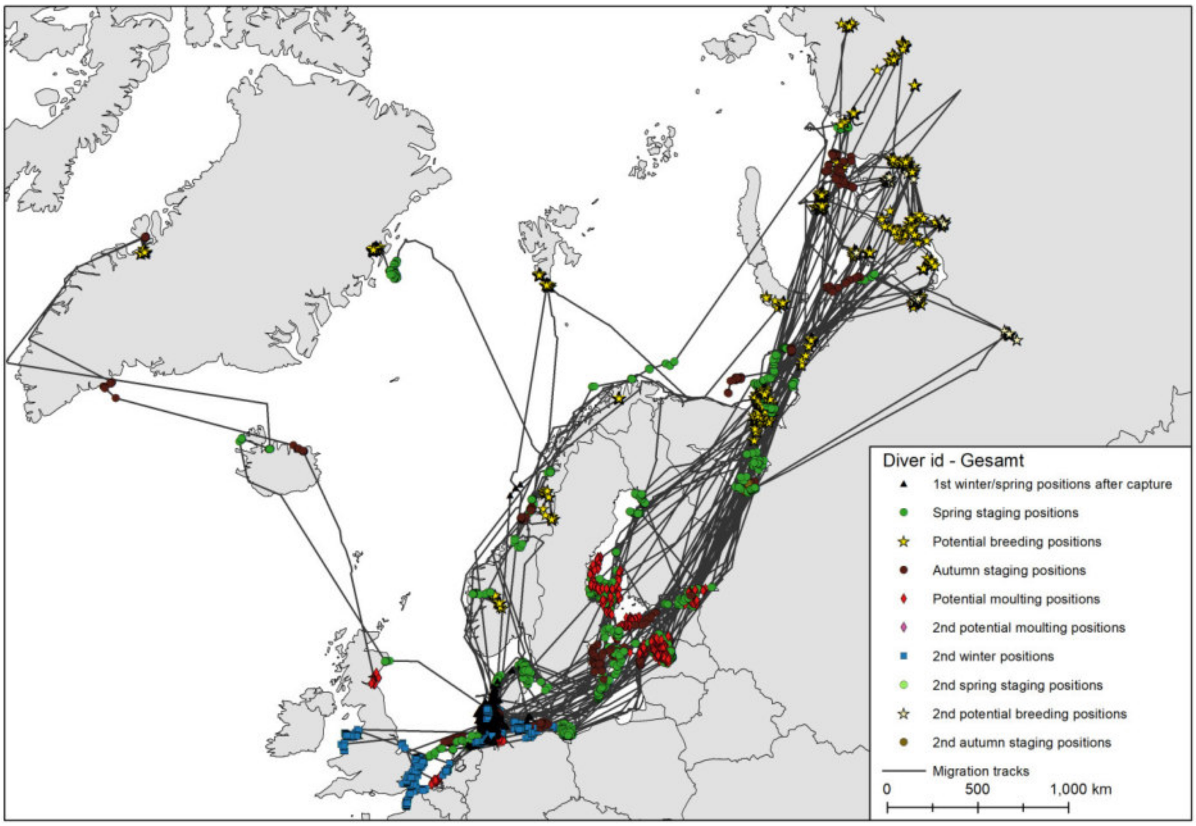


Figure A.1 Migration tracks of all red-throated divers tracked during the project between April 2015 and August 2018.

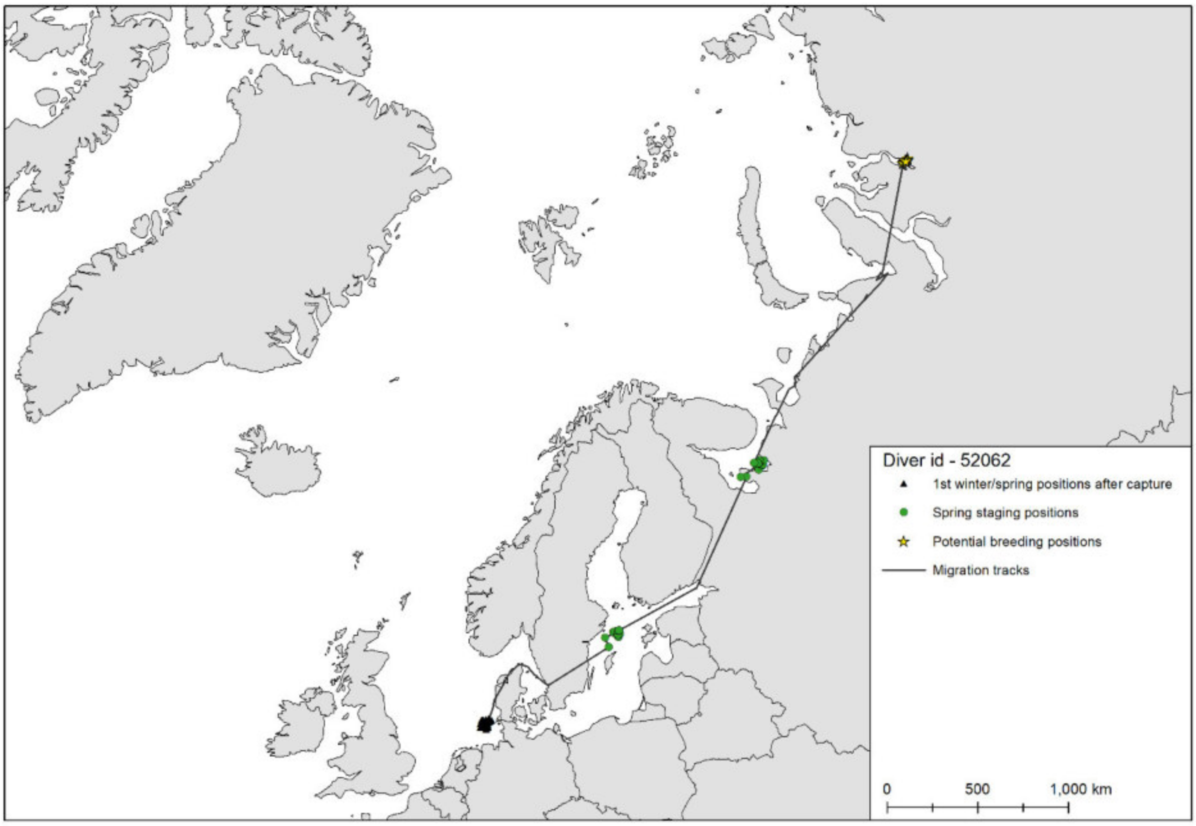


Figure A.2 Migration track of red-throated diver id-52062 covering the period between 11 April 2017 and 01 July 2017.

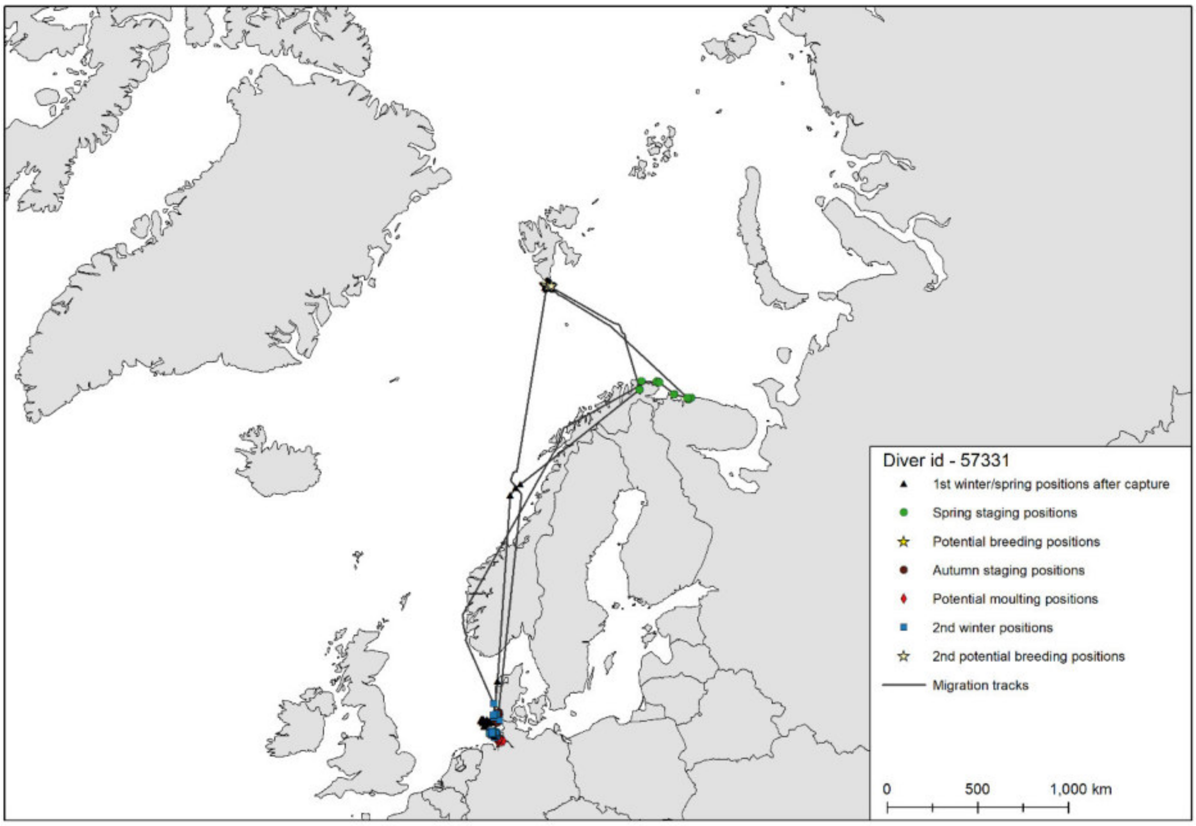


Figure A.3 *Migration track of red-throated diver id-52331 covering the period between 12 April 2017 and 06 August 2018.*

Figure A.4 *Migration track of red-throated diver id-52332 covering the period between 11 April 2017 and 30 July 2017.*

Figure A.5 Migration track of red-throated diver id-52335 covering the period between 11 April 2017 and 12 July 2017.

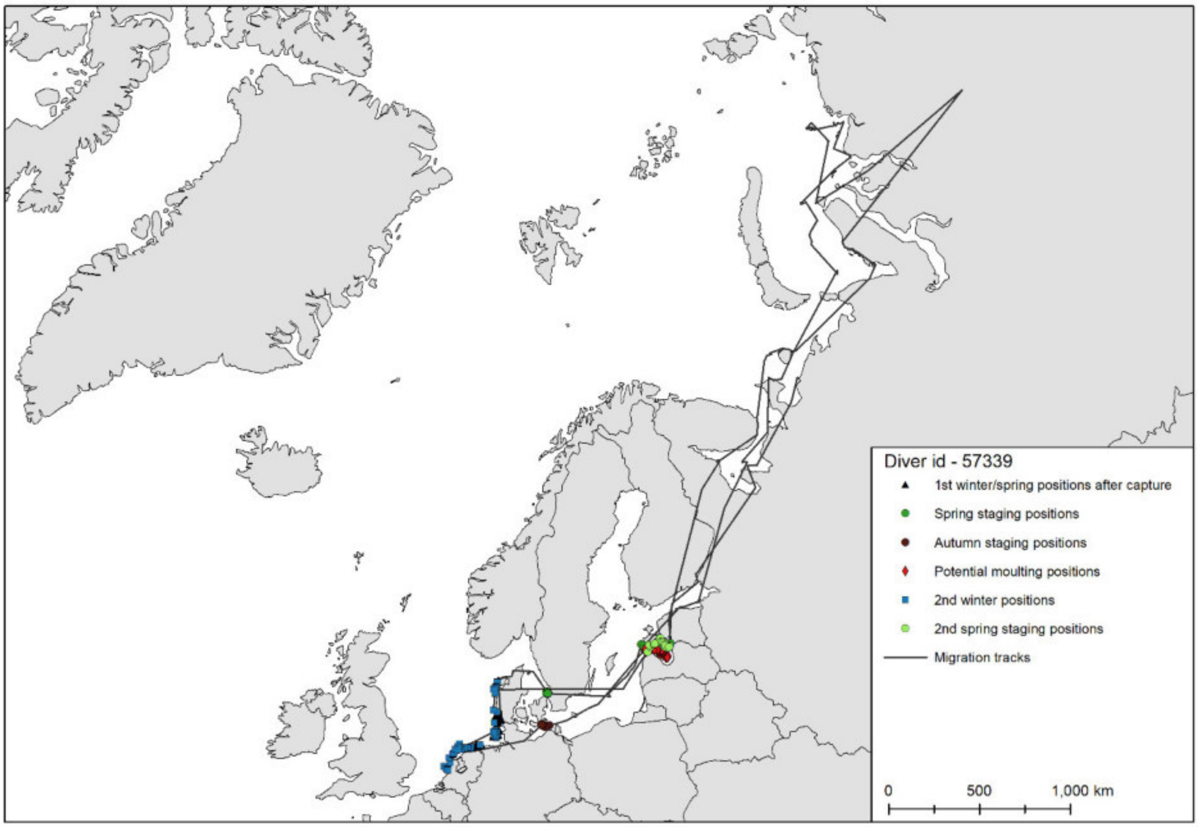


Figure A.6 *Migration track of red-throated diver id-52339 covering the period between 11 April 2017 and 04 June 2018.*

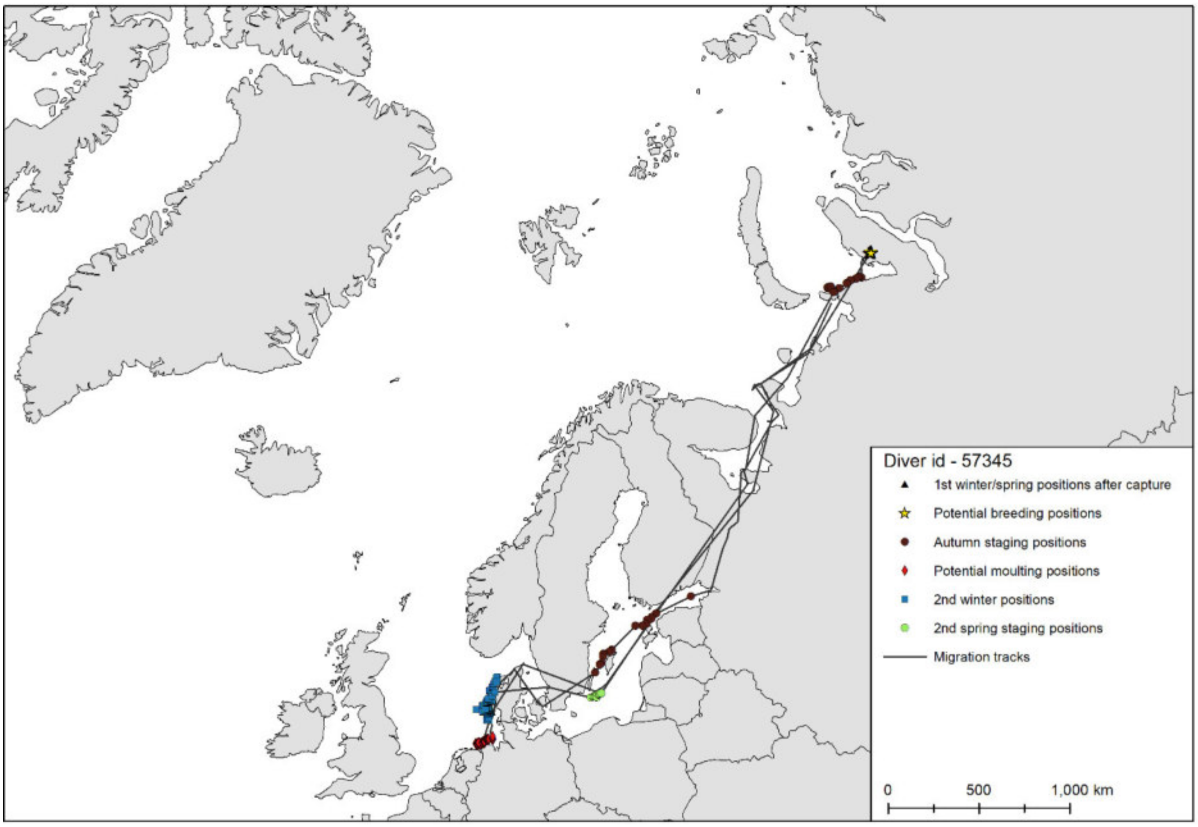


Figure A.7 *Migration track of red-throated diver id-57345 covering the period between 11 April 2017 and 12 June 2018.*

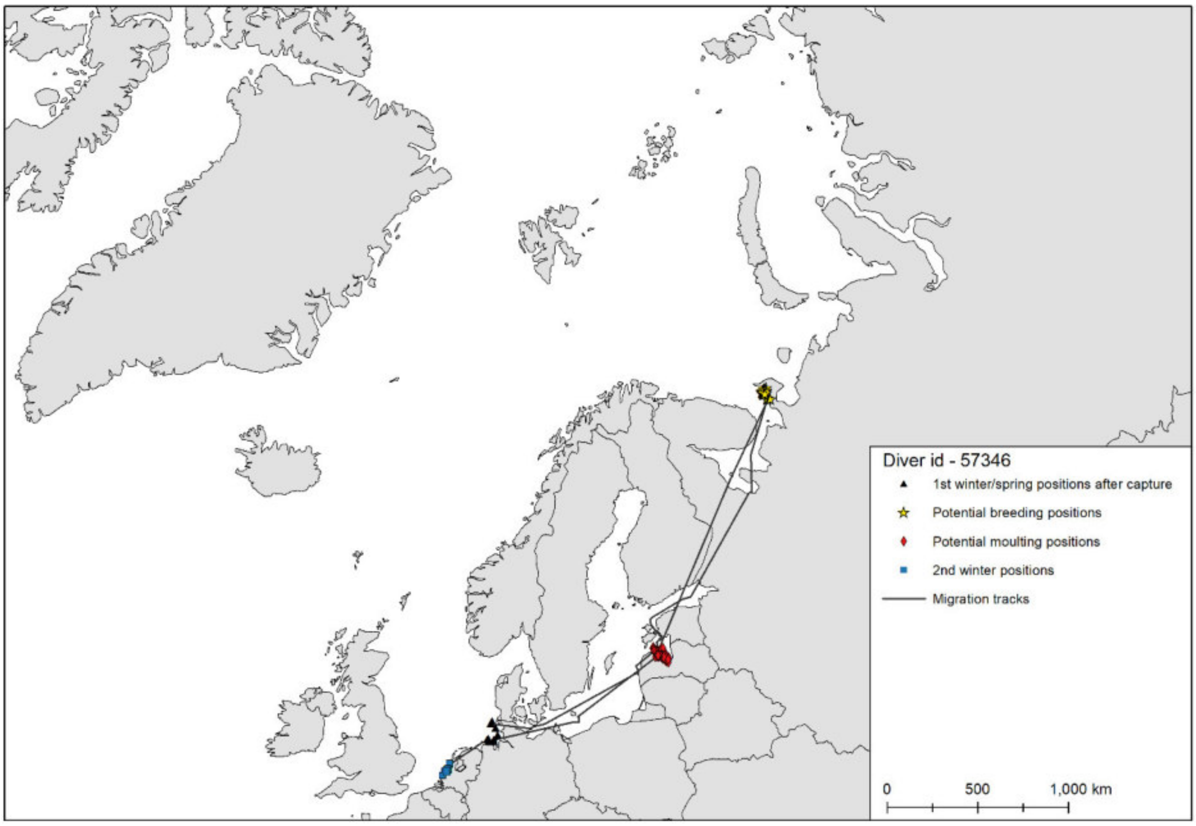


Figure A.8 Migration track of red-throated diver id-57345 covering the period between 11 April 2017 and 29 January 2018.

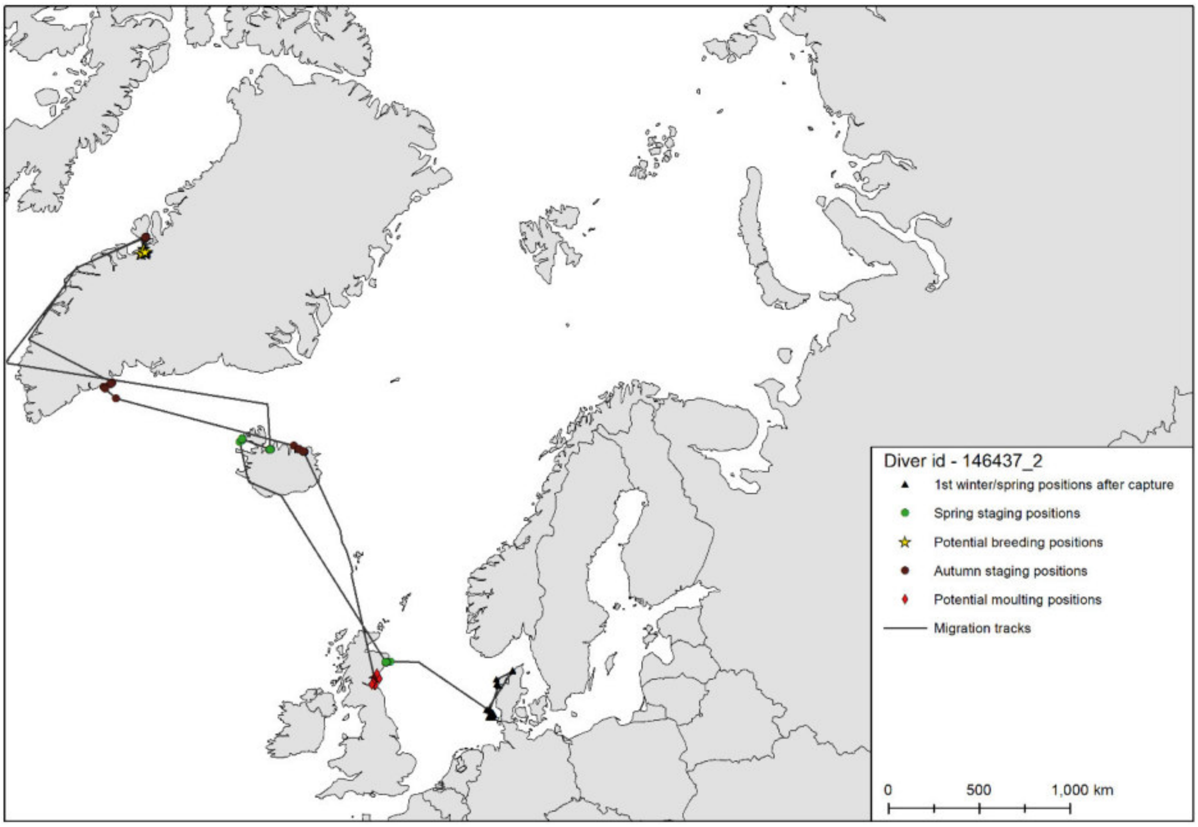


Figure A.9 *Migration track of red-throated diver id-146437_2 covering the period between 05 May 2015 and 05 December 2015.*

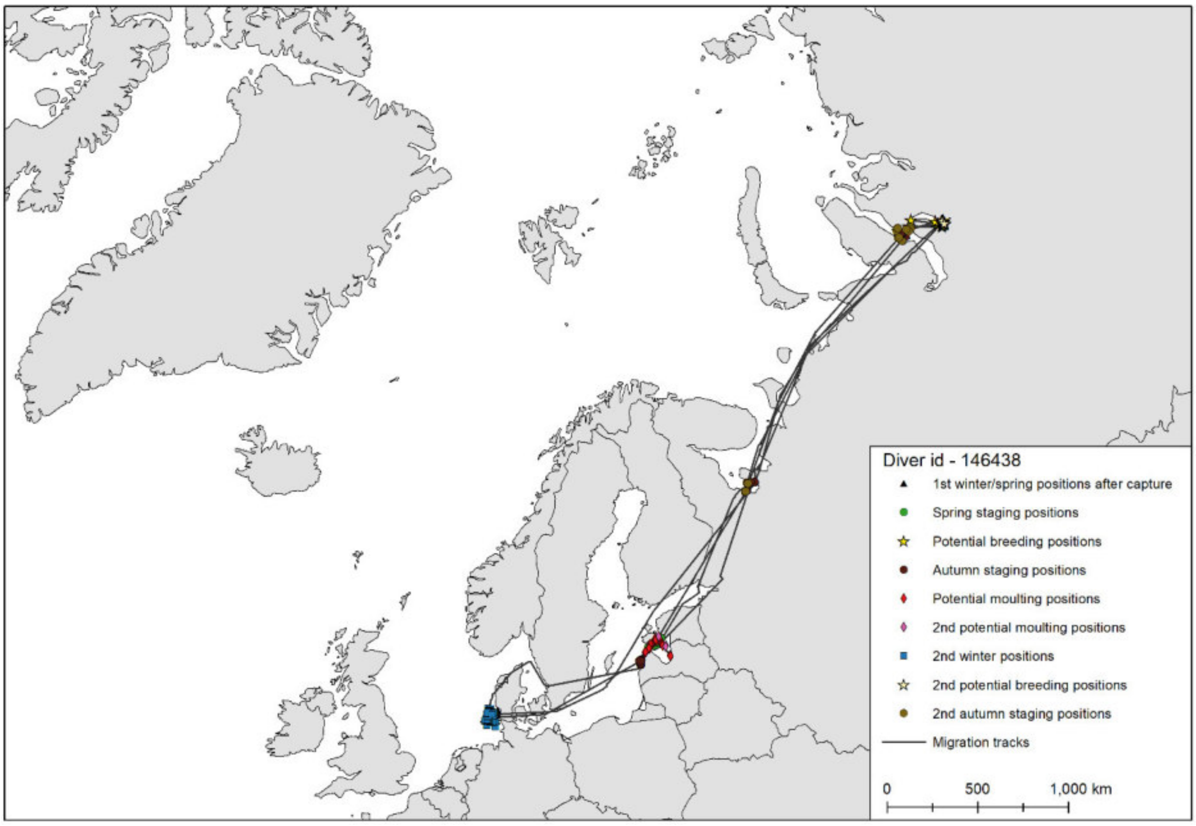


Figure A.10 *Migration track of red-throated diver id-146438 covering the period between 05 April 2015 and 17 October 2016.*

Figure A.11 Migration track of red-throated diver id-146439 covering the period between 05 April 2015 and 15 June 2015.

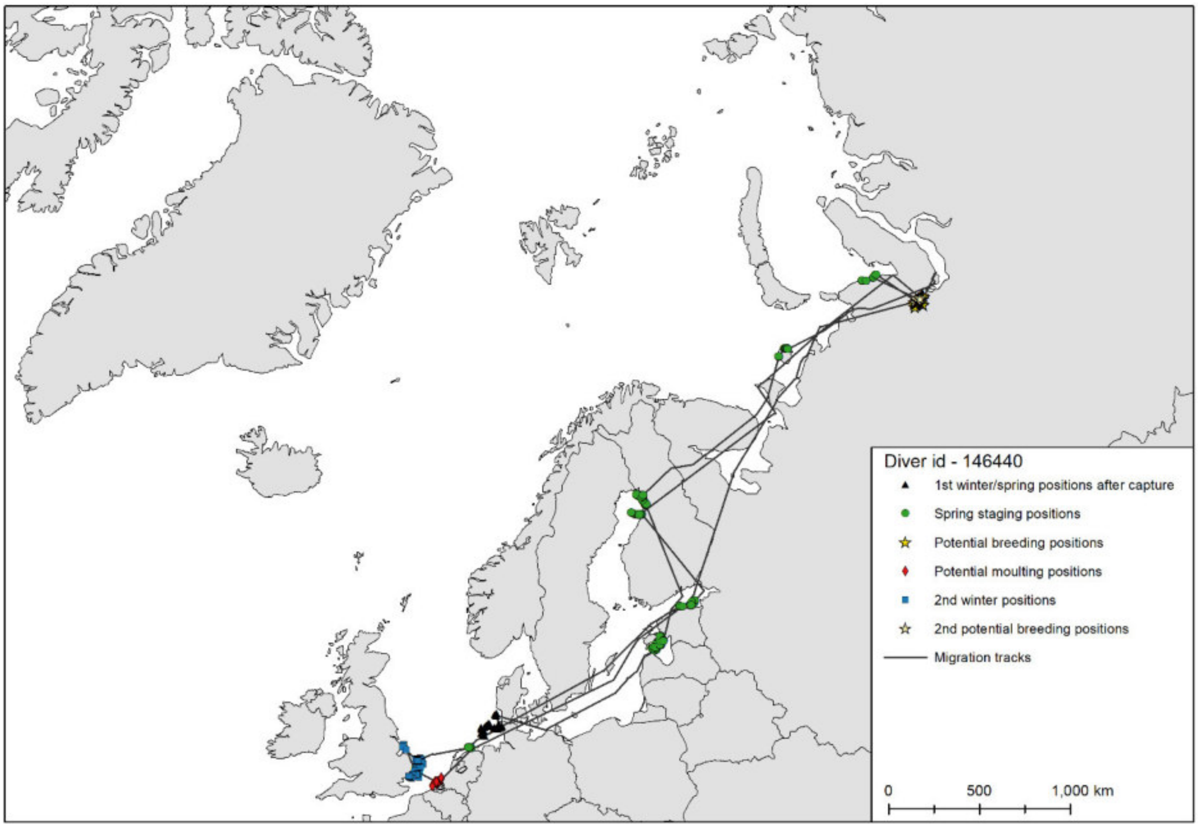


Figure A.12 Migration track of red-throated diver id-146440 covering the period between 05 April 2015 and 20 August 2016.

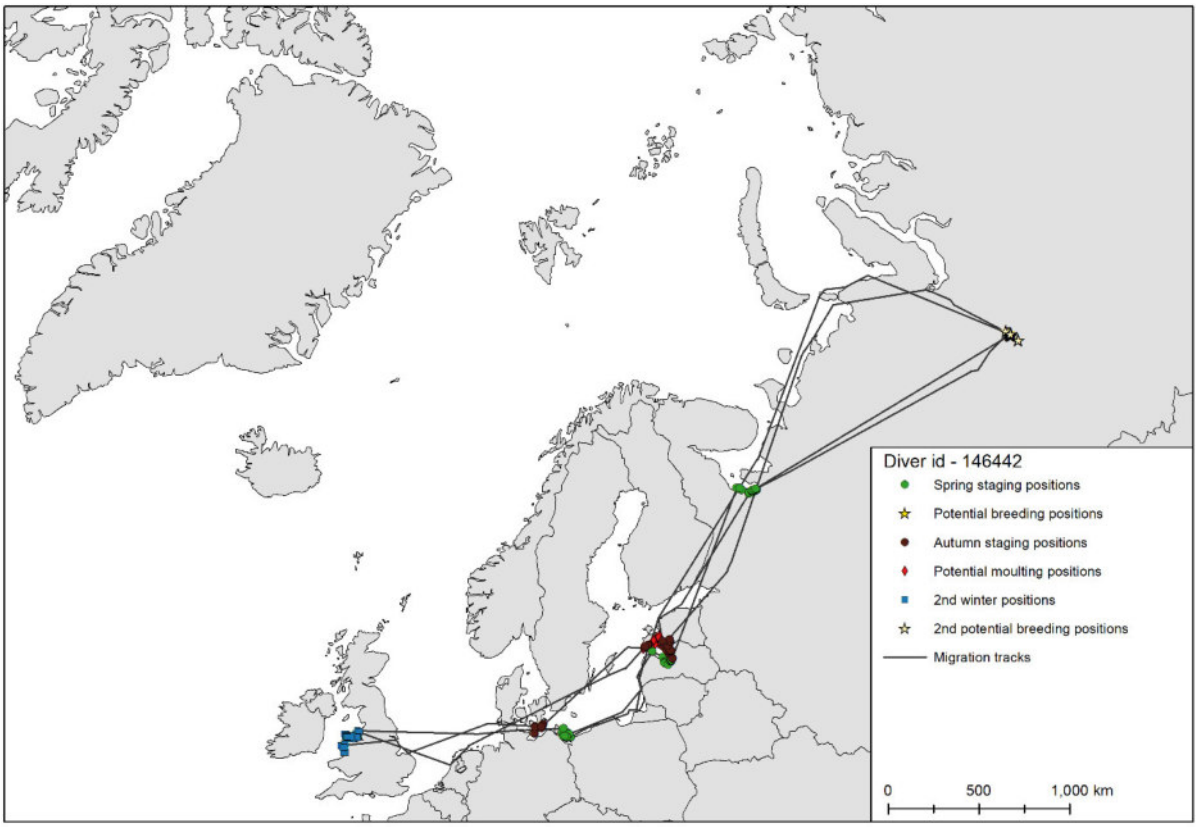


Figure A.13 Migration track of red-throated diver id-146442 covering the period between 05 April 2015 and 06 February 2017.

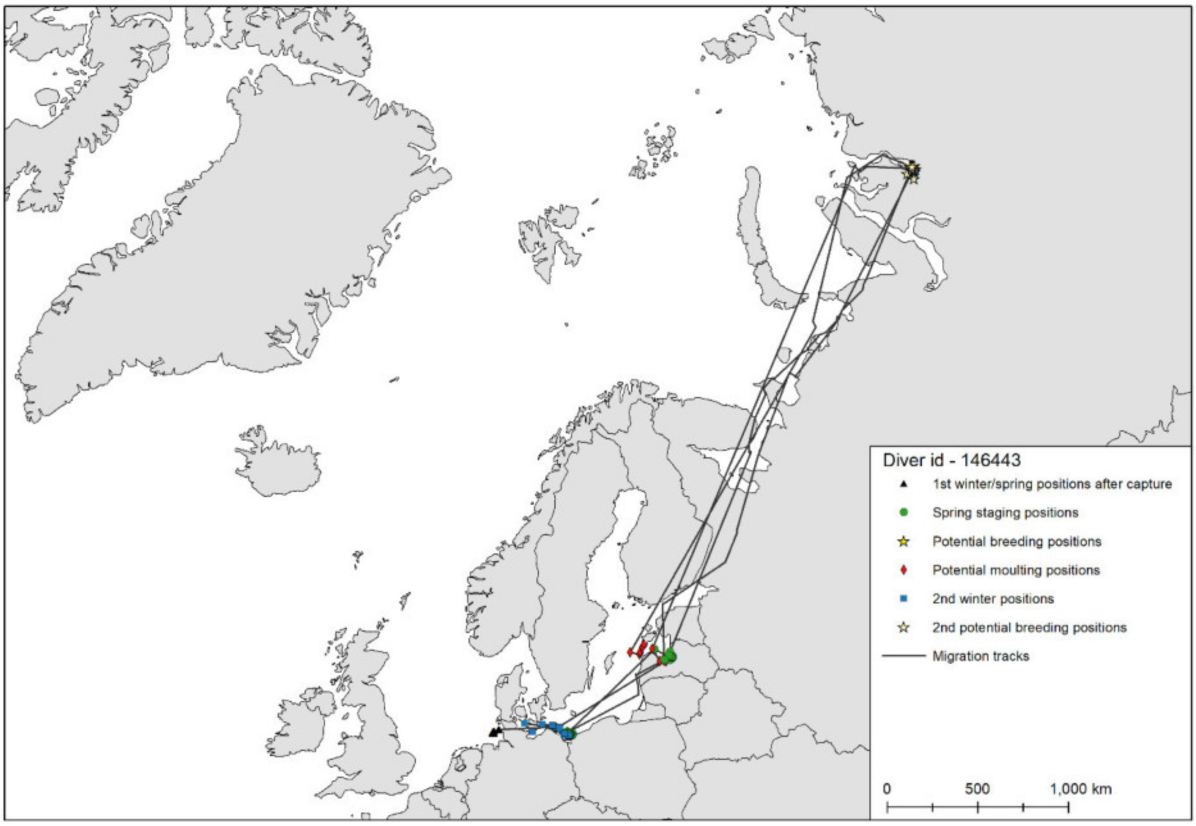


Figure A.14 Migration track of red-throated diver id-146443 covering the period between 05 April 2015 and 10 November 2016.

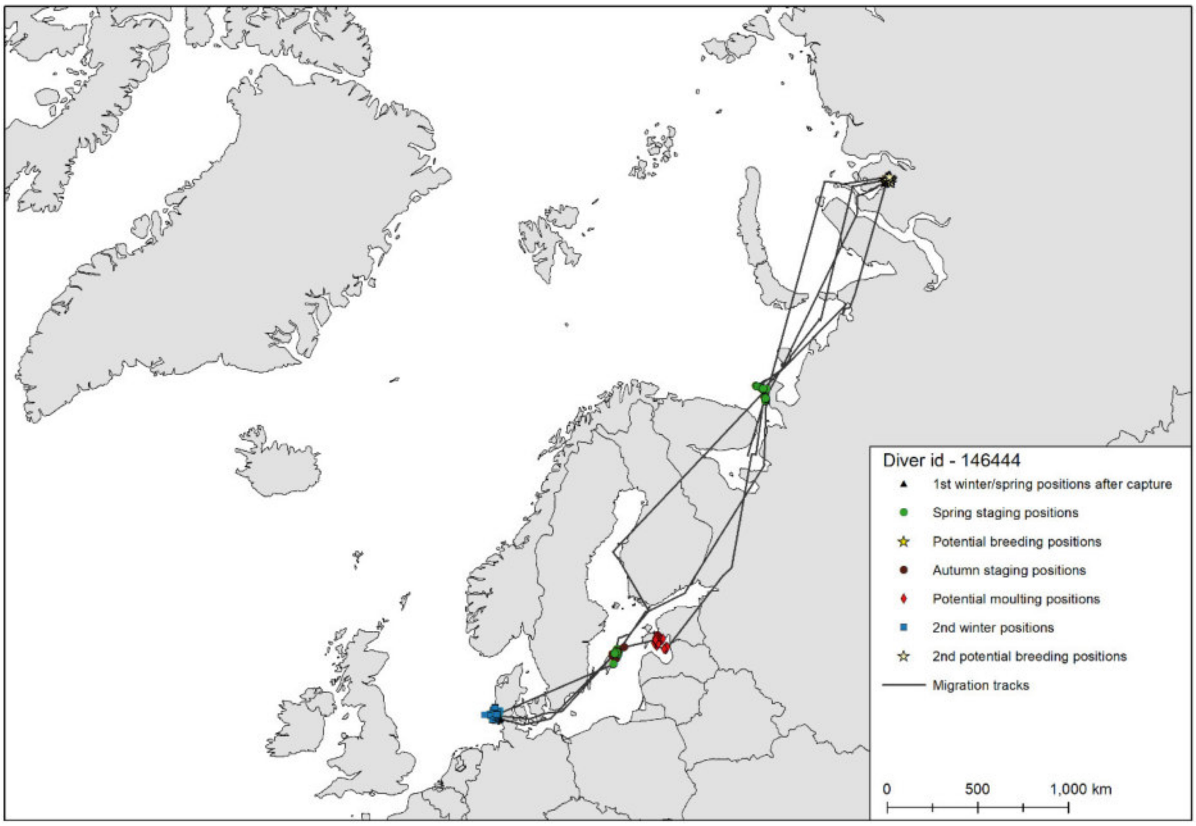


Figure A.15 *Migration track of red-throated diver id-146444 covering the period between 09 April 2015 and 29 September 2016.*

Figure A.16 *Migration track of red-throated diver id-146449 covering the period between 04 May 2015 and 17 June 2015.*

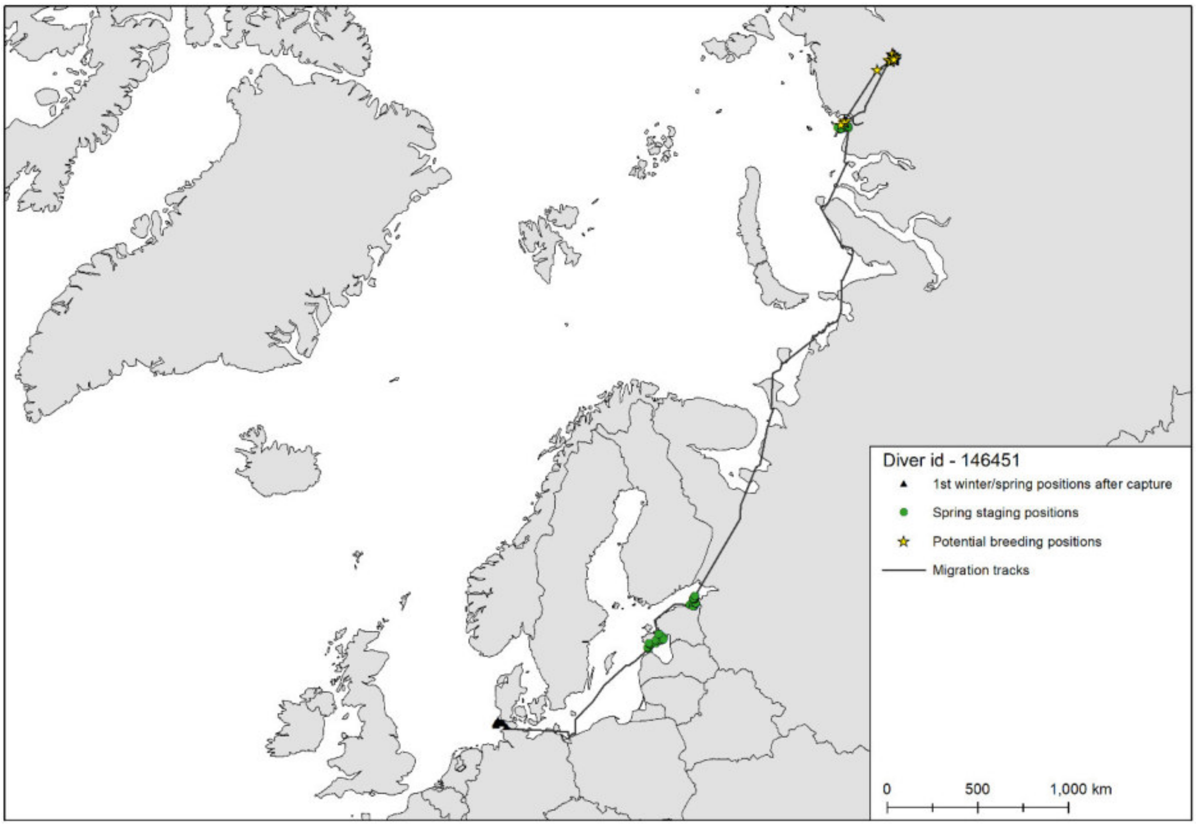


Figure A.17 Migration track of red-throated diver id-146451 covering the period between 05 May 2015 and 29 July 2015.

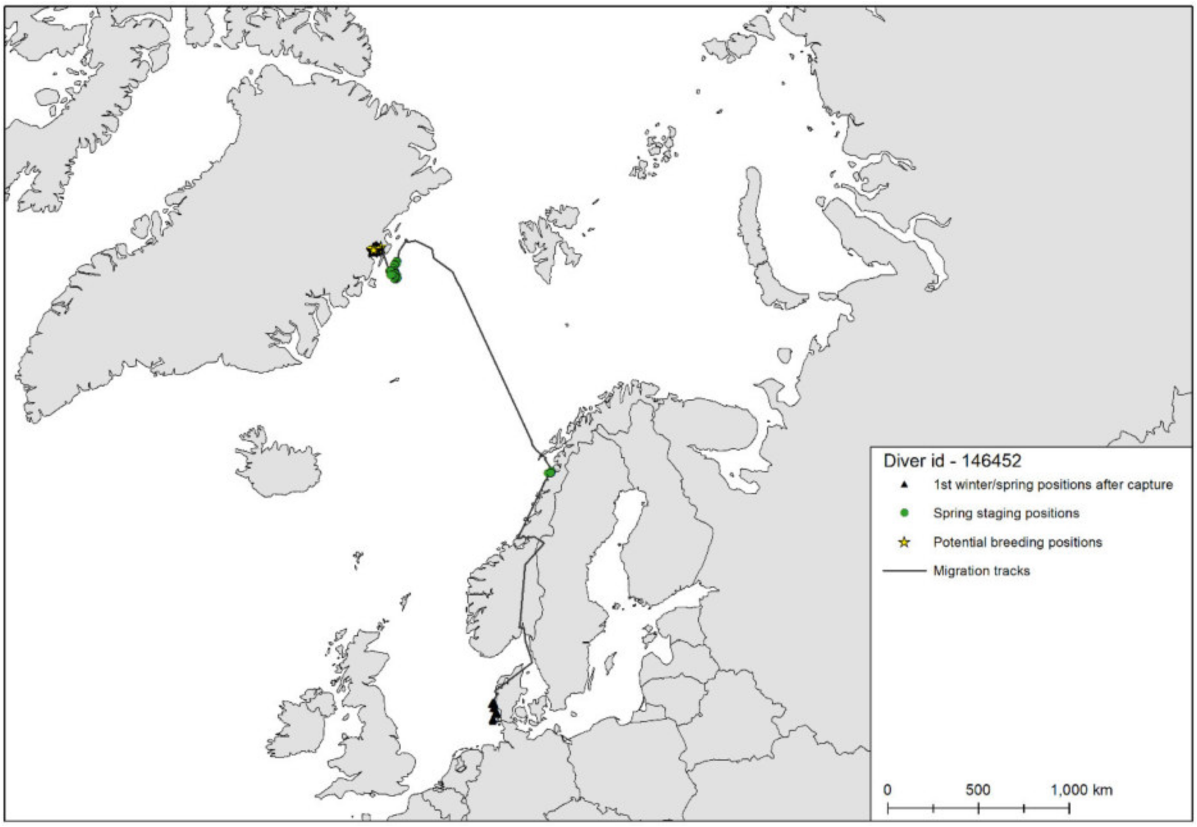


Figure A.18 Migration track of red-throated diver id-146452 covering the period between 04 May 2015 and 04 September 2015.

Figure A.19 Migration track of red-throated diver id-146453 covering the period between 05 May 2015 and 22 September 2015.

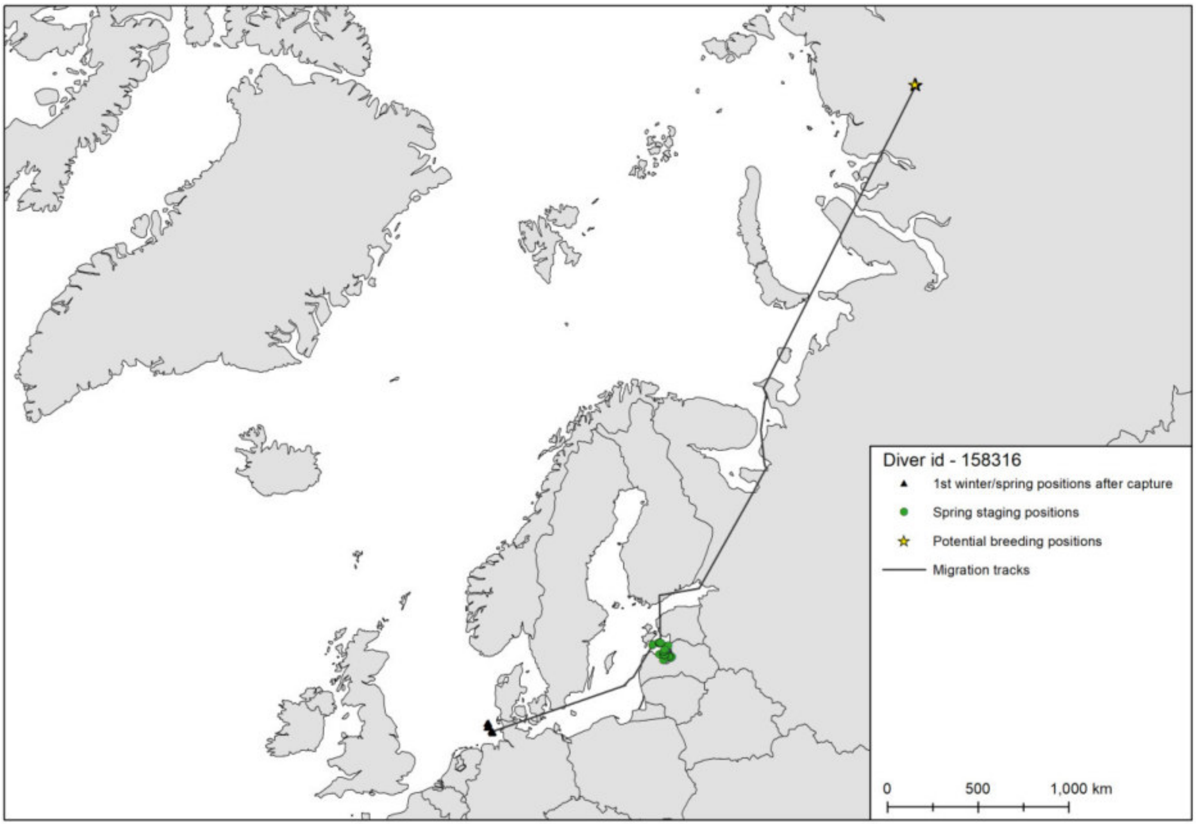


Figure A.20 Migration track of red-throated diver id-158316 covering the period between 27 March 2016 and 12 August 2016.

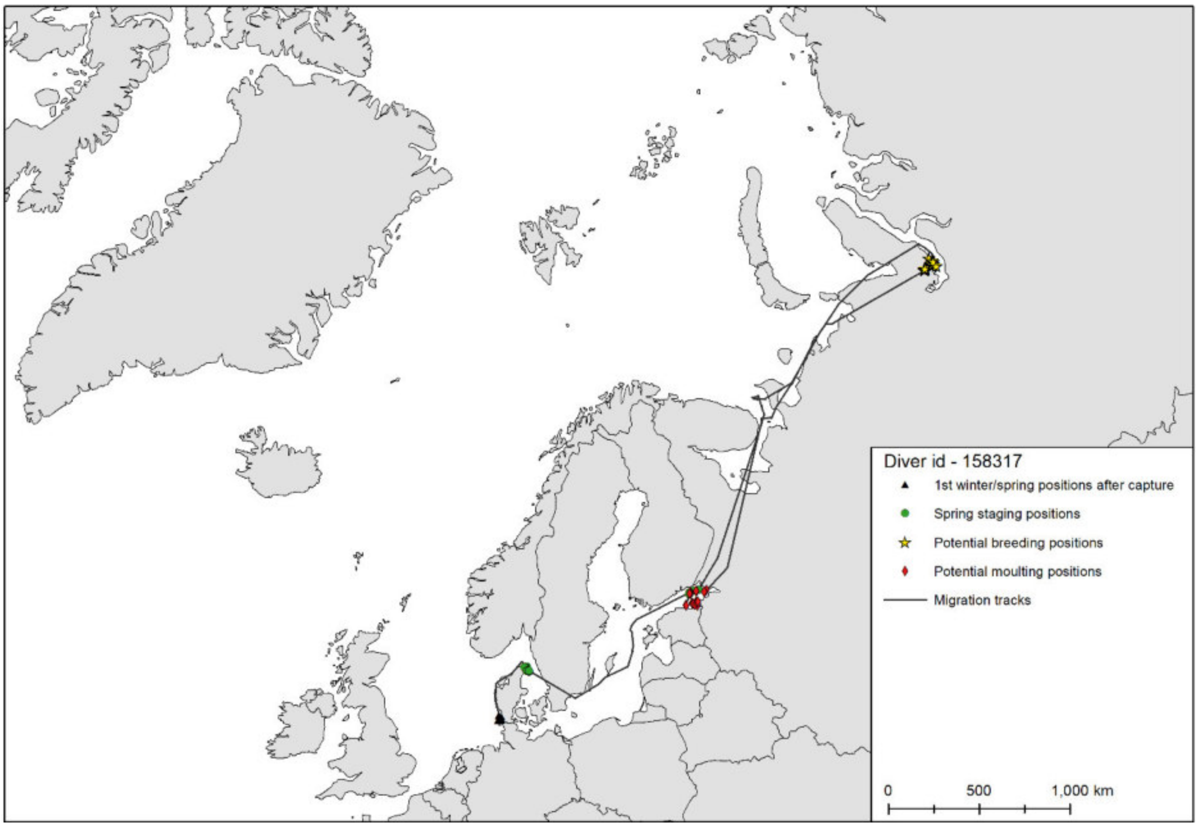


Figure A.21 Migration track of red-throated diver id-158317 covering the period between 27 March 2016 and 19 October 2016.

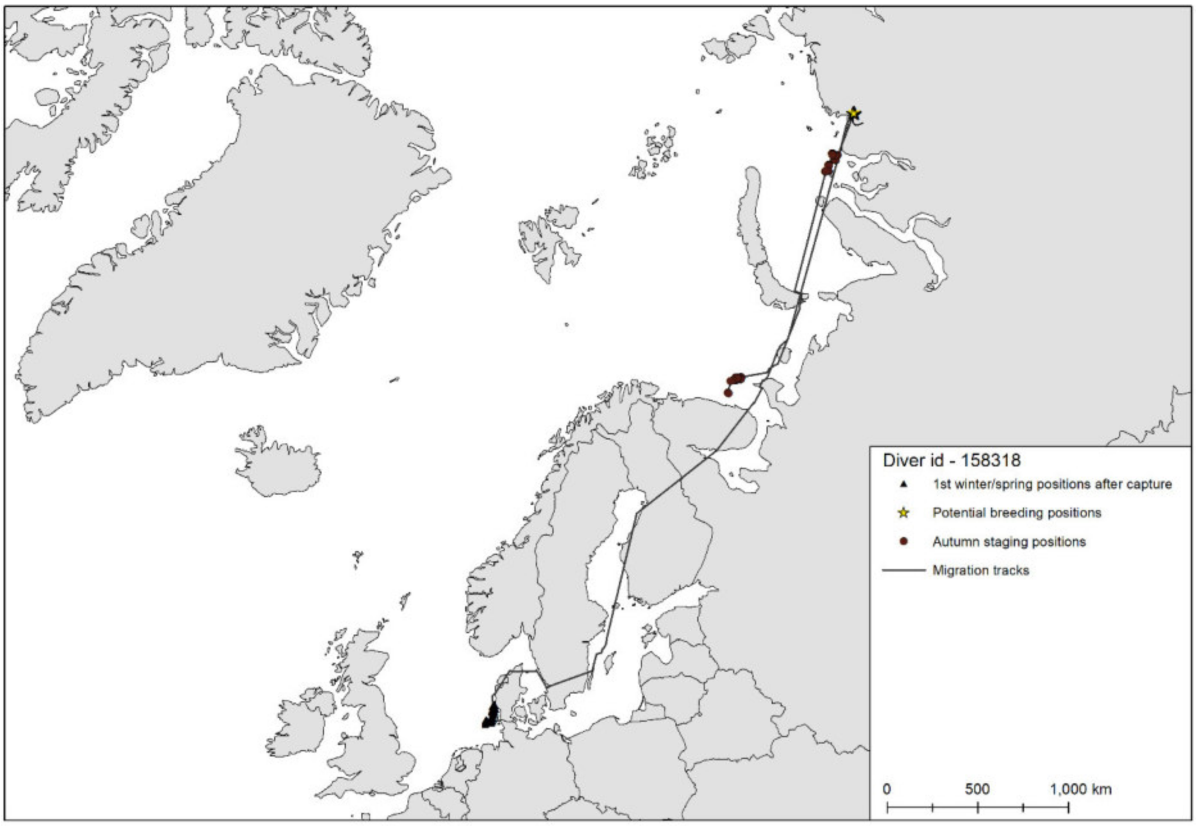


Figure A.22 Migration track of red-throated diver id-158318 covering the period between 26 March 2016 and 02 October 2016.

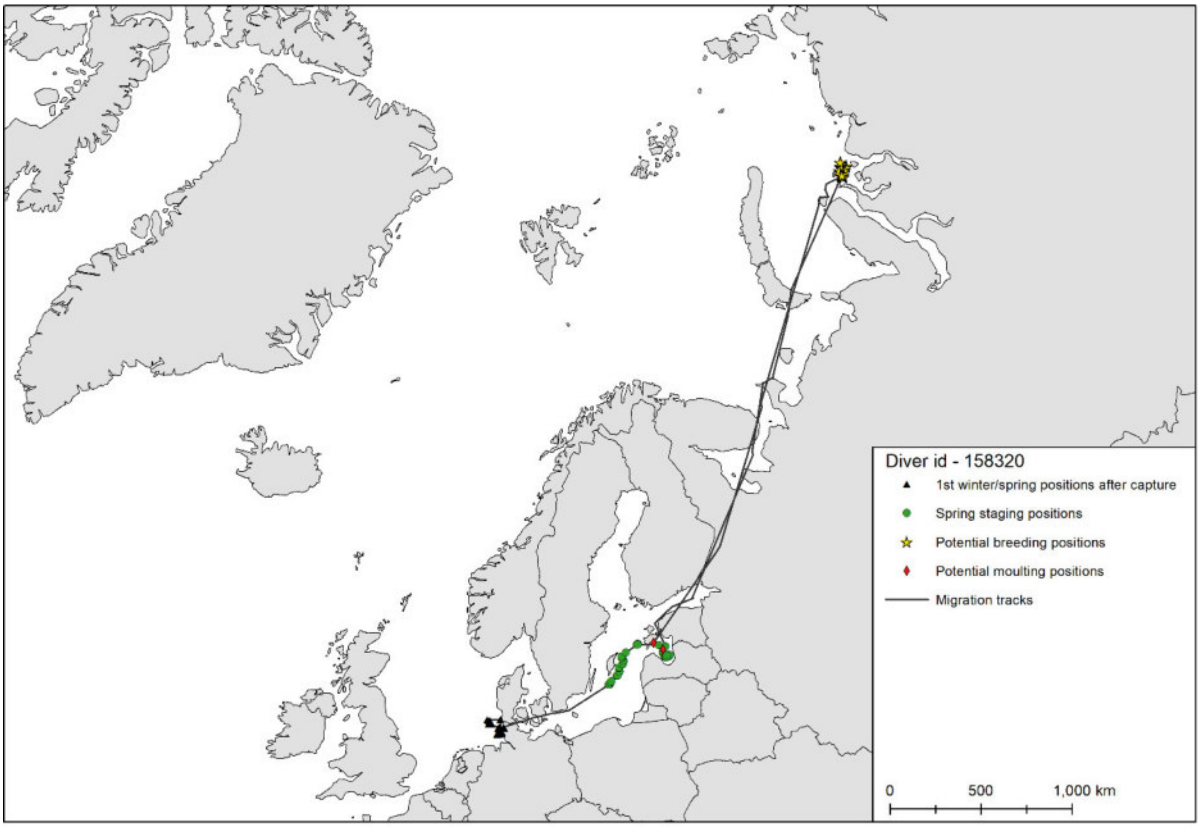


Figure A.23 Migration track of red-throated diver id-158320 covering the period between 27 March 2016 and 07 November 2016.

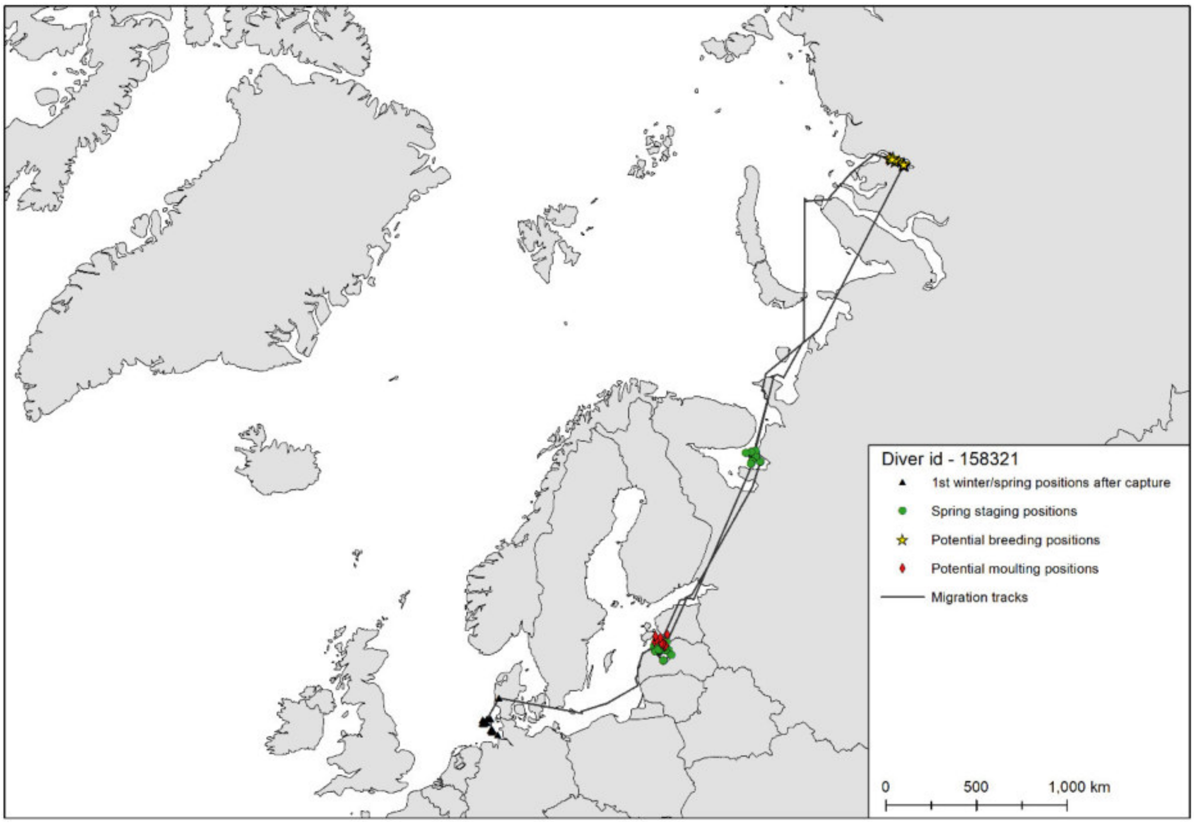


Figure A.24 Migration track of red-throated diver id-158321 covering the period between 27 March 2016 and 21 October 2016.

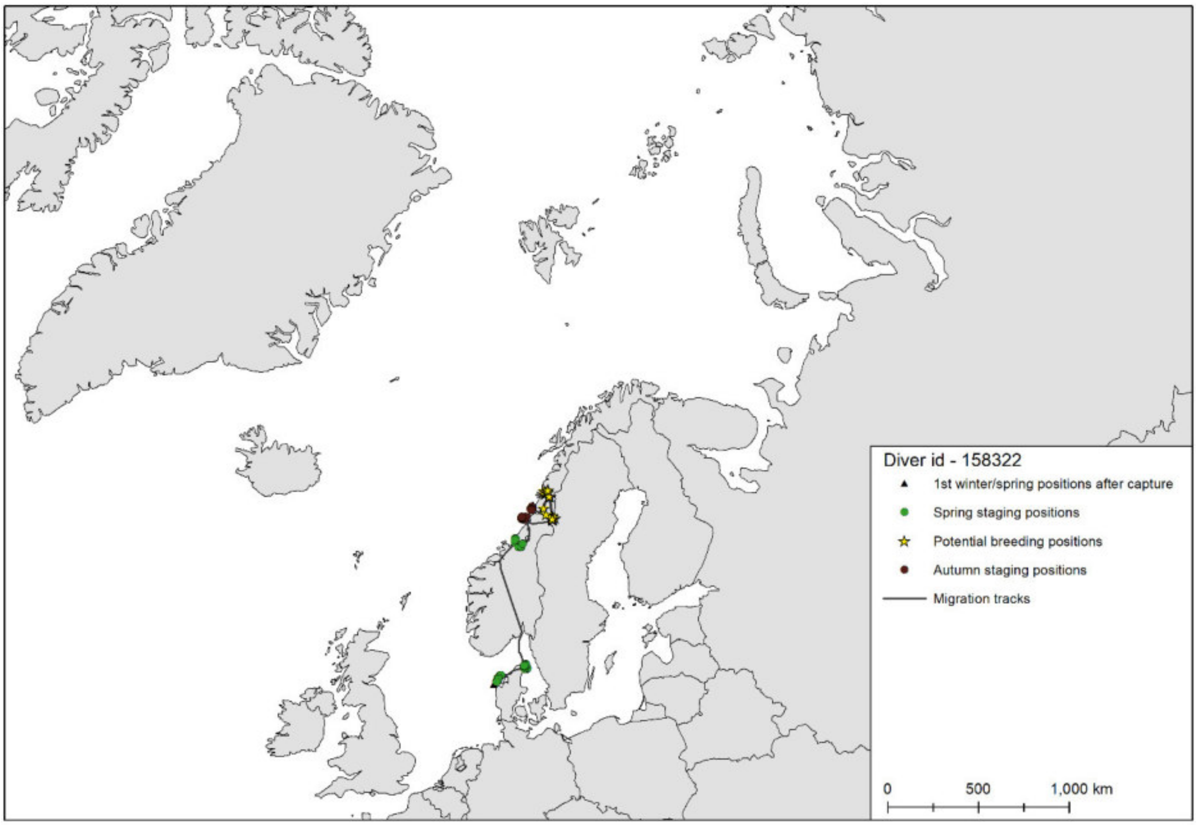


Figure A.25 Migration track of red-throated diver id-158322 covering the period between 27 March 2016 and 11 September 2016.

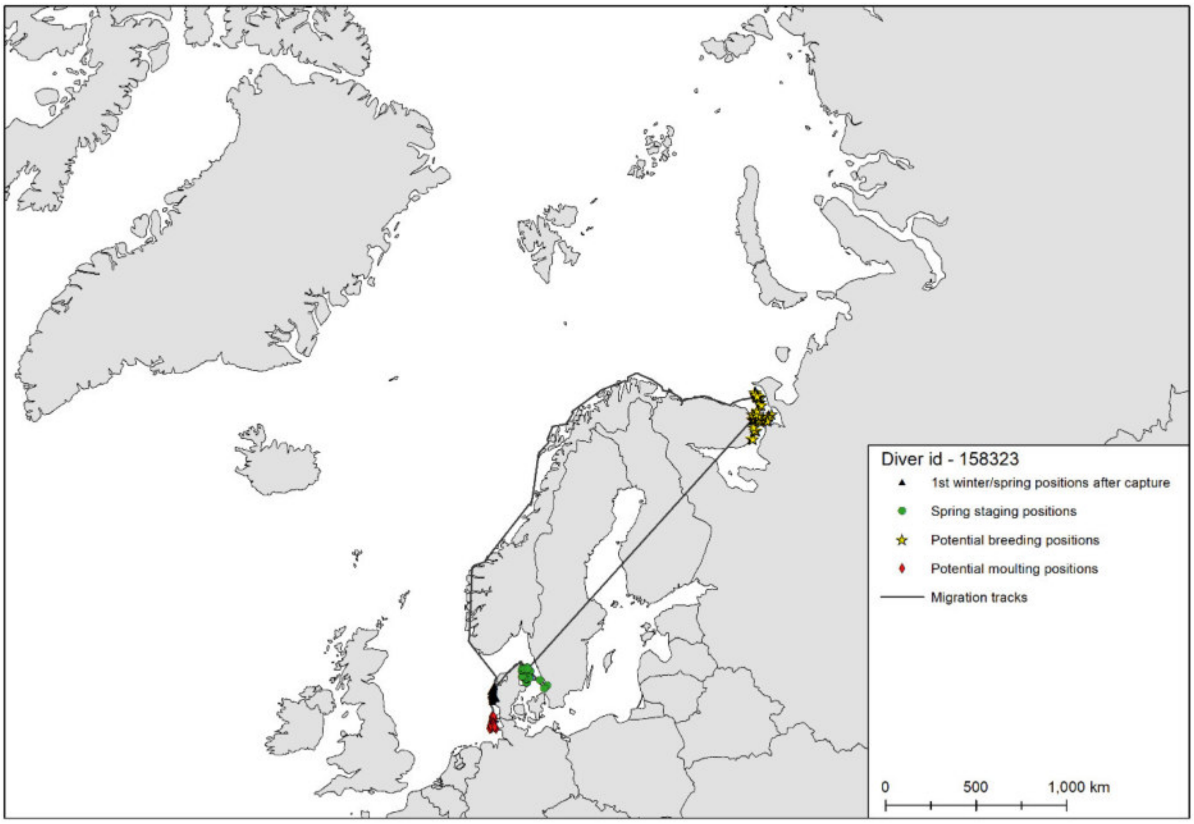


Figure A.26 Migration track of red-throated diver id-158323 covering the period between 27 March 2016 and 13 November 2016.

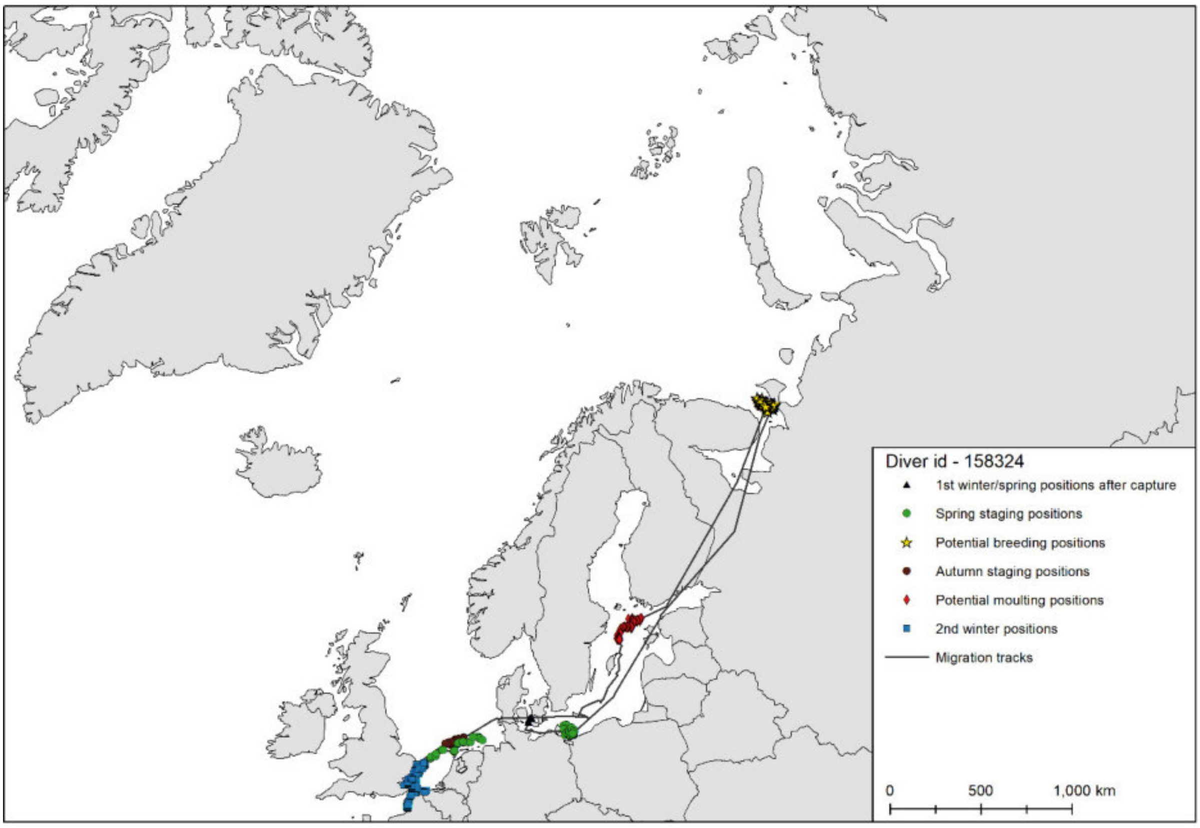


Figure A.27 Migration track of red-throated diver id-158324 covering the period between 27 March 2016 and 08 April 2017.

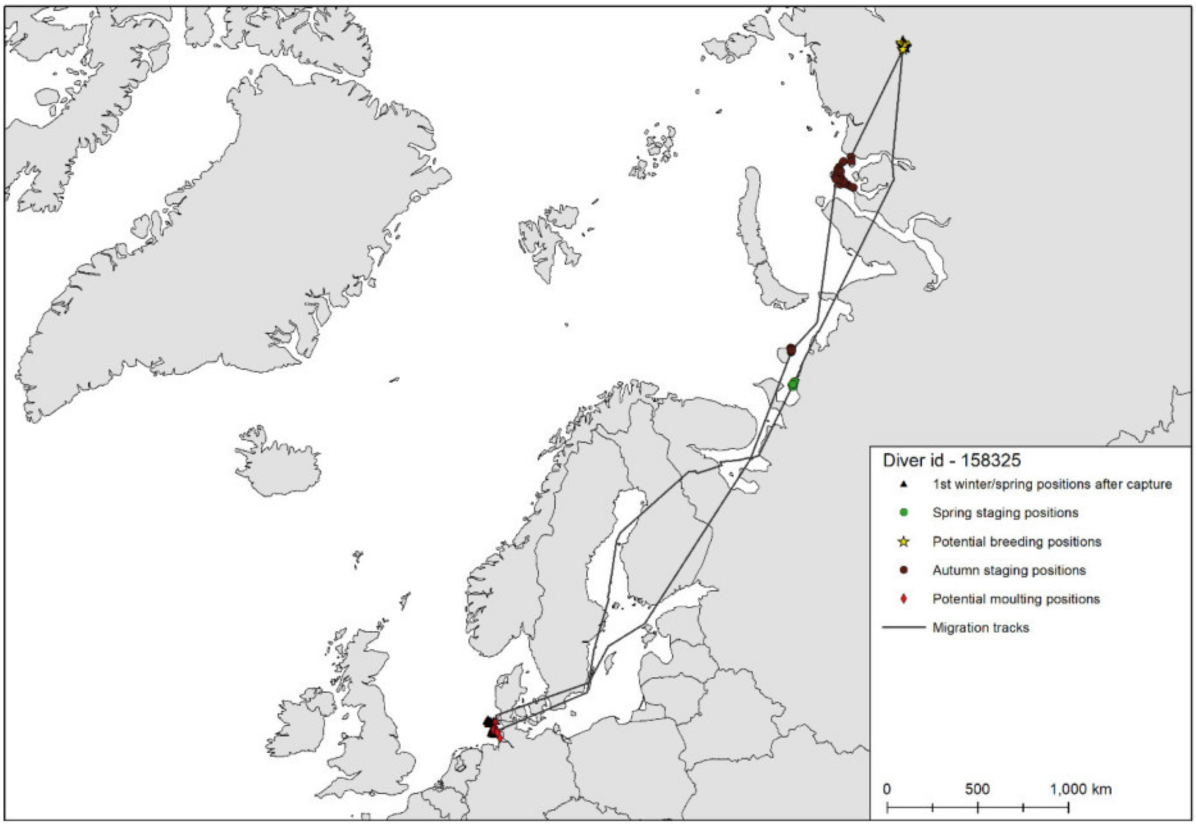


Figure A.28 Migration track of red-throated diver id-158325 covering the period between 28 March 2016 and 21 October 2016.

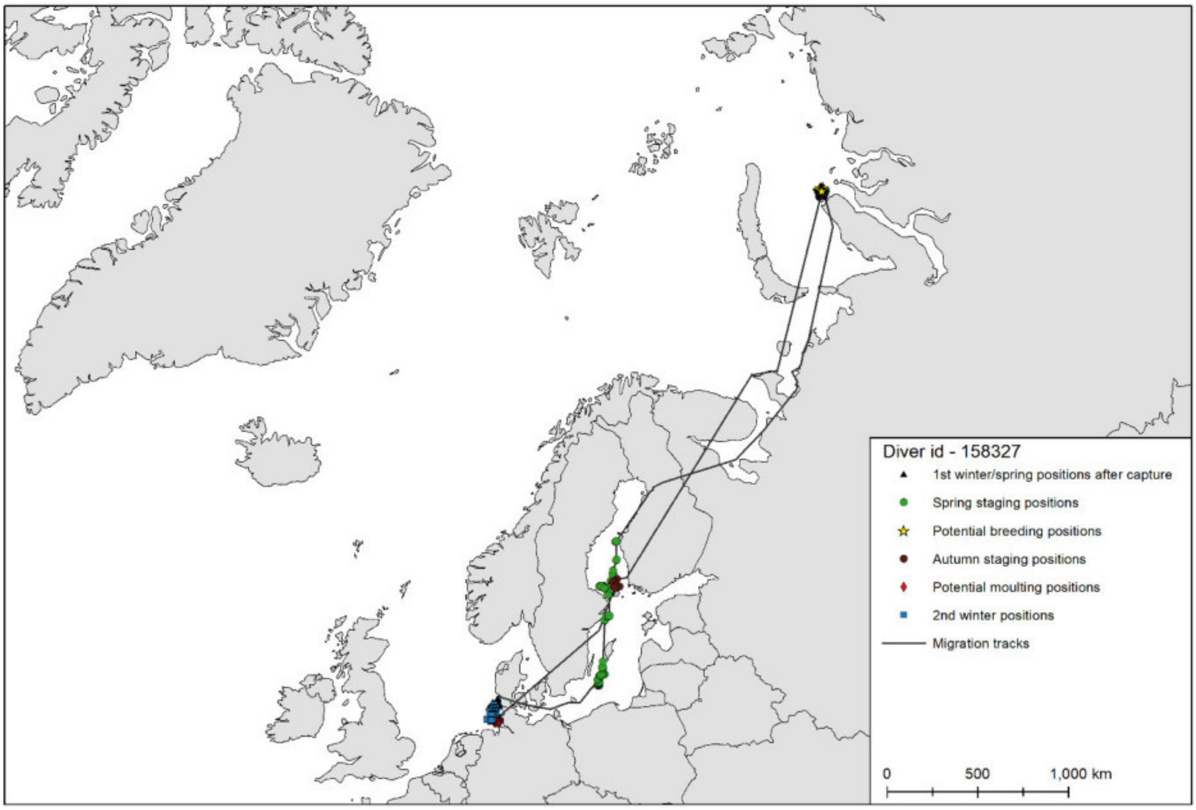


Figure A.29 Migration track of red-throated diver id-158327 covering the period between 13 March 2016 and 28 February 2017.

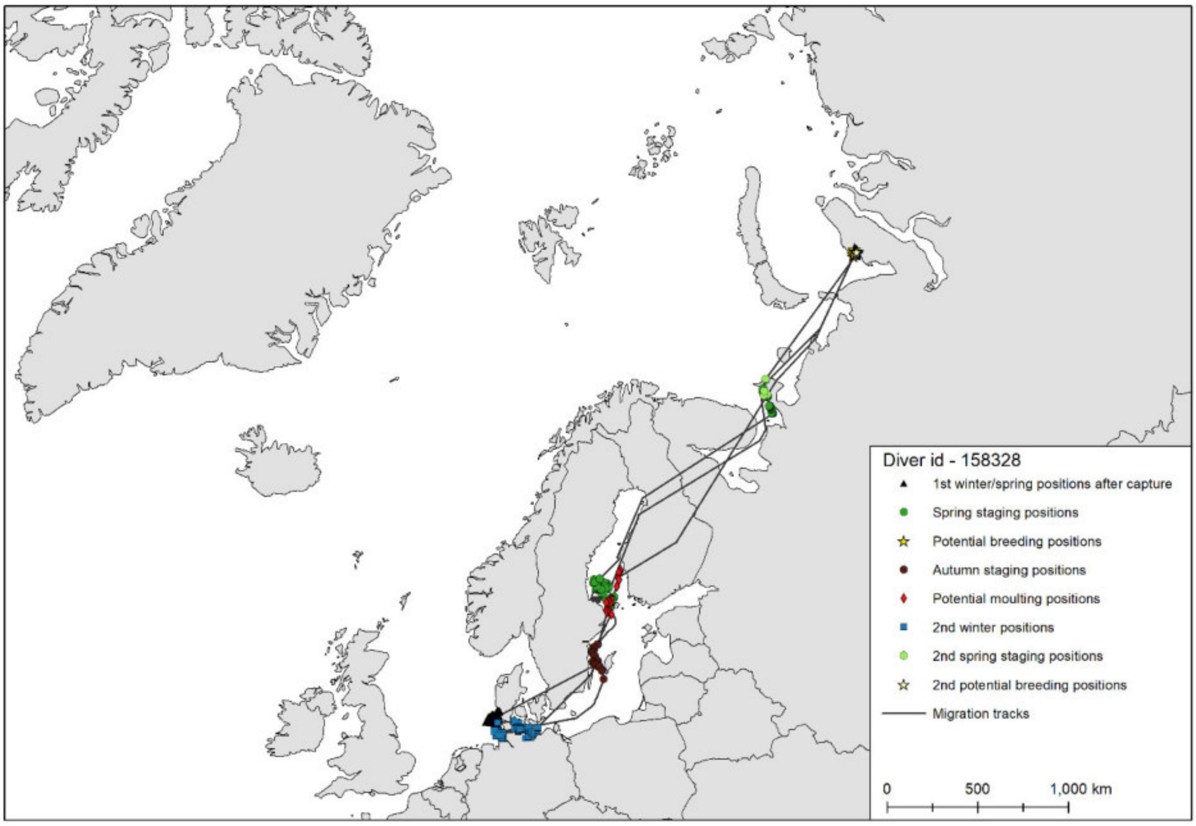


Figure A.30 Migration track of red-throated diver id-158328 covering the period between 14 March 2016 and 28 June 2017.

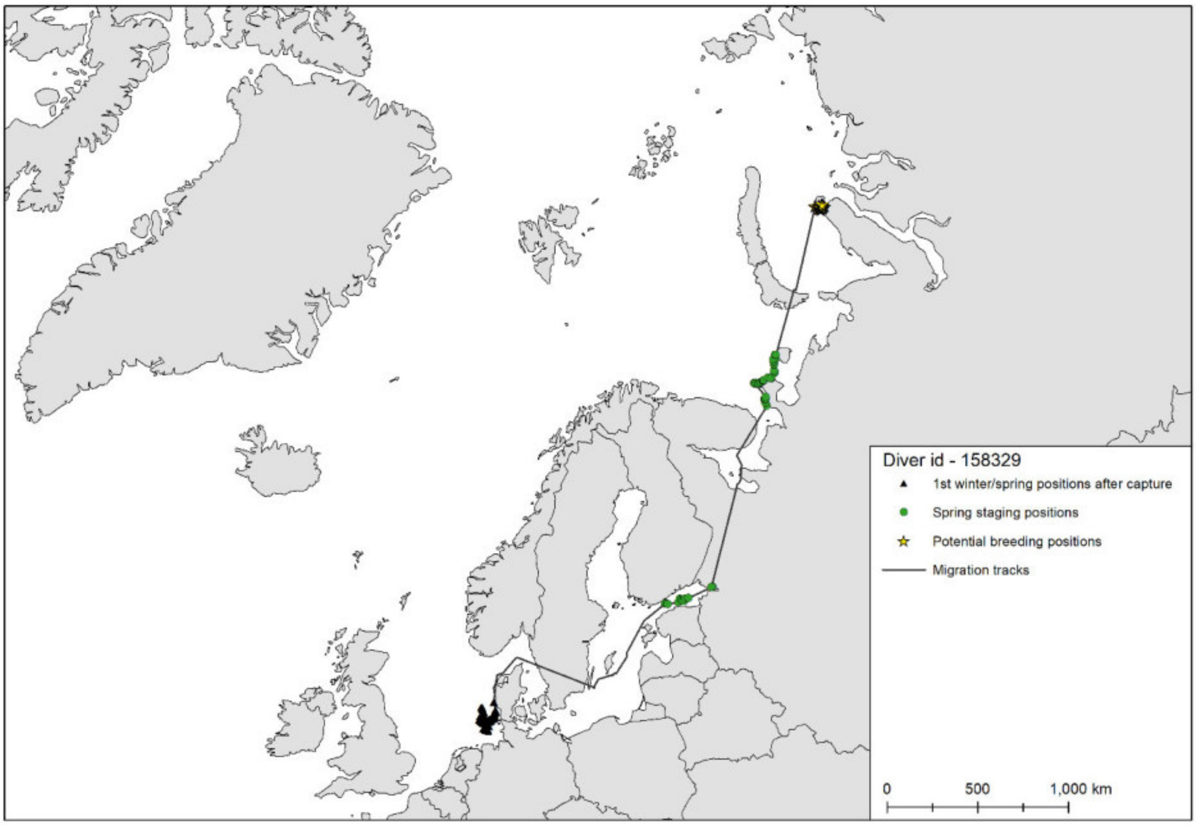


Figure A.31 Migration track of red-throated diver id-158329 covering the period between 14 March 2016 and 20 August 2016.

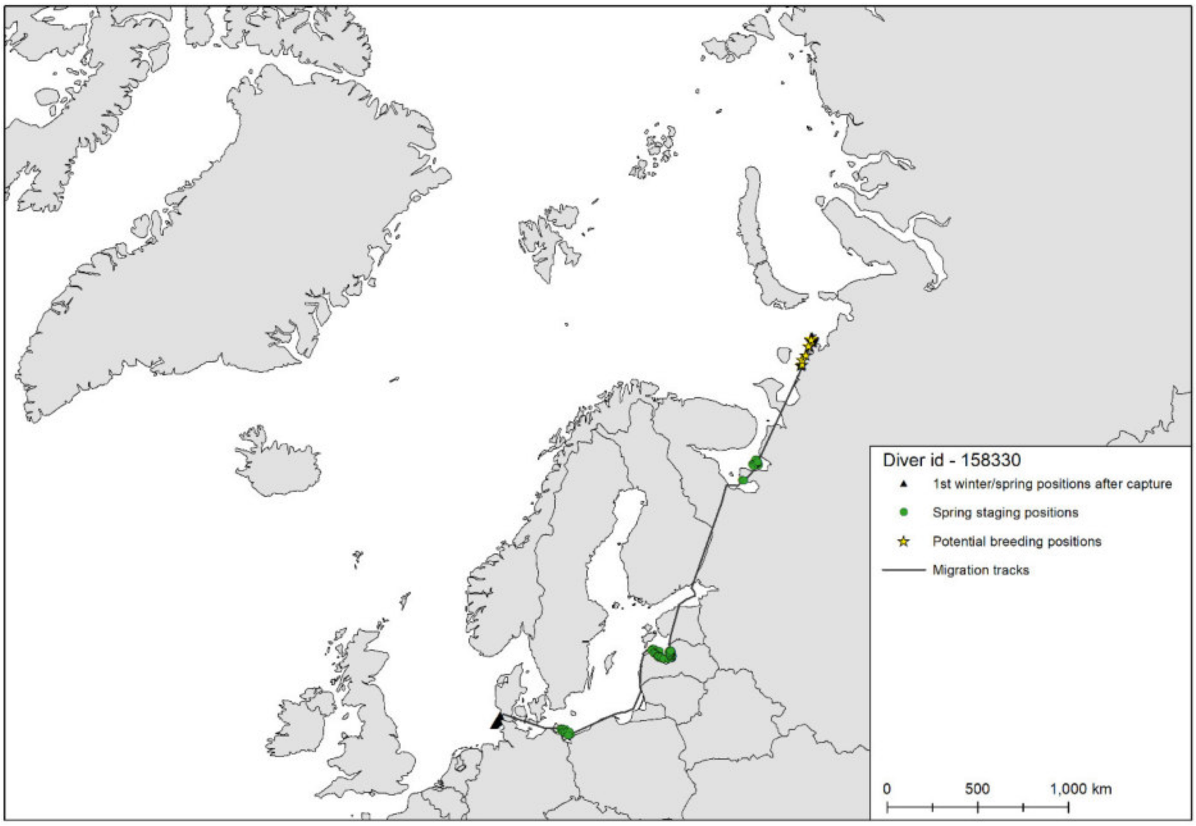


Figure A.32 Migration track of red-throated diver id-158330 covering the period between 14 March 2016 and 02 September 2016.

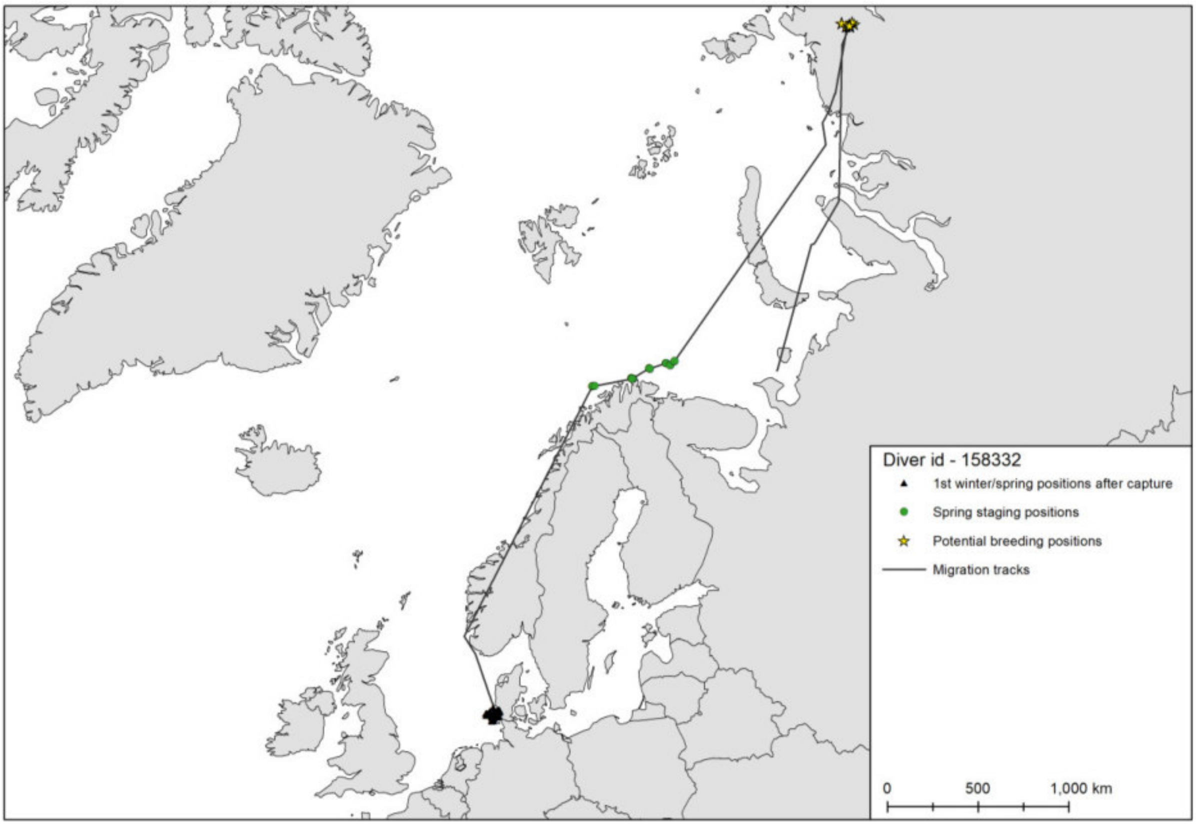


Figure A.33 Migration track of red-throated diver id-158332 covering the period between 13 March 2016 and 09 September 2016.

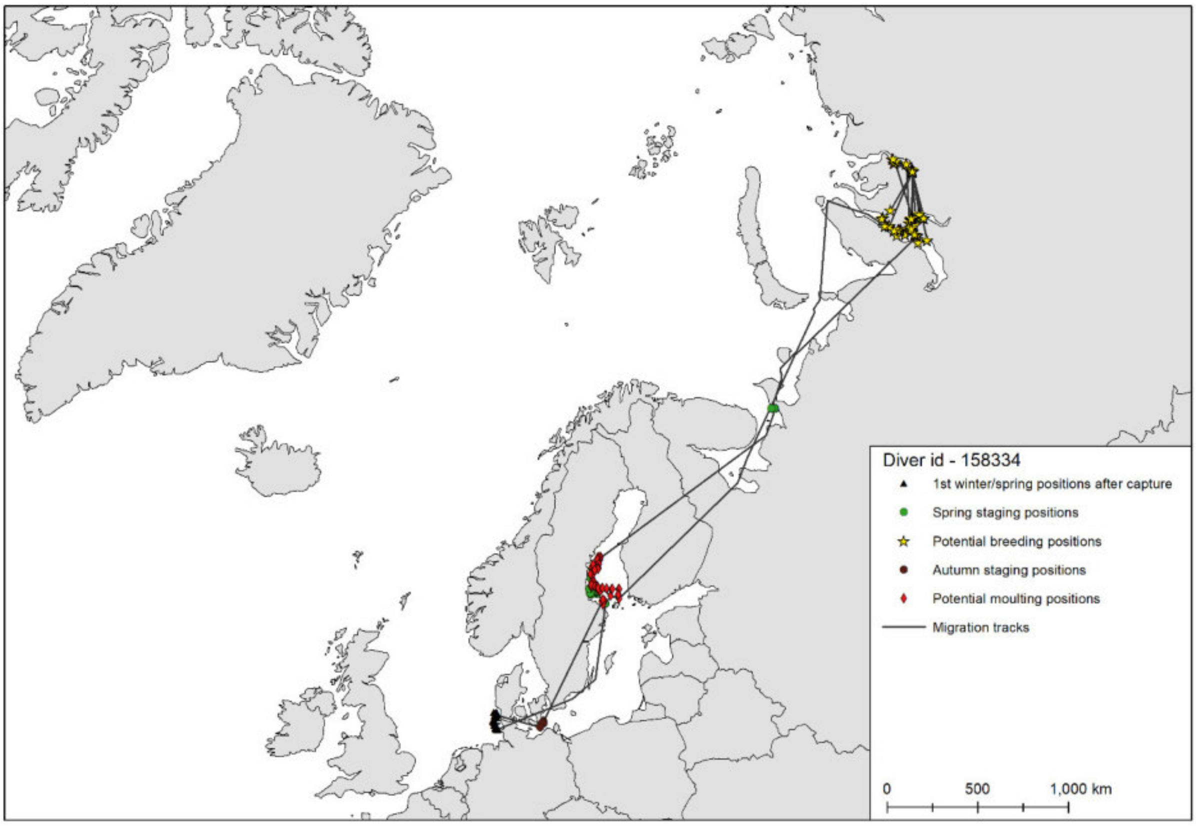


Figure A.34 Migration track of red-throated diver id-158334 covering the period between 27 March 2016 and 13 December 2016.

A.2 Red-throated diver winter home ranges

This chapter contains maps of all winter home ranges calculated as described in chapter 5.3.6.1.

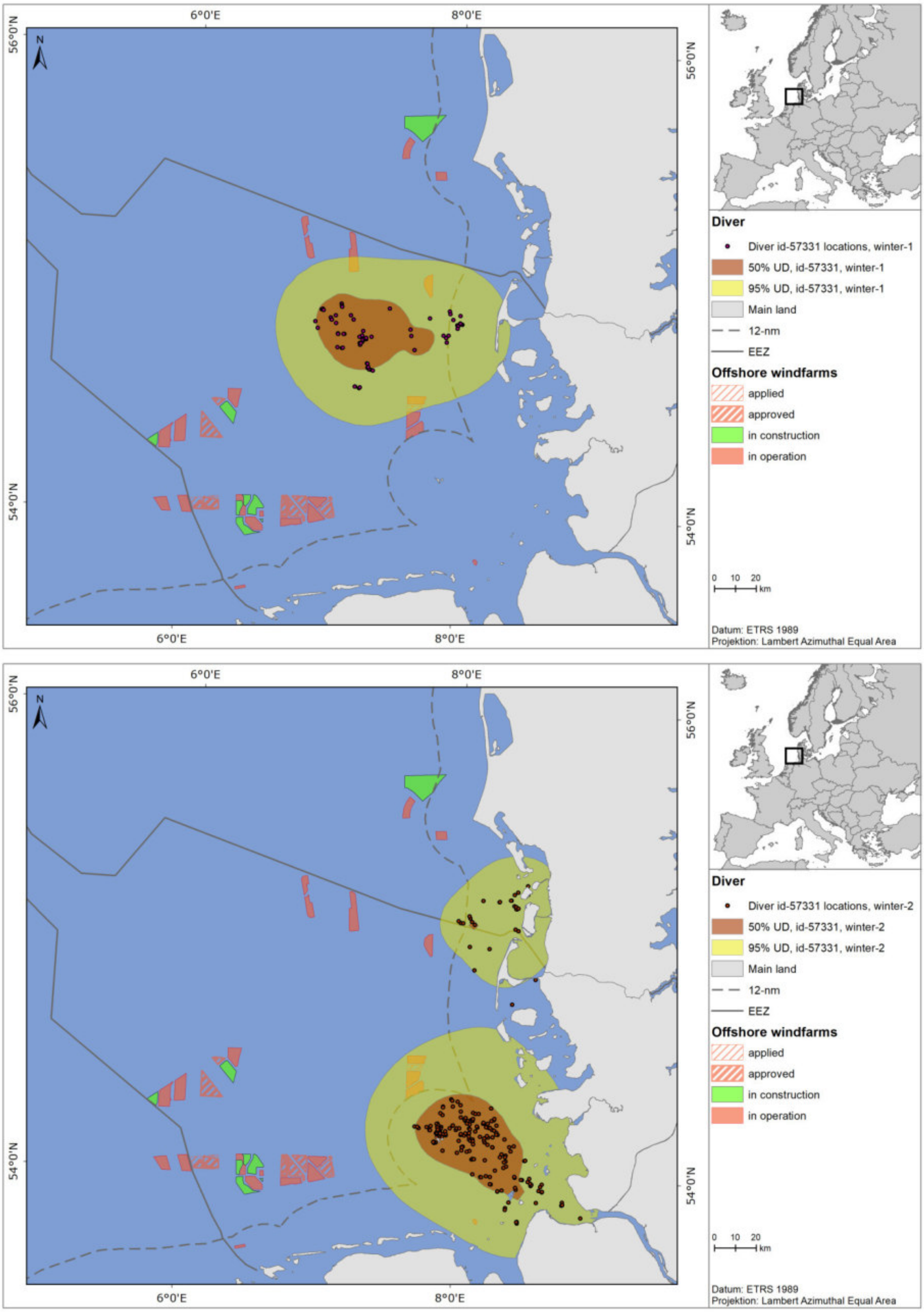


Figure A.35 *Distribution of diver id-57331 in the German Bight presented as 95% UD winter distribution and 50% UD core areas during the first winter (April 12 – May 13, 2017; upper map) and second winter of tracking (September 20, 2017 – May 8, 2018; lower map).*

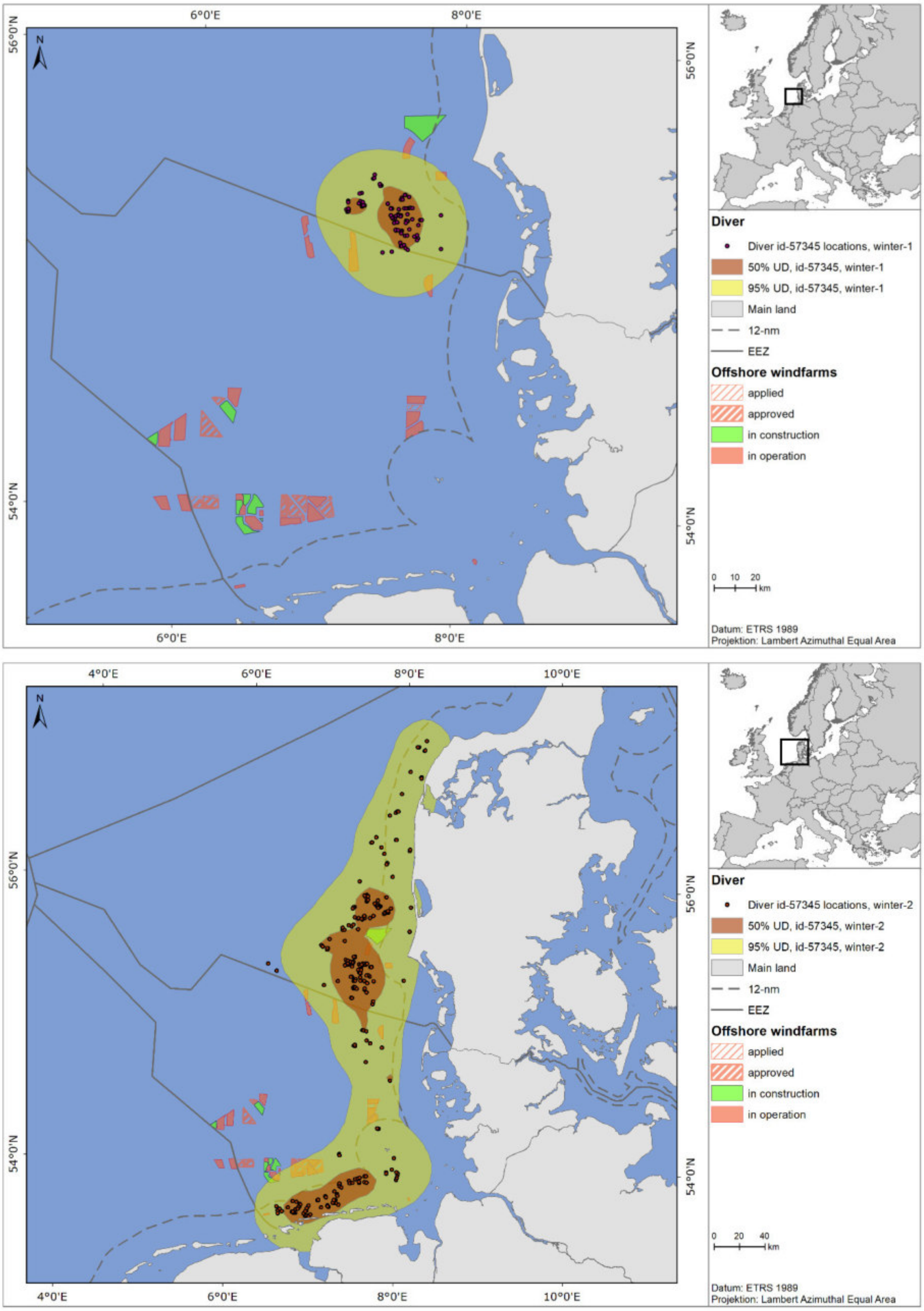
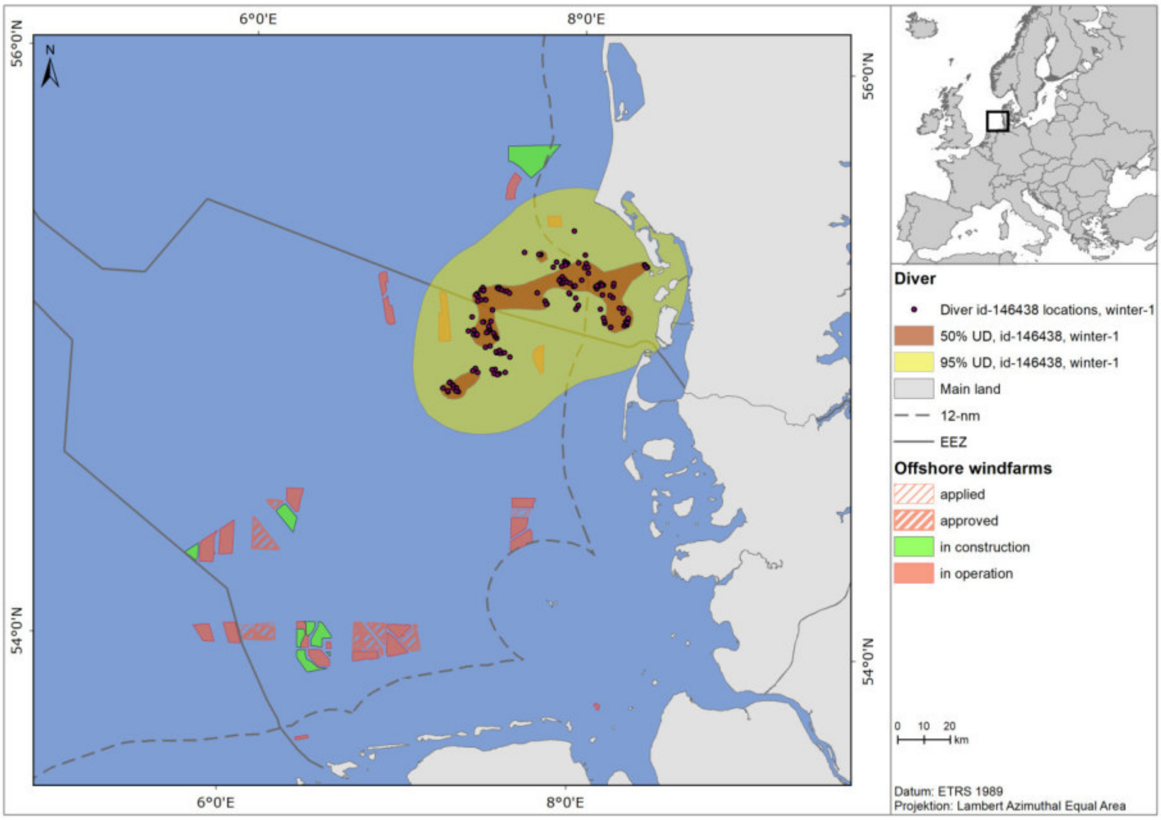


Figure A.36 *Distribution of diver id-57345 in the German Bight presented as 95% UD winter distribution and 50% UD core areas during the first winter (April 8 – May 14, 2017; upper map) and second winter of tracking (October 26, 2017 – May 16, 2018; lower map).*



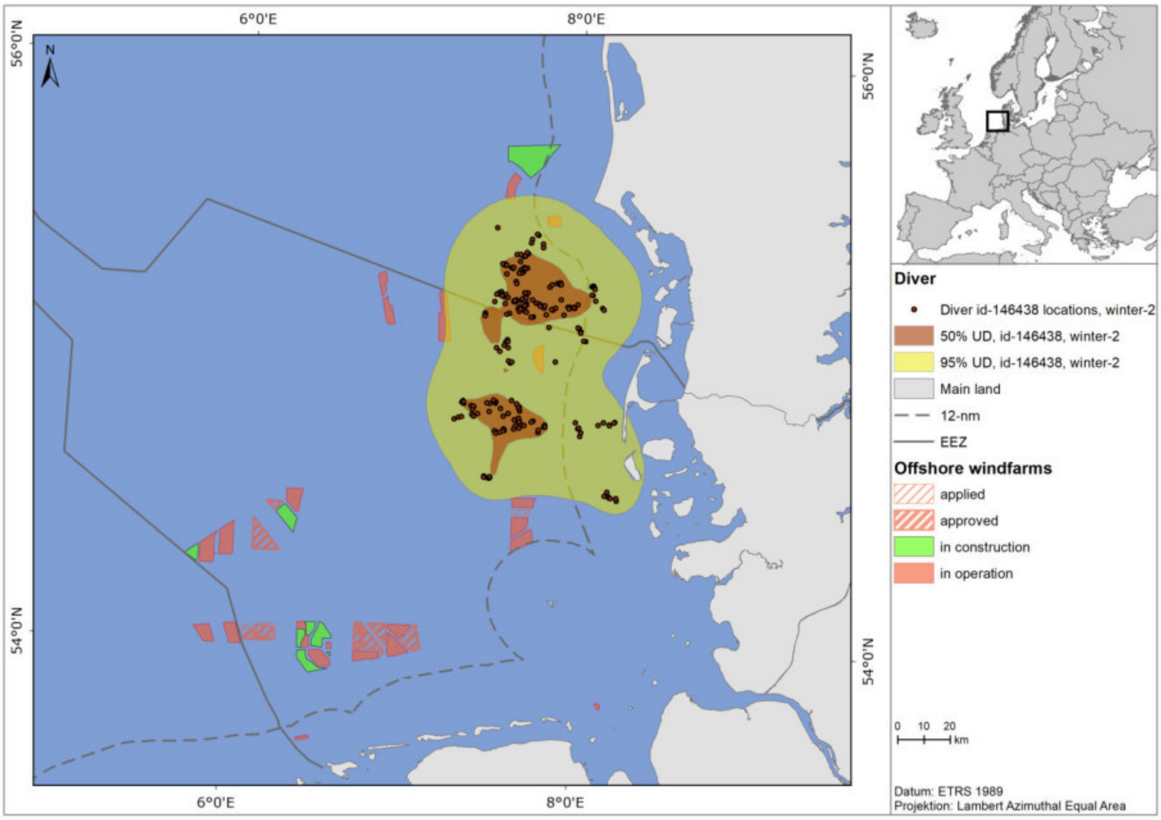
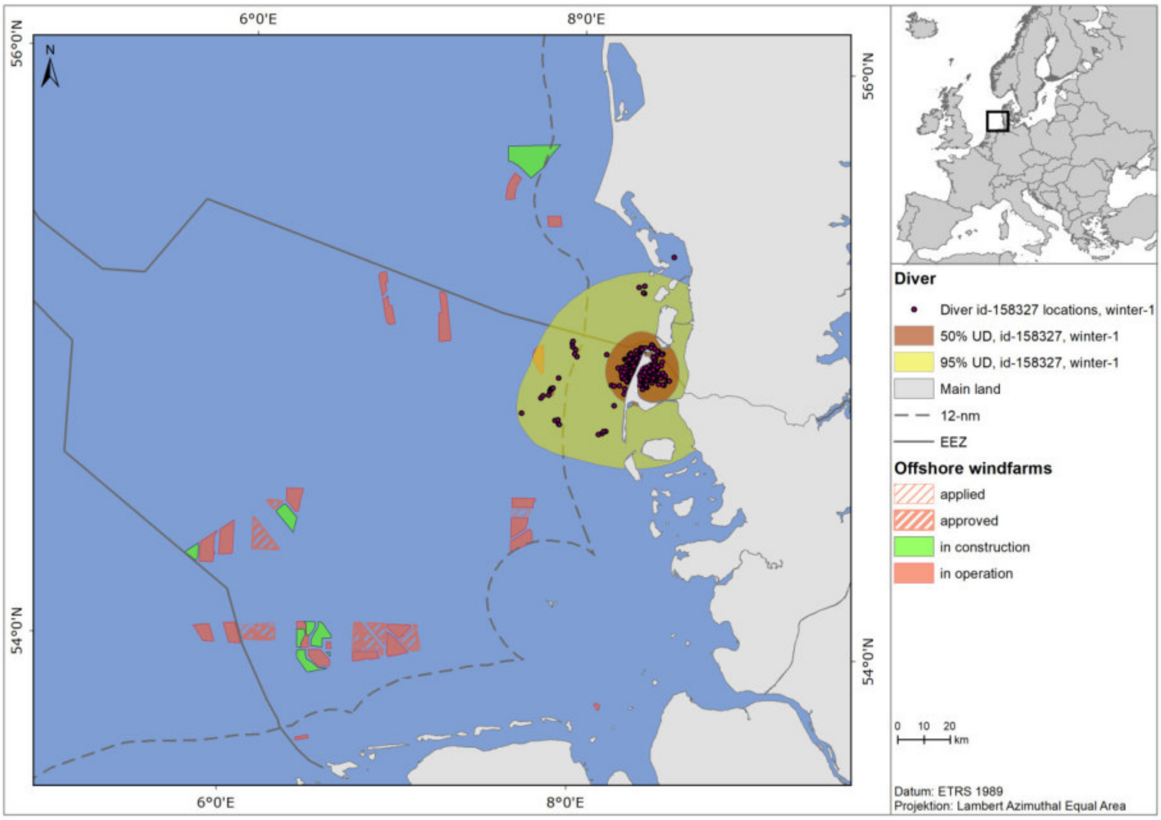


Figure A.37 Distribution of diver id-146438 in the German Bight presented as 95% UD winter distribution and 50% UD core areas during the first winter (April 3 – May 3, 2015; upper map) and second winter of tracking (January 6 – April 27, 2016; lower map).


6°0'E
8°0'E
56°0'N
54°0'N
N
Diver
Diver id-158327 locations, winter-1
50% UD, id-158327, winter-1
95% UD, id-158327, winter-1
Main land
12-nm
EEZ
Offshore windfarms
applied
approved
in construction
in operation
0 10 20 km
Datum: ETRS 1989
Projektion: Lambert Azimuthal Equal Area

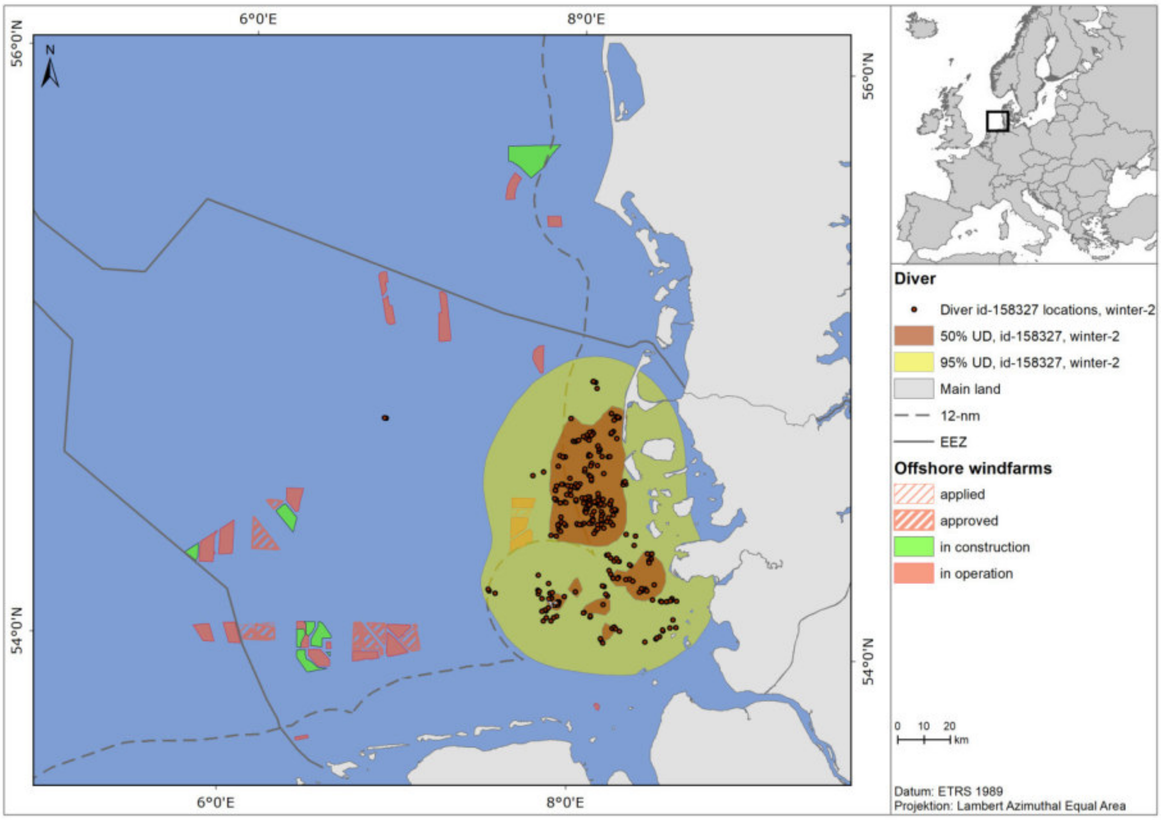
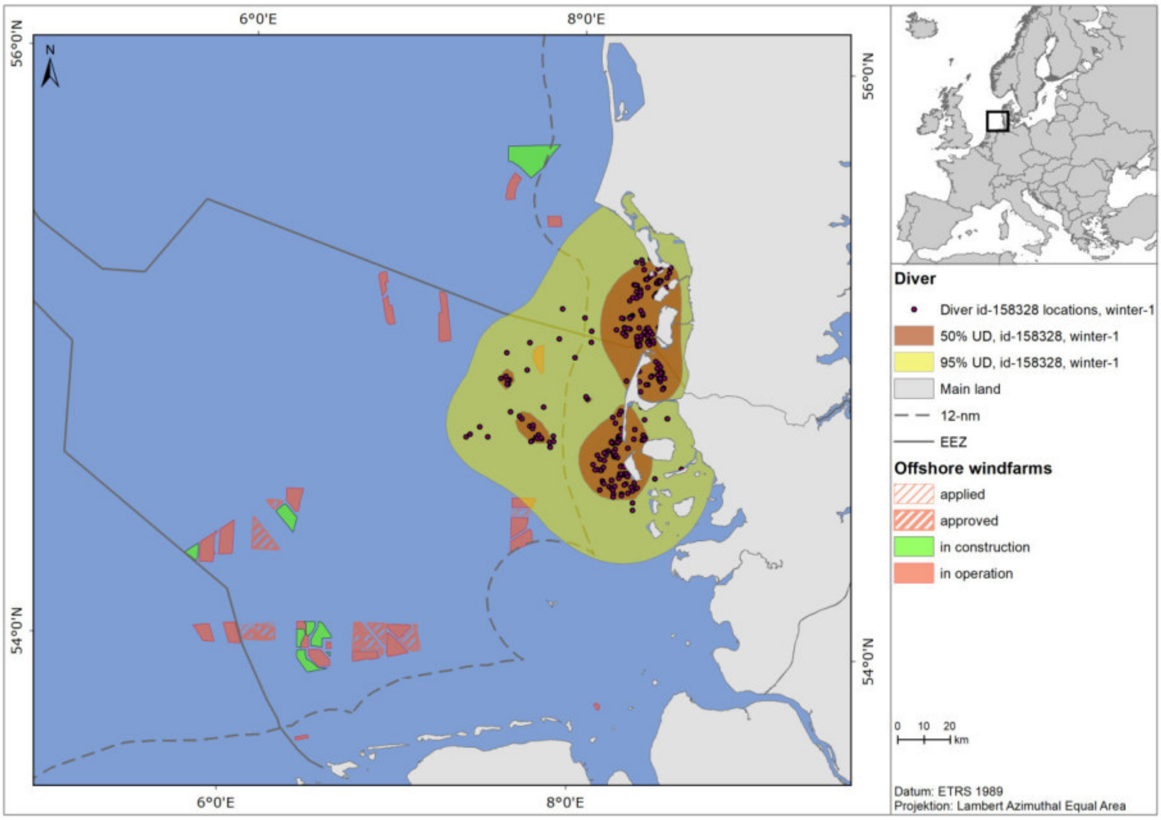

6°0'E
8°0'E
56°0'N
54°0'N
N
Diver
Diver id-158327 locations, winter-2
50% UD, id-158327, winter-2
95% UD, id-158327, winter-2
Main land
12-nm
EEZ
Offshore windfarms
applied
approved
in construction
in operation
0 10 20 km
Datum: ETRS 1989
Projektion: Lambert Azimuthal Equal Area

Figure A.38 *Distribution of diver id-158327 in the German Bight and southern Baltic Sea presented as 95% UD winter distribution and 50% UD core areas during the first winter (March 13 – May 4, 2016; upper map) and second winter of tracking (October 22, 2016 – February 28, 2017; lower map).*


6°0'E
8°0'E
56°0'N
54°0'N
N
Diver
Diver id-158328 locations, winter-1
50% UD, id-158328, winter-1
95% UD, id-158328, winter-1
Main land
12-nm
EEZ
Offshore windfarms
applied
approved
in construction
in operation
0 10 20
km
Datum: ETRS 1989
Projektion: Lambert Azimuthal Equal Area

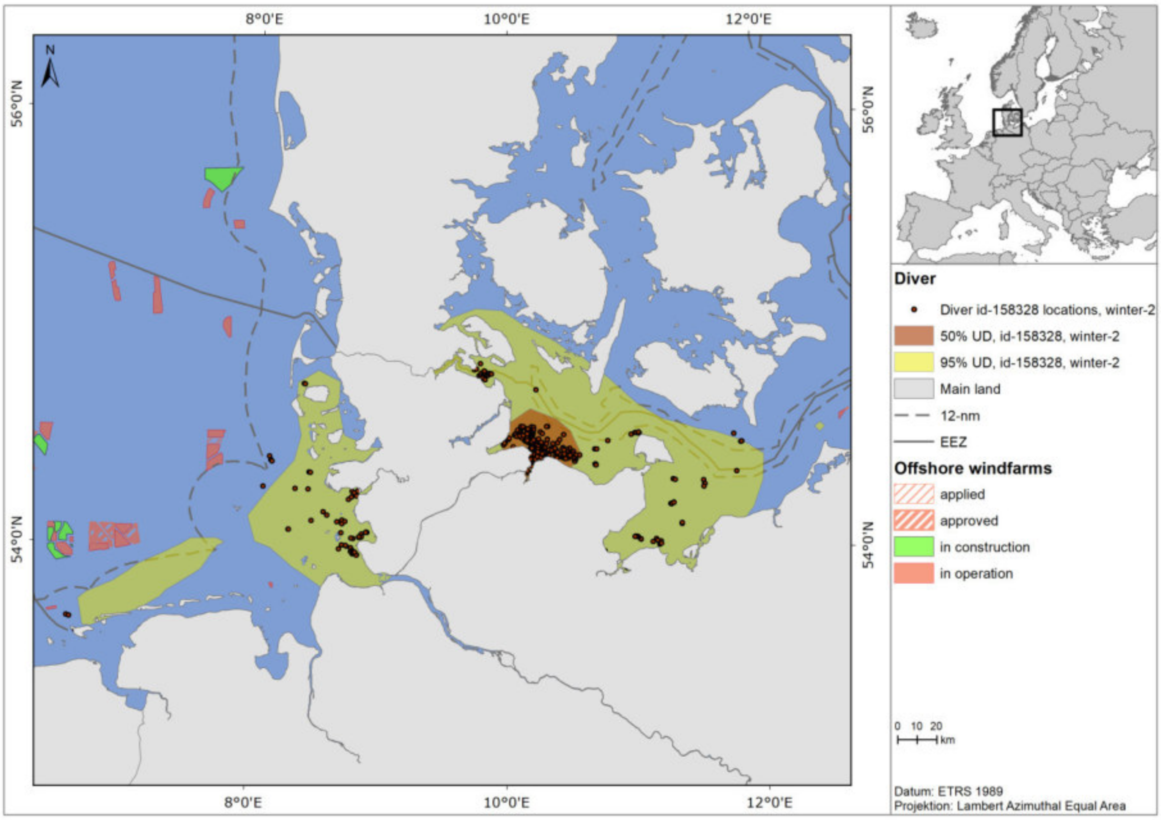

8°0'E
10°0'E
12°0'E
56°0'N
54°0'N
N
Diver
Diver id-158328 locations, winter-2
50% UD, id-158328, winter-2
95% UD, id-158328, winter-2
Main land
12-nm
EEZ
Offshore windfarms
applied
approved
in construction
in operation
0 10 20
km
Datum: ETRS 1989
Projektion: Lambert Azimuthal Equal Area

Figure A.39 Distribution of diver id-158328 in the German Bight and southern Baltic Sea presented as 95% UD winter distribution and 50% UD core areas during the first winter (March 14 – April 28, 2016; upper map) and second winter of tracking (December 3, 2016 – April 14, 2017; lower map).

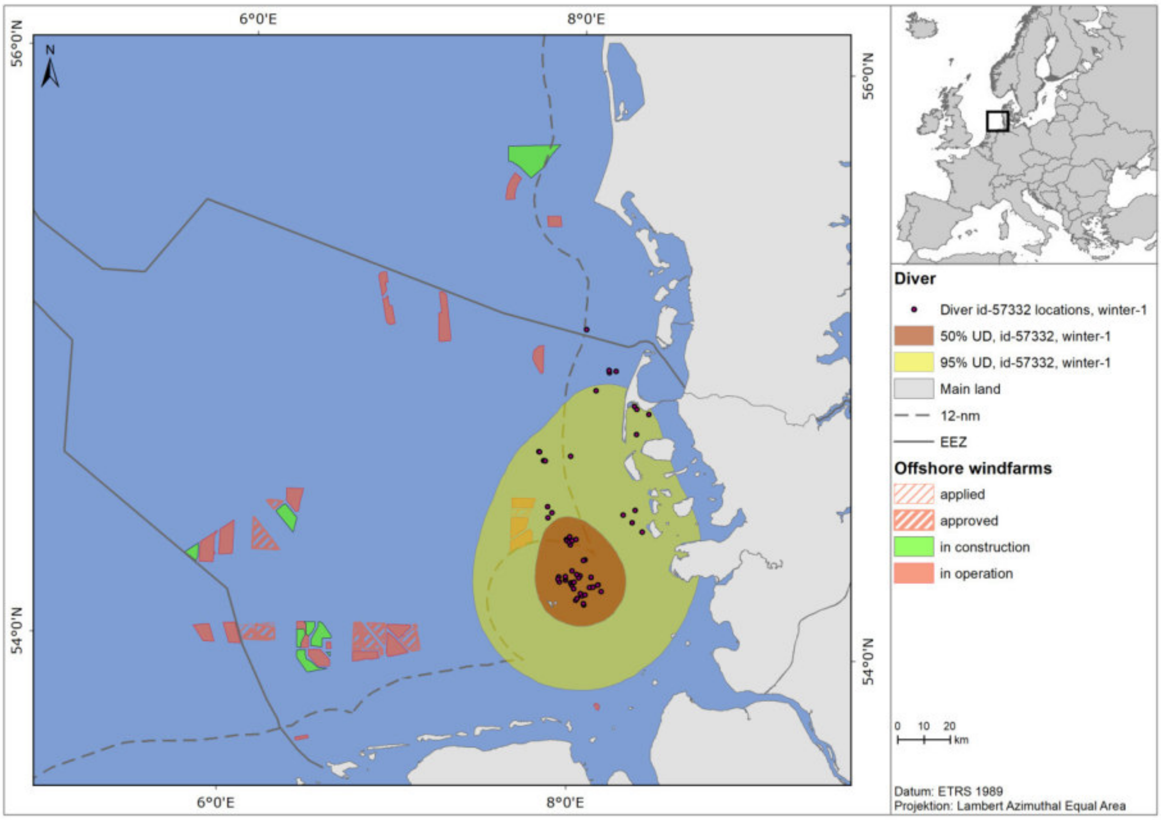


Figure A.40 Distribution of diver id-57332 in the German Bight presented as 95% UD winter distribution and 50% UD core area during the first winter of tracking (April 8 – May 9, 2017).

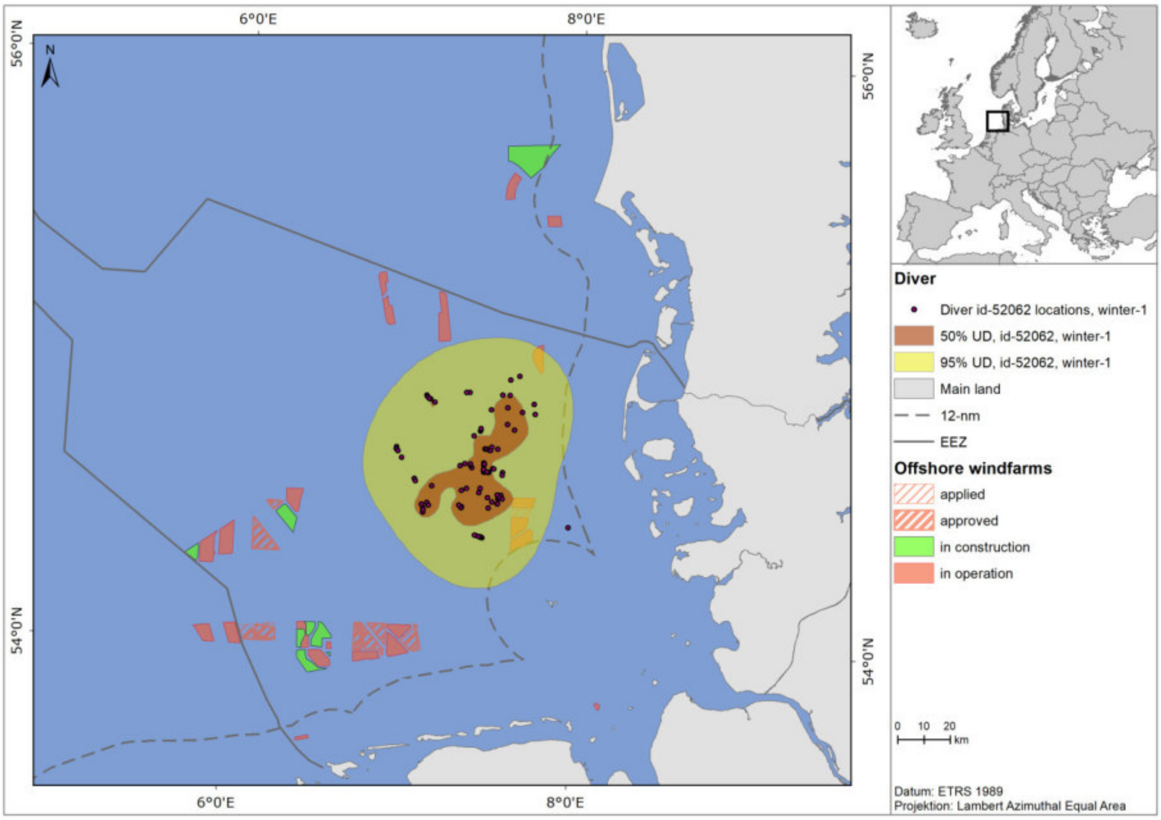


Figure A.41 Distribution of diver id-52062 in the German Bight presented as 95% UD winter distribution and 50% UD core area during the first winter of tracking (April 8 – May 9, 2017).

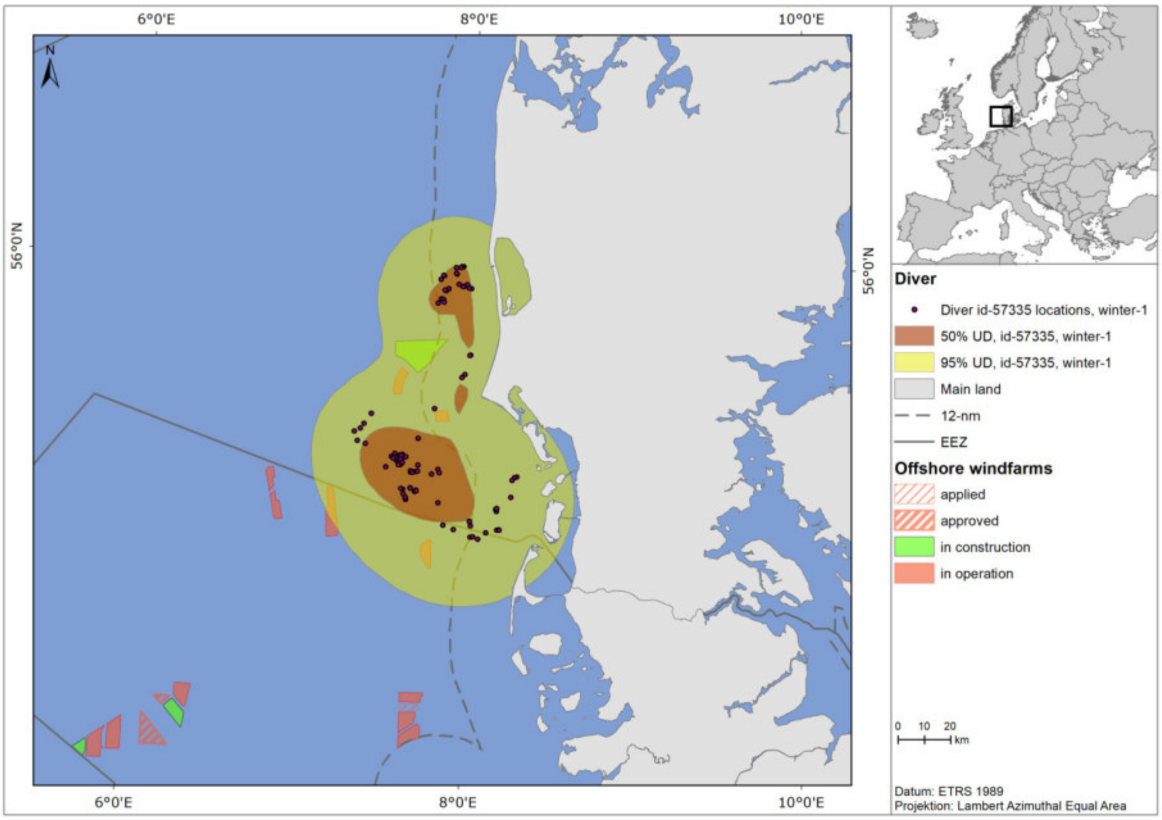


Figure A.42 *Distribution of diver id-57335 in the German Bight presented as 95% UD winter distribution and 50% UD core area during the first winter of tracking (April 11 – May 11, 2017).*

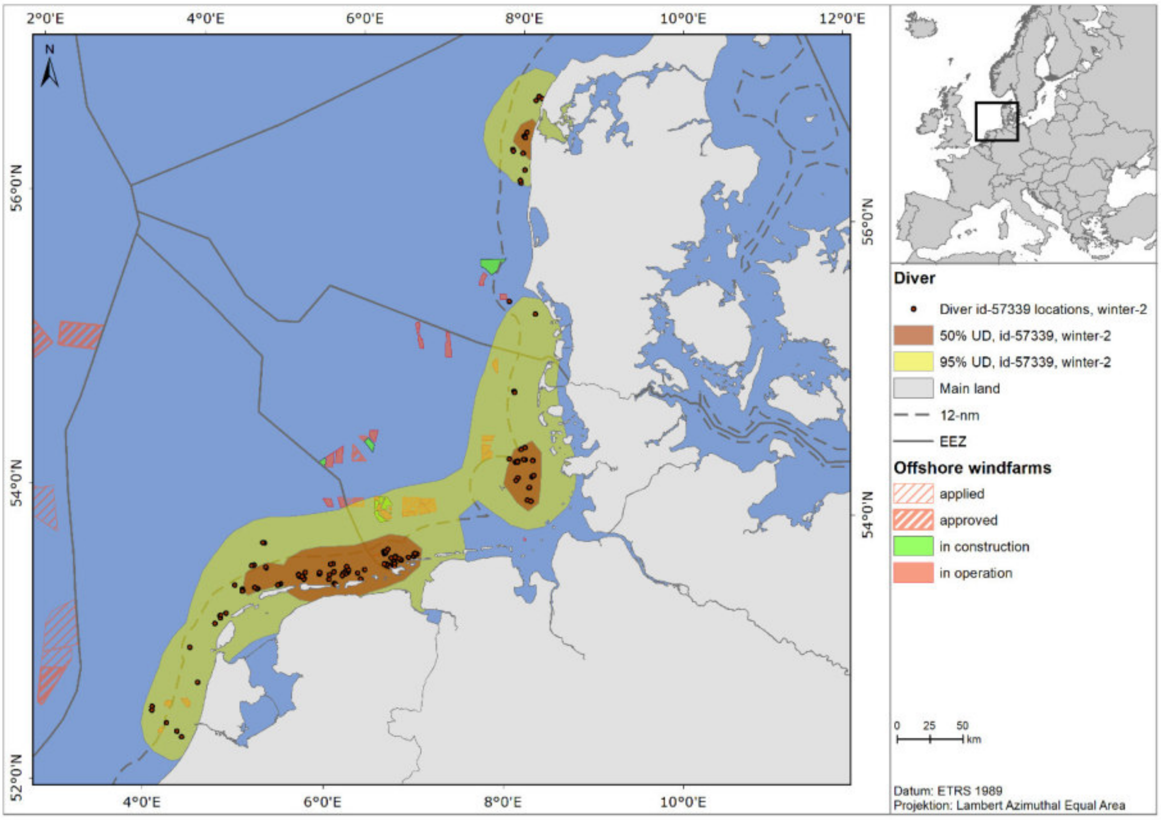


Figure A.43 *Distribution of diver id-57339 in the eastern North Sea presented as 95% UD winter distribution and 50% UD core area during the second winter of tracking (Jan 9 – Apr 20, 2018).*

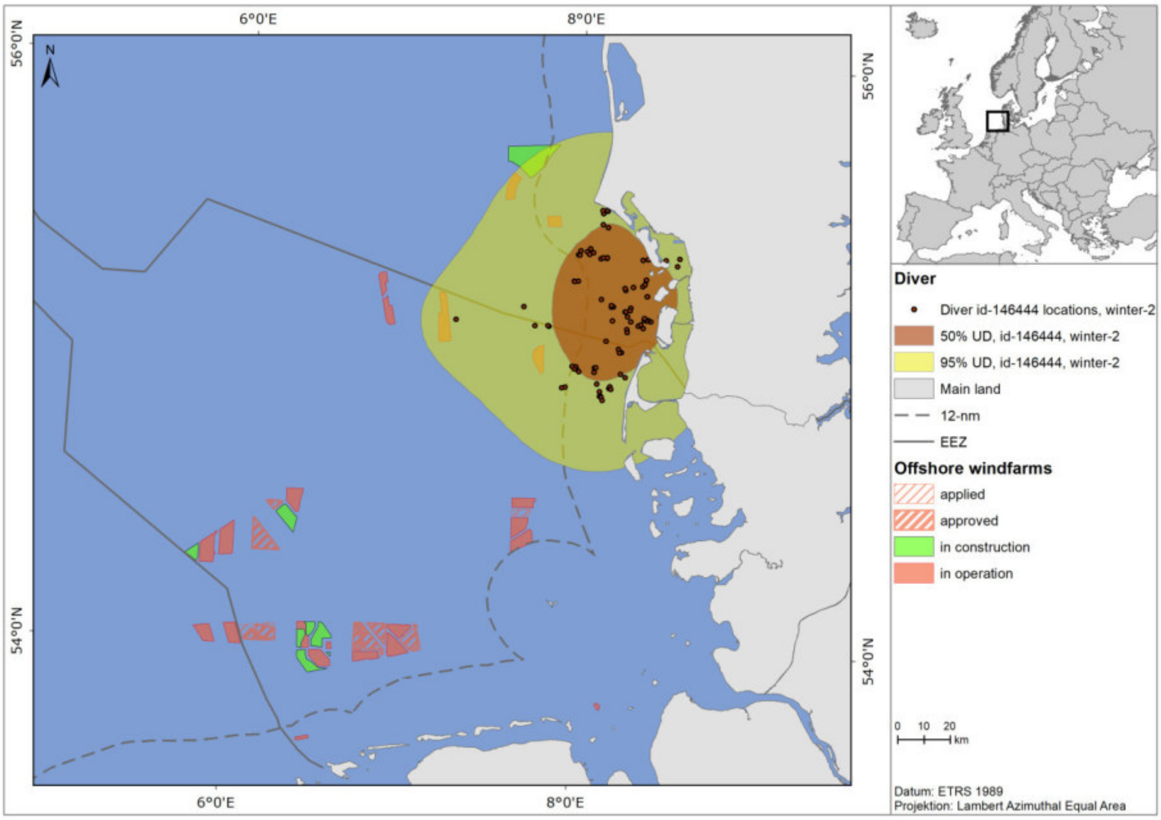


Figure A.44 Distribution of diver id-146444 in the German Bight presented as 95% UD winter distribution and 50% UD core area during the second winter of tracking (January 9 – March 23, 2016).

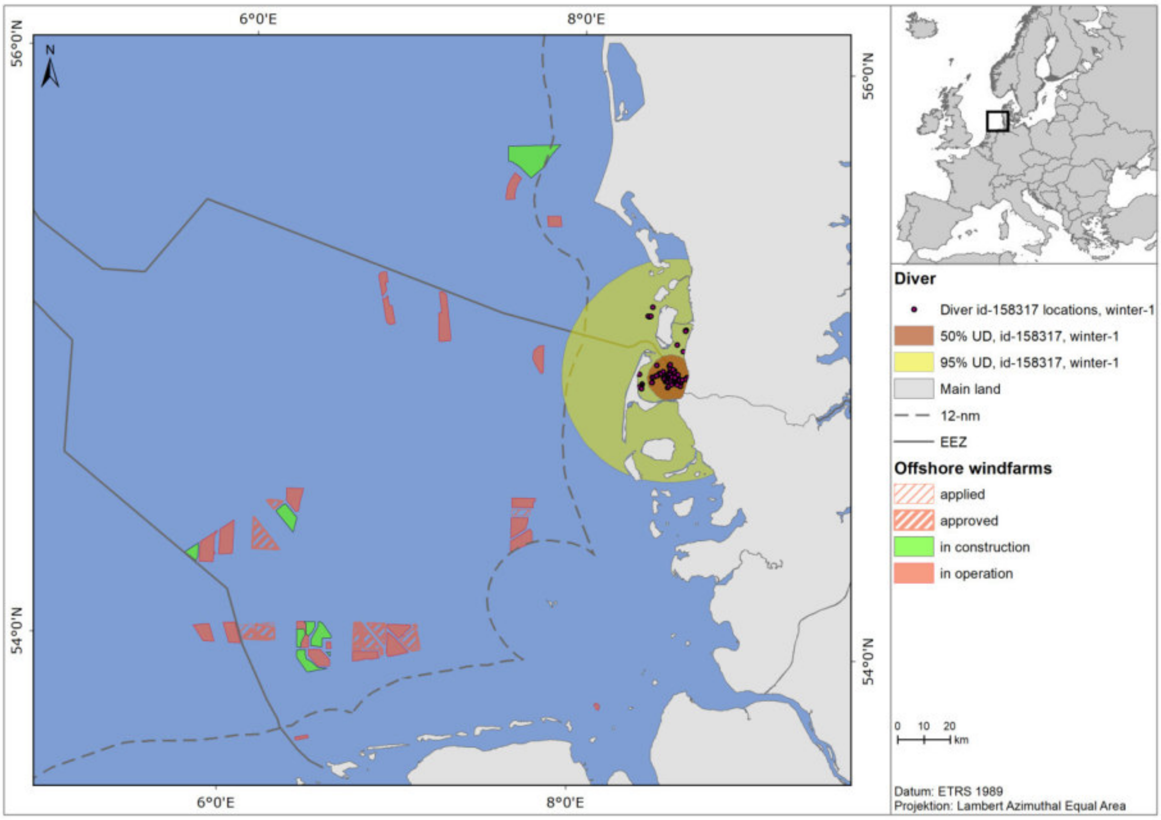


Figure A.45 Distribution of diver id-158317 in the German Bight presented as 95% UD winter distribution and 50% UD core area during the first winter of tracking (March 26 – May 2, 2016).

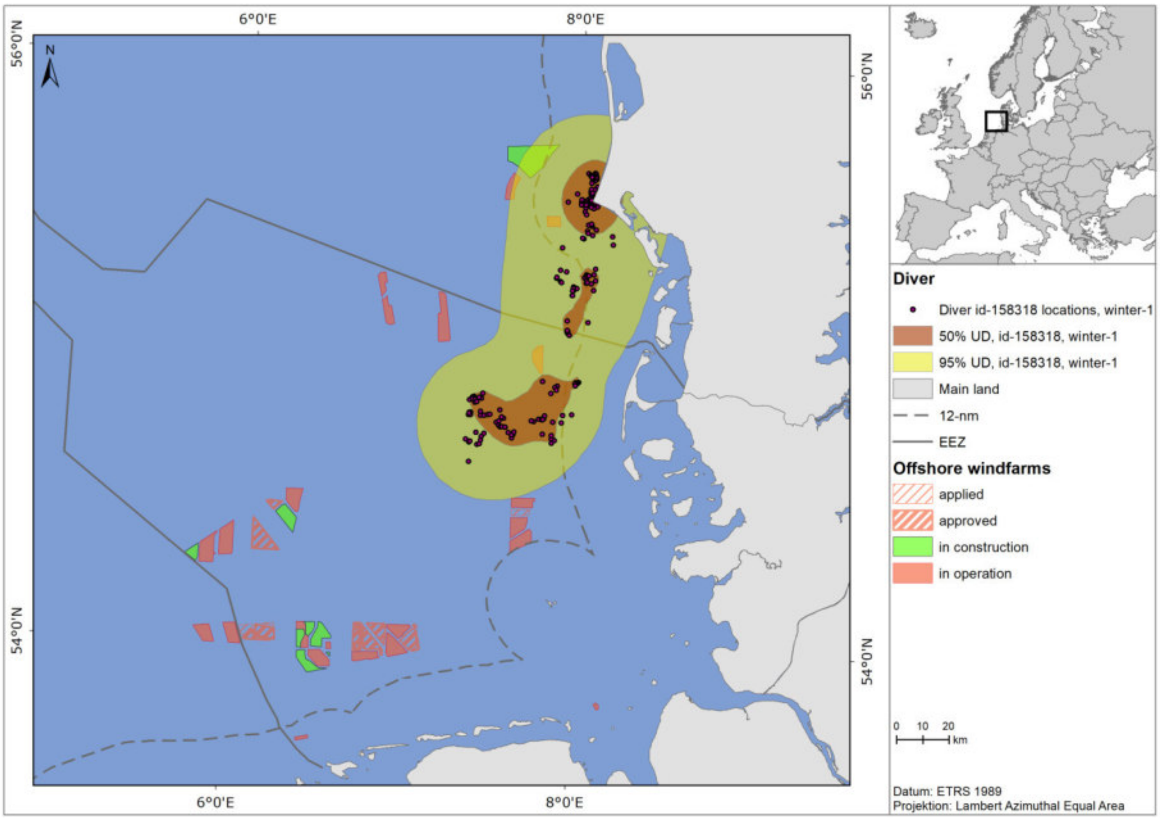


Figure A.46 Distribution of diver id-158318 in the German Bight presented as 95% UD winter distribution and 50% UD core area during the first winter of tracking (March 26 – May 20, 2016).

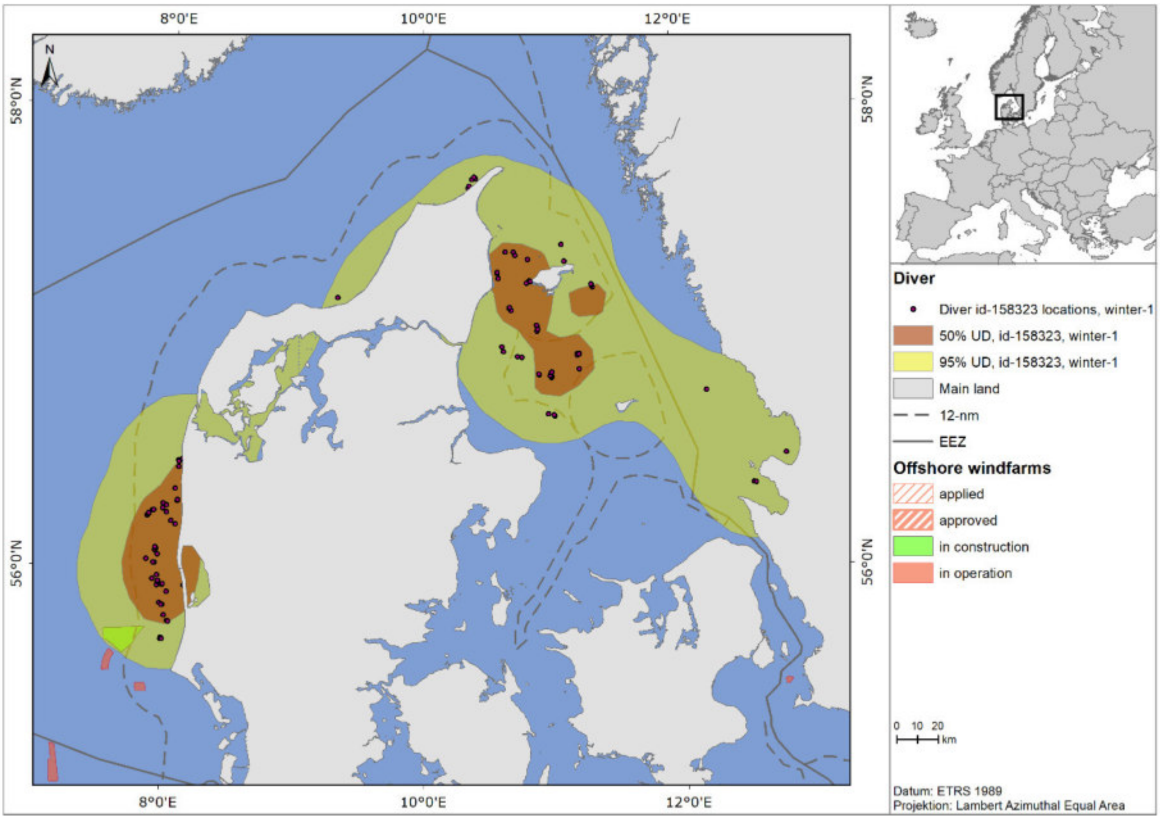


Figure A.47 *Distribution of diver id-158323 in the German Bight and Kattegat presented as 95% UD winter distribution and 50% UD core area during the first winter of tracking (March 27 – May 16, 2016).*

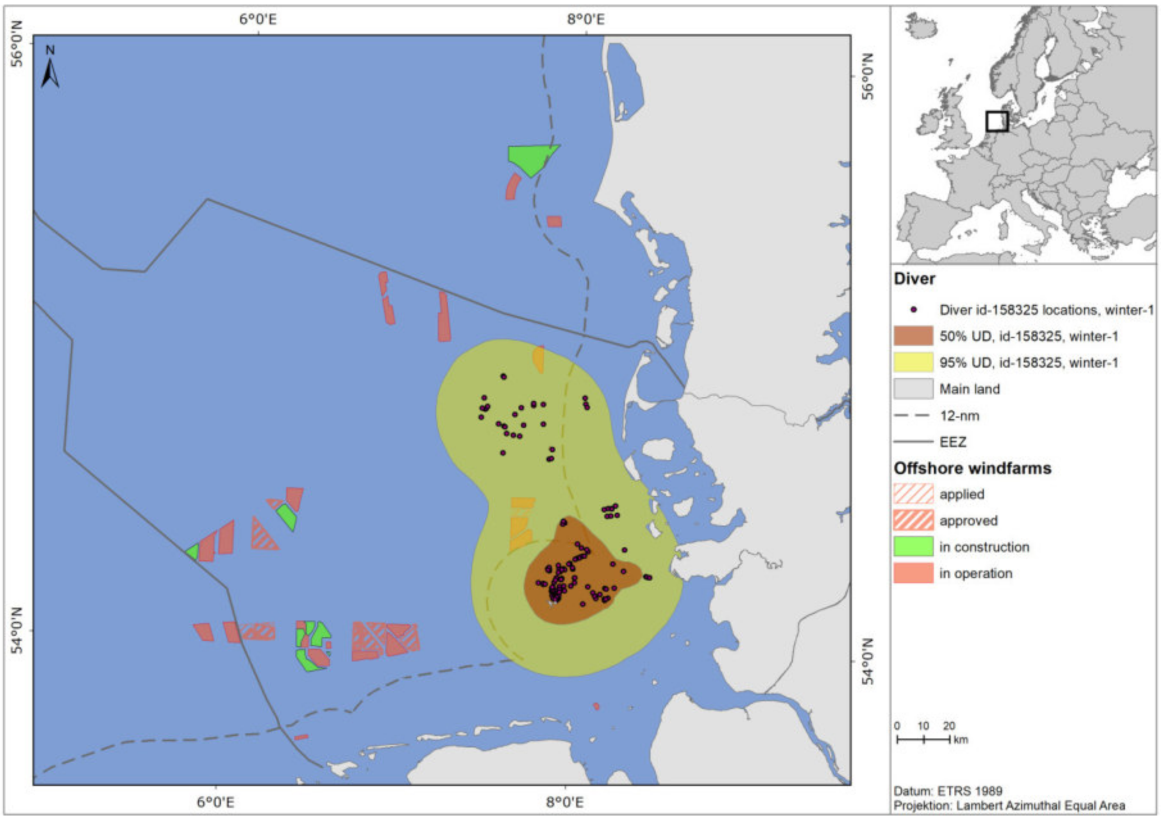


Figure A.48 *Distribution of diver id-158325 in the German Bight presented as 95% UD winter distribution and 50% UD core area during the first winter of tracking (March 28 – May 17, 2016).*

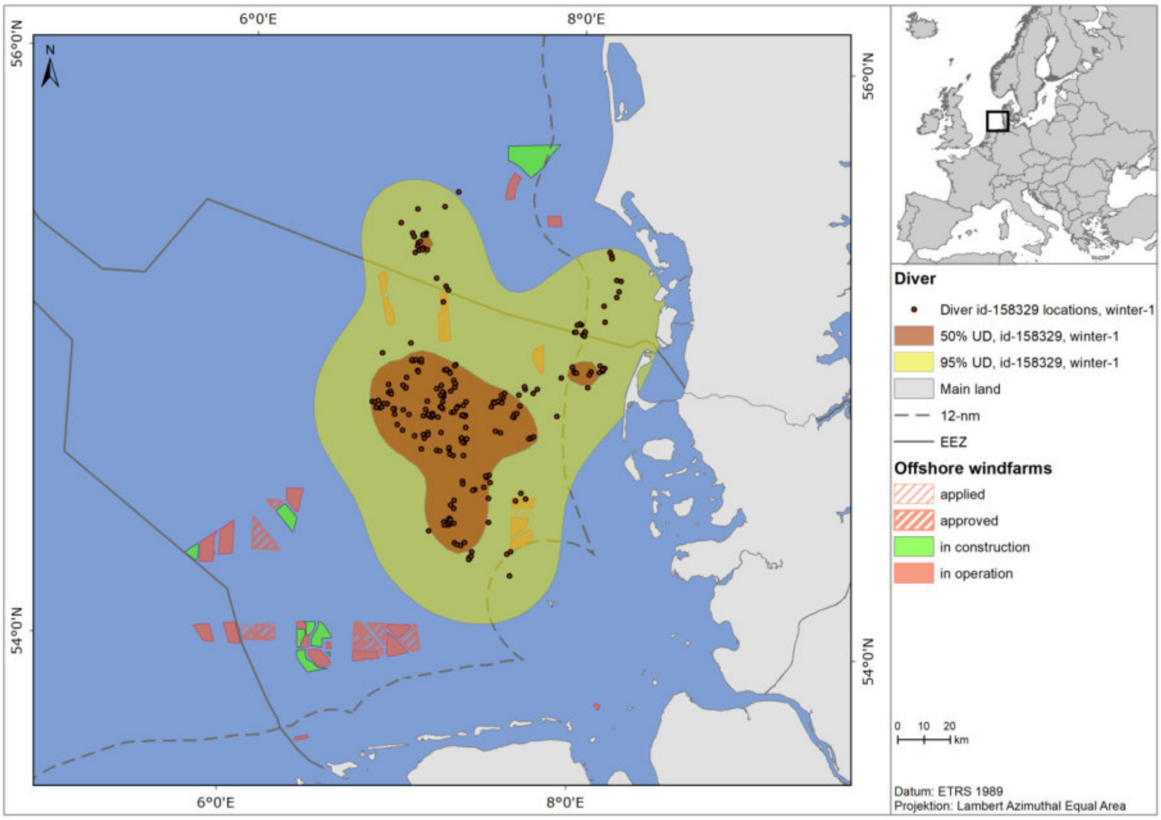


Figure A.49 Distribution of diver id-158329 in the German Bight presented as 95% UD winter distribution and 50% UD core area during the first winter of tracking (March 14 – May 9, 2016).

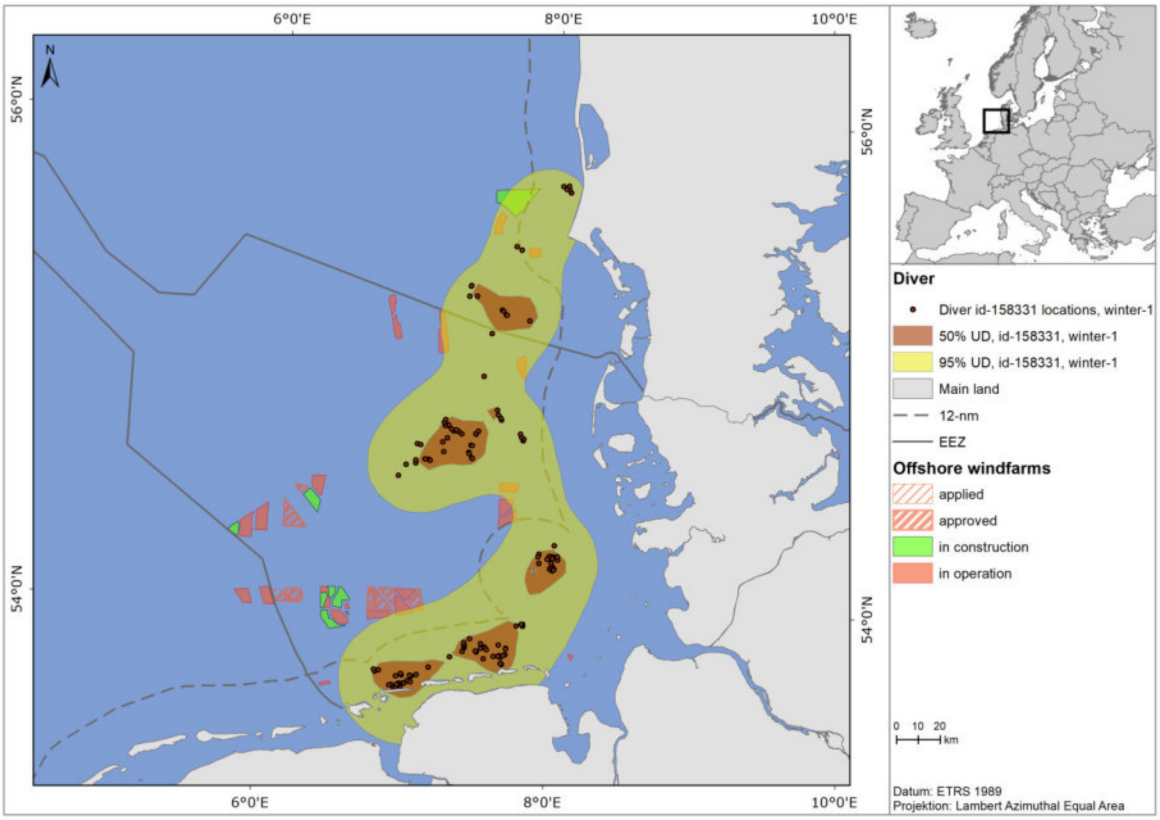


Figure A.50 *Distribution of diver id-158331 in the German Bight presented as 95% UD winter distribution and 50% UD core area during the first winter of tracking (March 13 – May 14, 2016).*

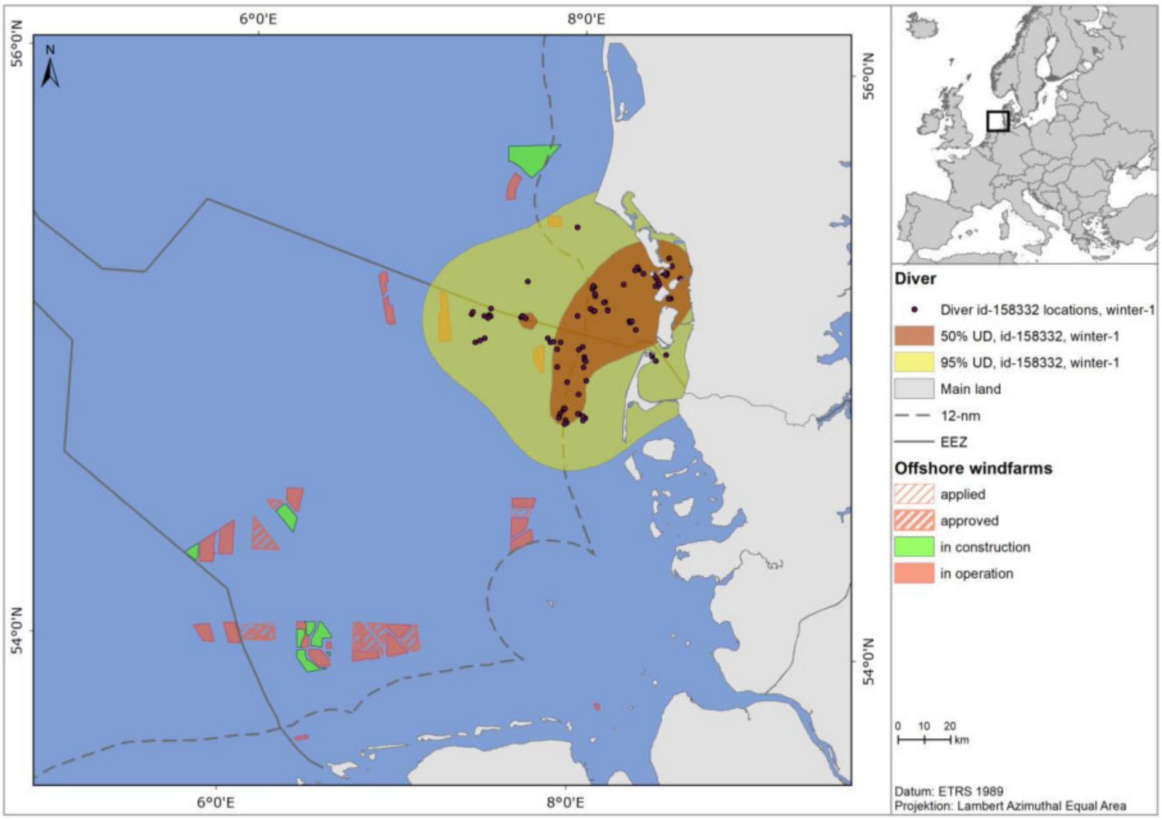


Figure A.51 *Distribution of diver id-158332 in the German Bight presented as 95% UD winter distribution and 50% UD core area during the first winter of tracking (March 13 – May 14, 2016).*

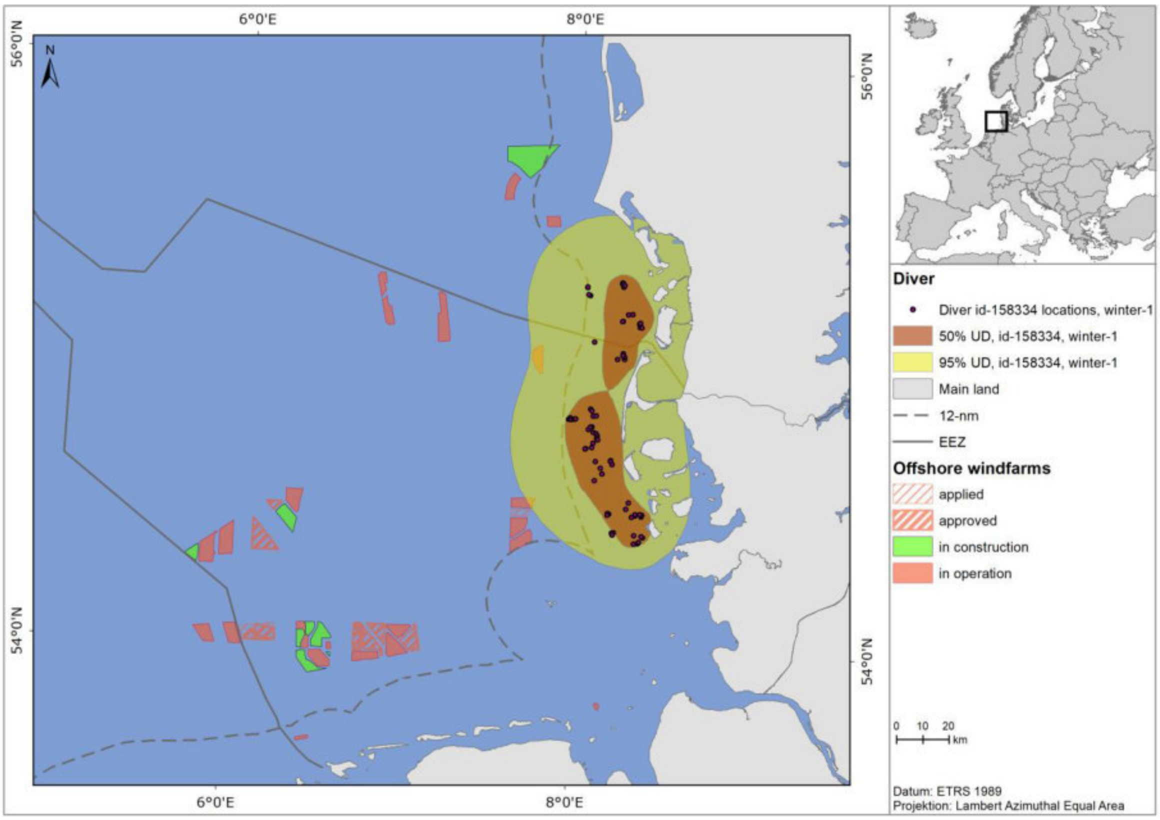


Figure A.52 Distribution of diver id-158334 in the German Bight presented as 95% UD winter distribution and 50% UD core area during the first winter of tracking (March 27 – May 28, 2016).

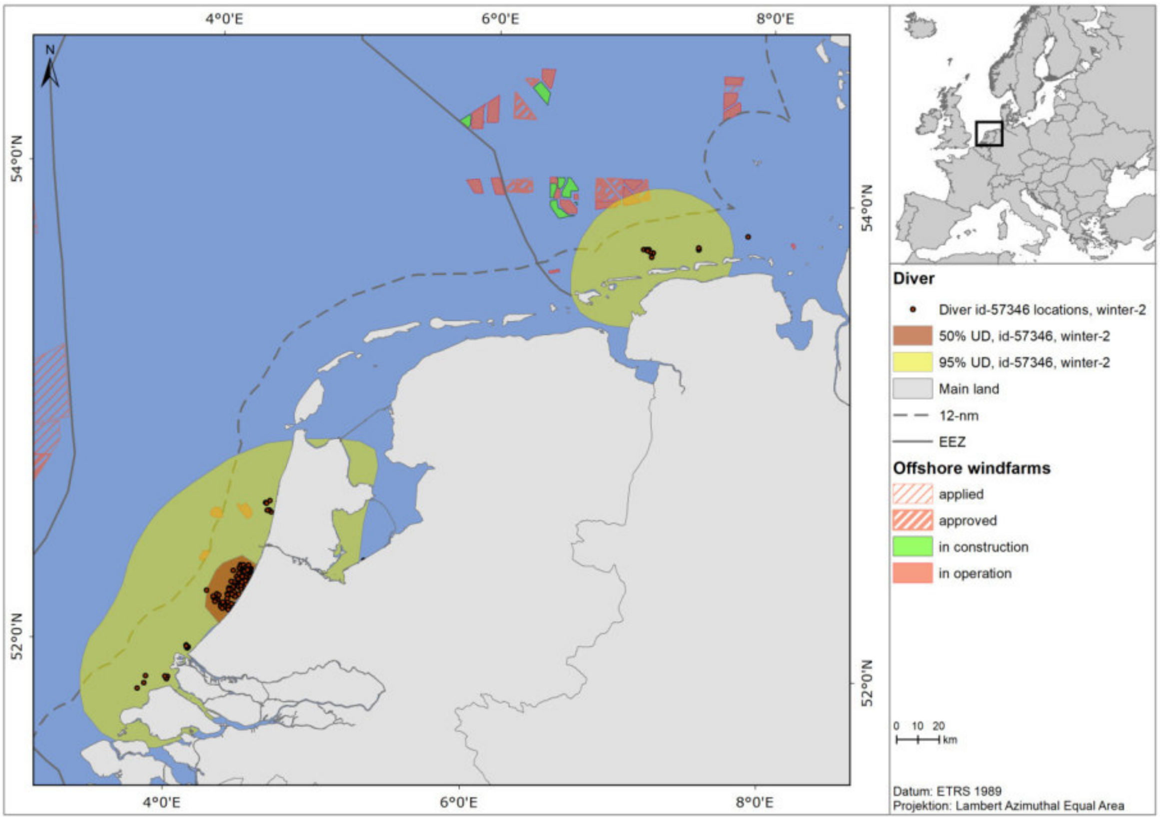


Figure A.53 Distribution of diver id-57346 in the Southern and German Bight presented as 95% UD winter distribution and 50% UD core area during the second winter of tracking (November 25, 2017 – February 7, 2018).

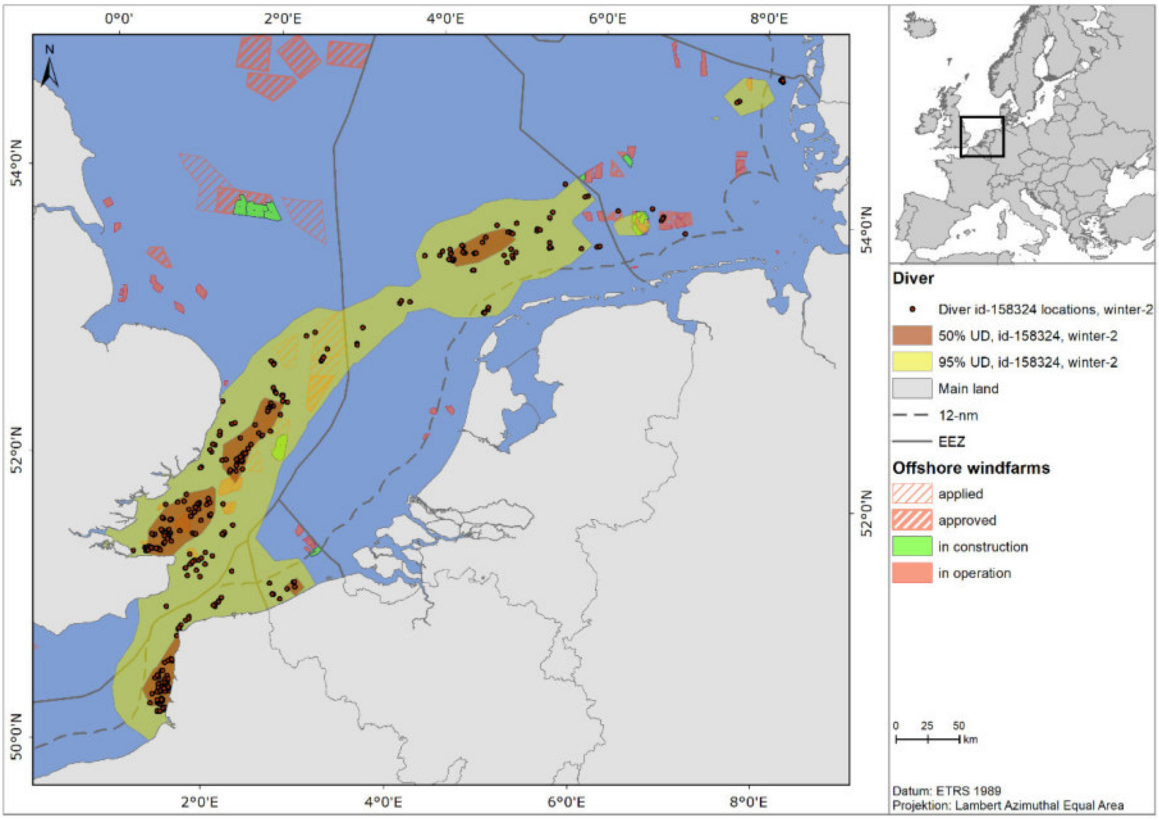


Figure A.54 *Distribution of diver id-158324 in the German and Southern Bight, and English Channel presented as 95% UD winter distribution and 50% UD core area during the second winter of tracking (November 22, 2016 – April 8, 2017).*

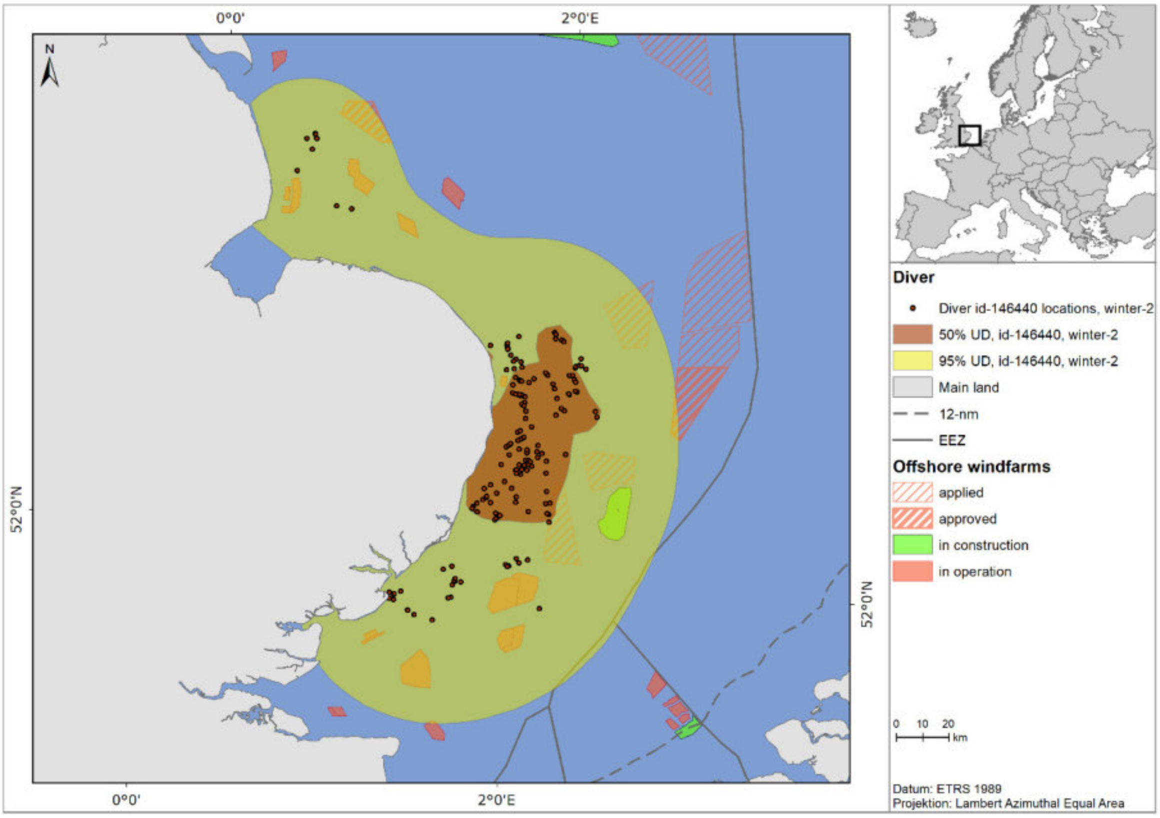


Figure A.55 *Distribution of diver id-146440 in the Southern Bight presented as 95% UD winter distribution and 50% UD core area during the second winter of tracking (December 2, 2015 – March 23, 2016).*

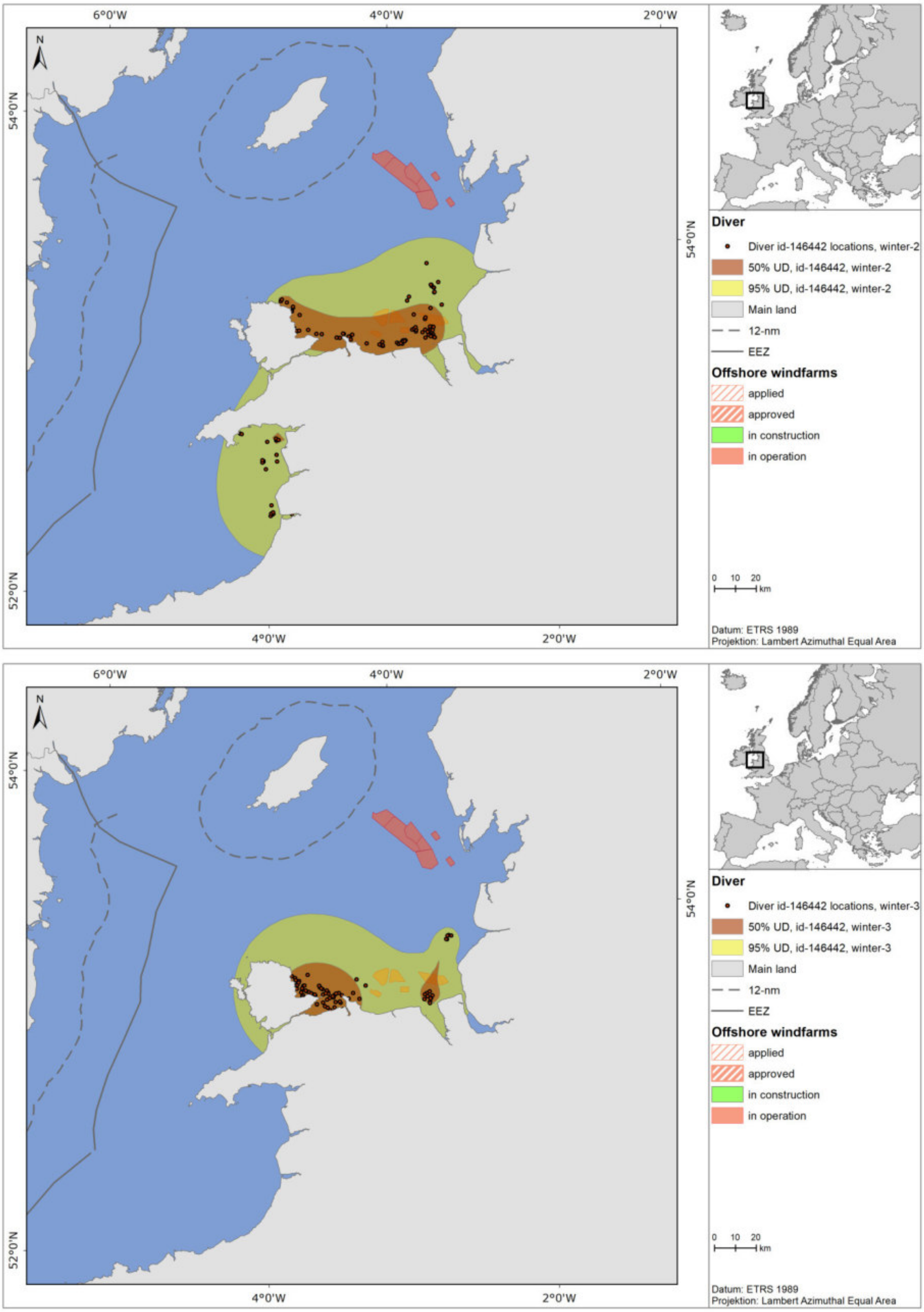


Figure A.56 Distribution of diver id-146442 in the Irish Sea presented as 95% UD winter distribution and 50% UD core areas during the second winter (December 16, 2015 – March 2, 2016; upper map) and third winter of tracking (December 4, 2016 – February 2, 2017; lower map).

B APPENDIX TO CHAPTER 6

B.1 Supplementary materials of HEINÄNEN et al. (unpublished data)

This chapter contains the supplementary materials for HEINÄNEN et al. (unpublished data): Strong displacement of red-throated divers (Gavia stellata) from offshore wind farms confirmed by two independent data sets, satellite telemetry and digital aerial surveys (chapters 6.1– 6.4).

Table B.11.1 Proportion of Argos quality classes (location classes) for the telemetry data within the study area (Figure 6.1 main article), the data in the table include locations in the Wadden Sea which were removed prior to analyses. See http://www.argos-system.org/manual/index.html#3-location/34_location_classes.htm for details regarding estimation methods.

Quality class	Estimated error radius	Count	%
3	< 250 m	452	16%
2	250–500 m	402	14%
1	500–1,500 m	306	11%
0	> 1,500 m	153	5%
A	No estimation	467	17%
B	No estimation	1,014	36%
Total		2,794	

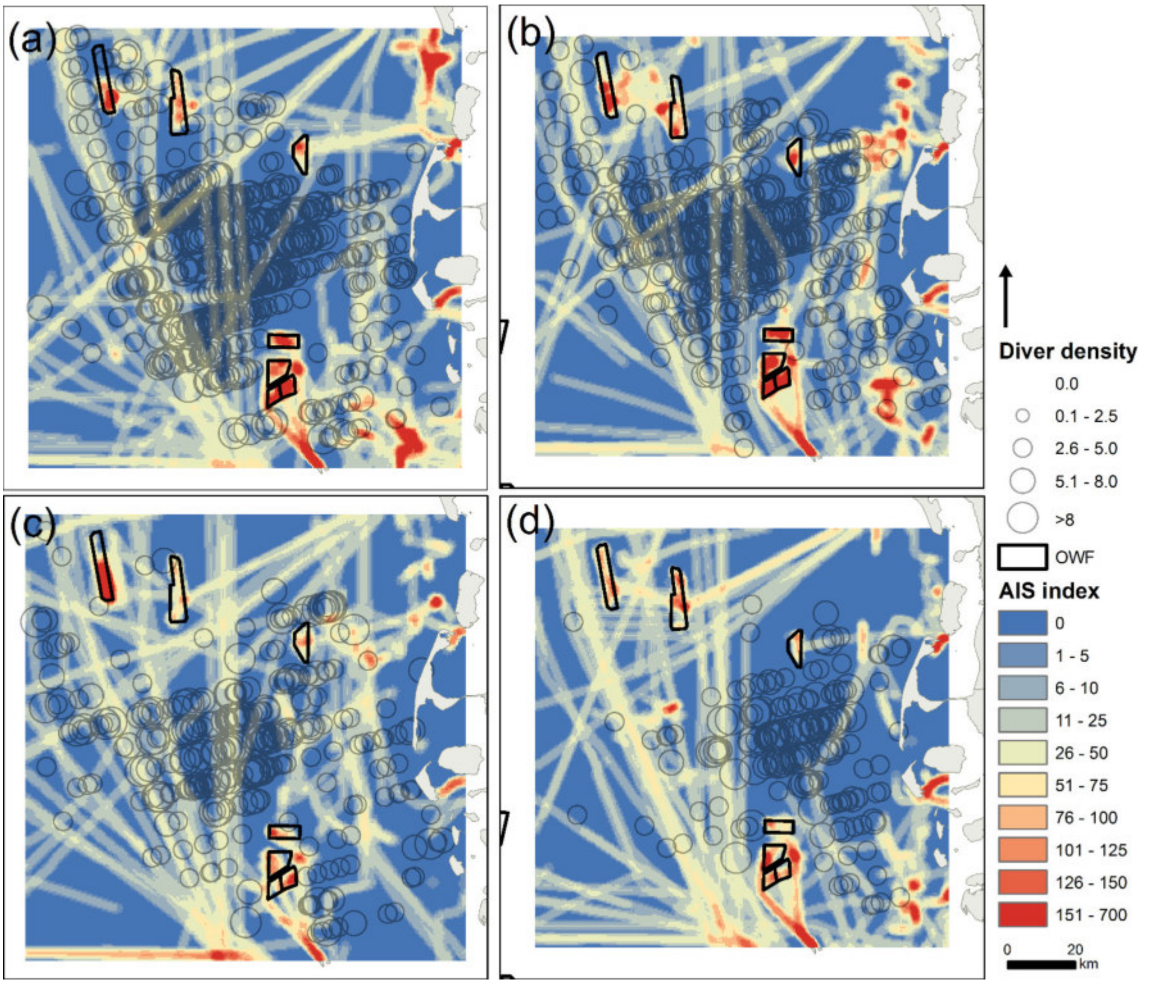


Figure B.1 *Index of shipping intensity (AIS) with observed red-throated diver densities during each survey are overlaid, a) 10 April 2016, b) 1 May 2016, c) 25 March 2017, d) 11 May 2017.*

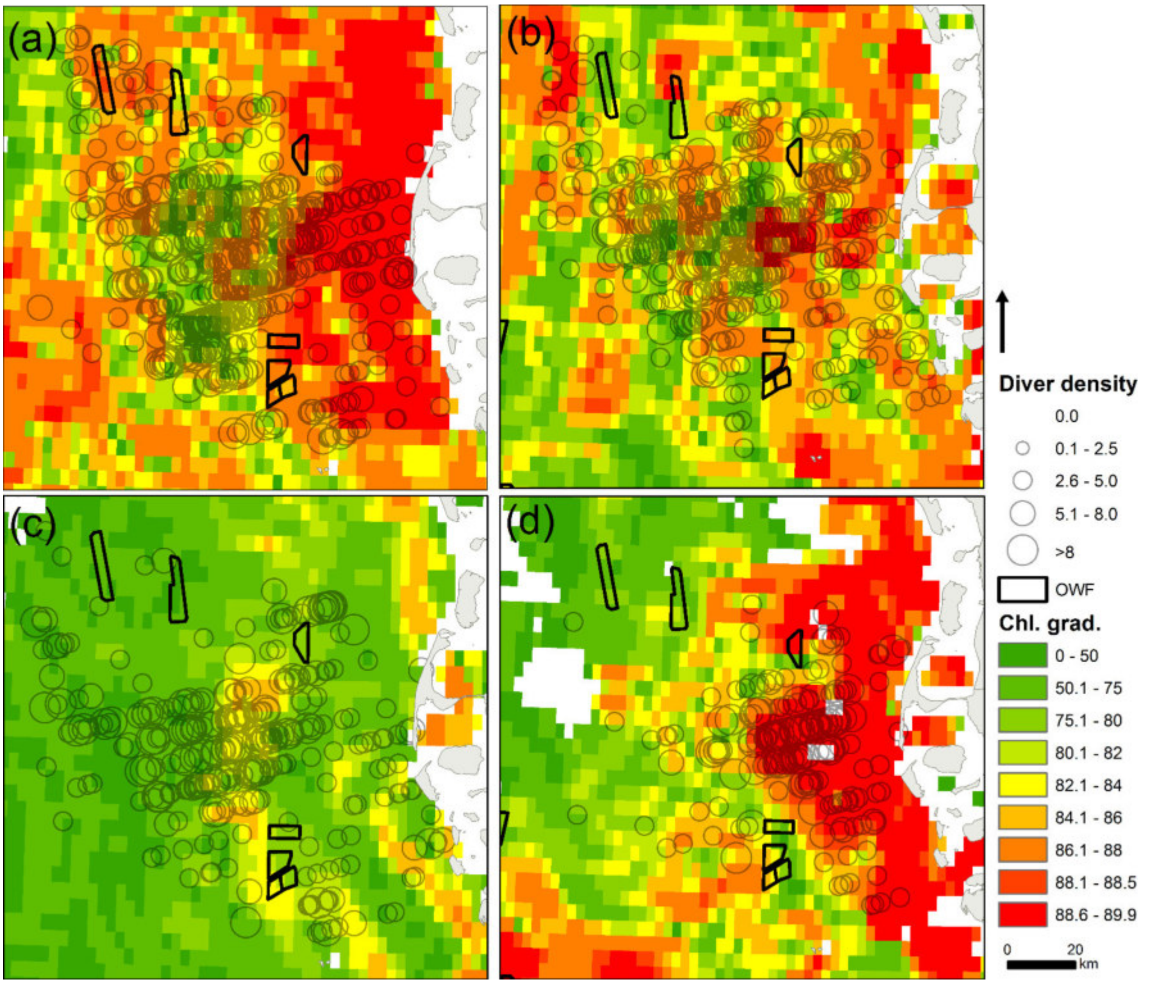


Figure B.2 *Chlorophyll a gradient (slope) with observed red-throated diver densities during each survey are overlaid, a) 10 April 2016, b) 1 May 2016, c) 25 March 2017, d) 11 May 2017.*

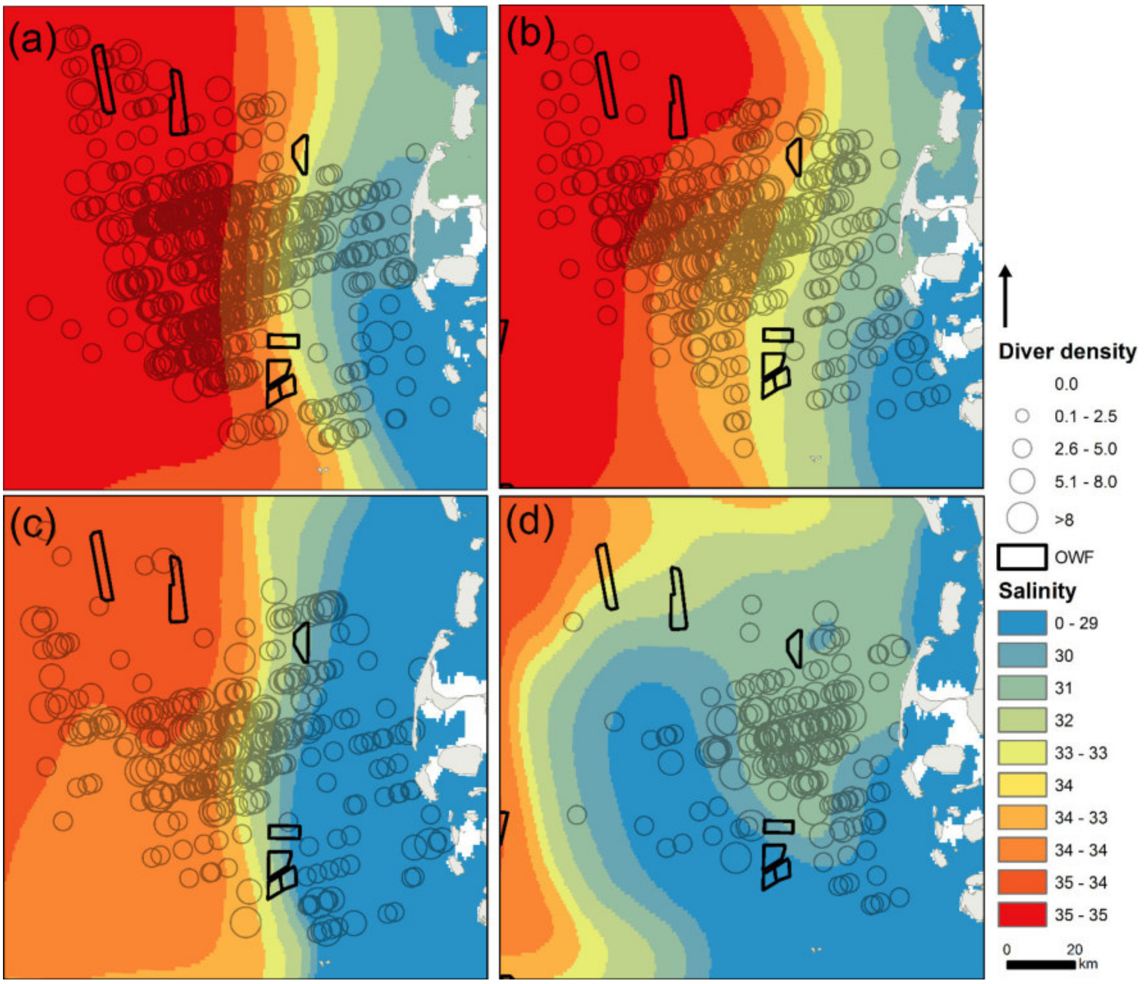


Figure B.3 Salinity (psu) with observed red-throated diver densities during each survey are overlaid, a) 10 April 2016, b) 1 May 2016, c) 25 March 2017, d) 11 May 2017.

B.2 Generalised additive model (GAM) results of red-throated diver proximity to OWF in relation to meteorological and day-night parameters

This appendix refers to chapter 6.5.

Plots of diver distance to OWF in relation to meteorological parameters show results of exploratory analyses using GAMs, when model residuals appeared to be autocorrelated. We nevertheless present these results as single variable response curves as we find them informative and logical, and did not notice irregularities that could be attributed to data structuring.

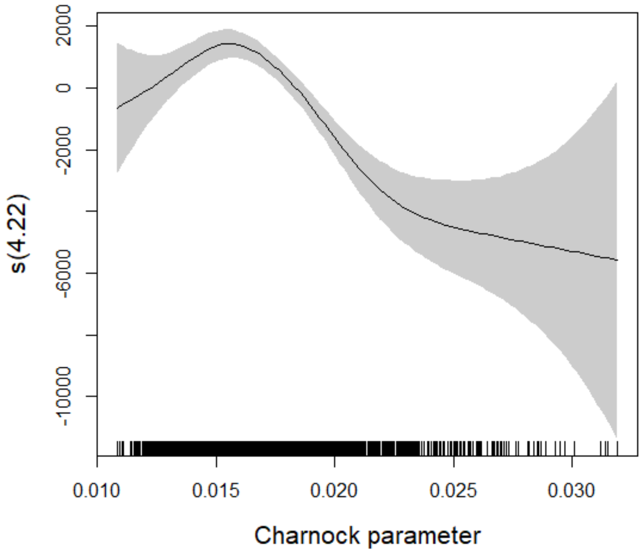


Figure B.4 *GAM response curve indicating that distance between red-throated divers and OWF declines as Charnock parameter value increases (F = 16.5, P < 0.001). Charnock parameter characterises sea surface roughness and this relationship suggests that birds occur closer to OWF in stormier seas.*

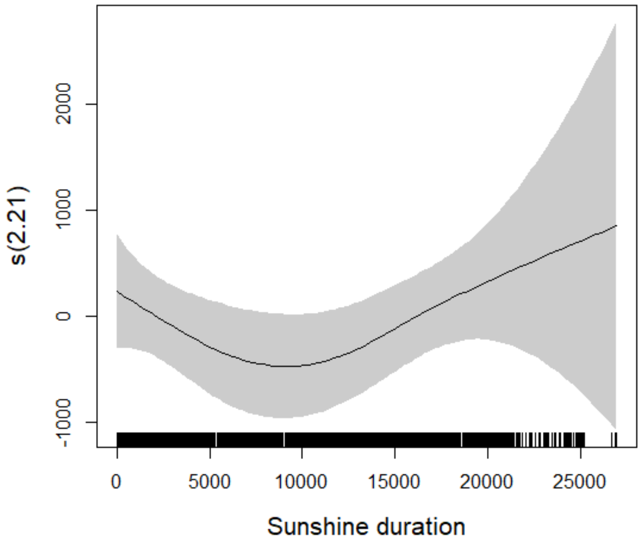


Figure B.5 *GAM response curve showing the relationship between distance of red-throated divers to OWF and daily sunshine duration, which was not significant (F = 1.68, P = 0.248).*

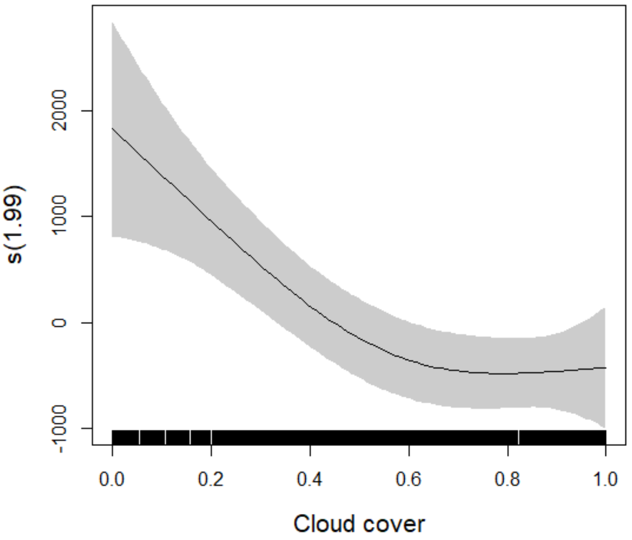


Figure B.6 GAM response curve indicating that distance between red-throated divers and OWF declines as total cloud cover increases (F = 6.83, P < 0.001). Cloud cover could be an indicator of reduced visibility (due to e.g. precipitation, reduced light conditions).

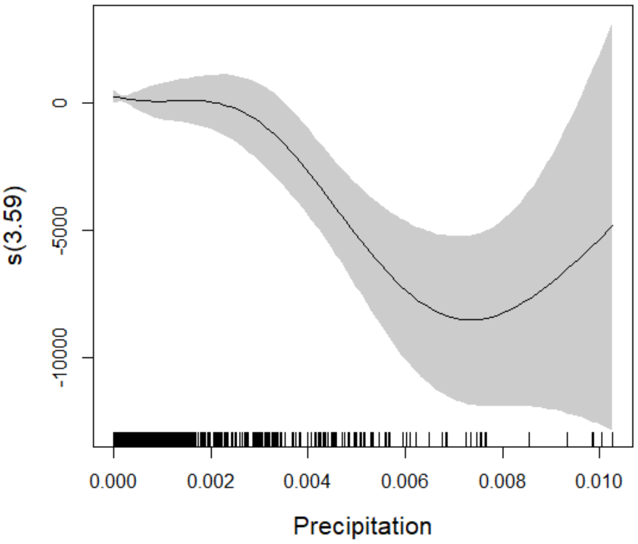


Figure B.7 GAM response curve indicating that distance between red-throated divers and OWF declines as amount of precipitation increases (F = 9.24, P < 0.001). Higher precipitation likely means lower visibility.

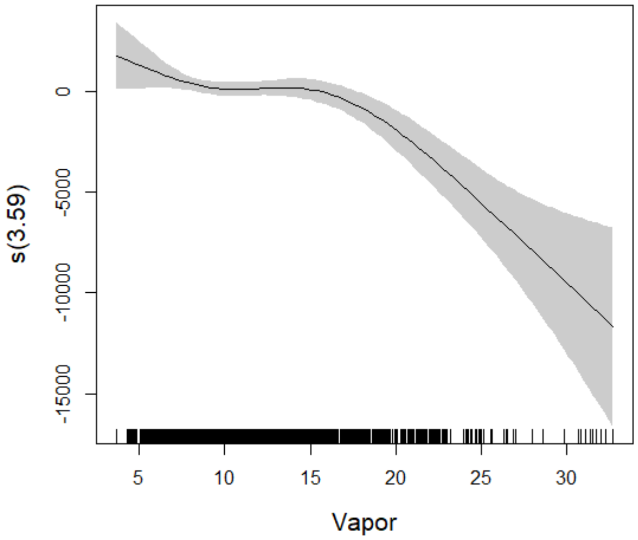


Figure B.8 GAM response curve indicating that distance between red-throated divers and OWF declines as amount of vapor in the air increases (F = 12, P < 0.001). Higher vapor concentration likely means lower visibility.

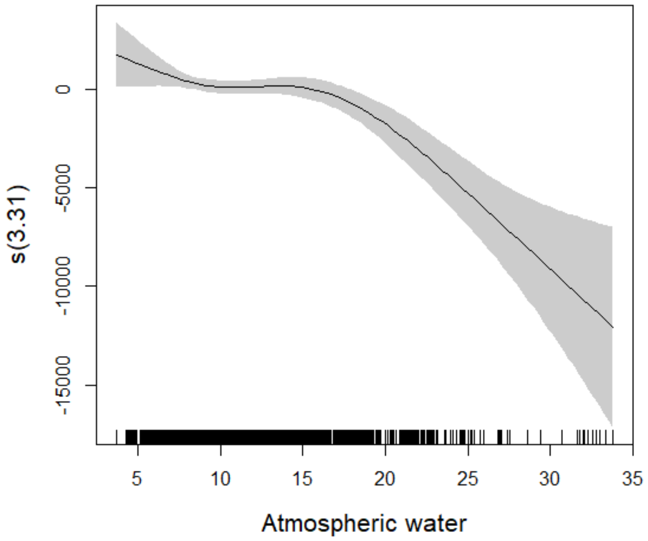


Figure B.9 GAM response curve indicating that distance between red-throated divers and OWF declines as amount of atmospheric water increases (F = 12.1, P < 0.001). This variable is nearly analogous to vapour concentration and thus it is likely that higher amount of atmospheric water is related to reduced visibility.

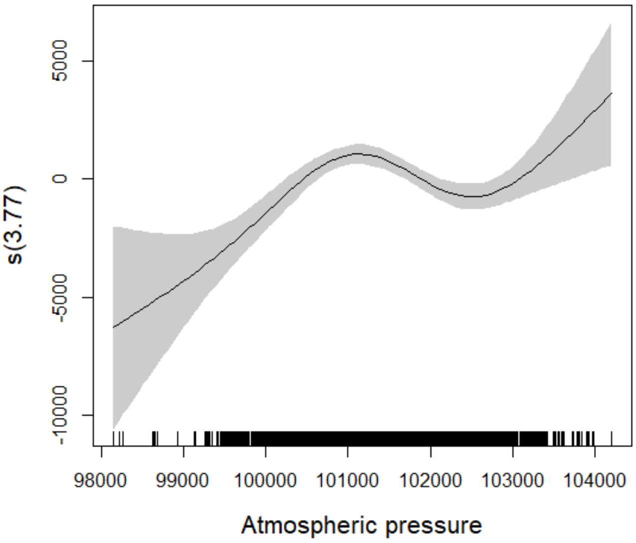


Figure B.10 *GAM response curve indicating that distance between red-throated divers and OWF increases as atmospheric pressure raises (F = 9.89, P < 0.001). Higher atmospheric pressure can be linked to fewer clouds and precipitation and therefore better visibility.*

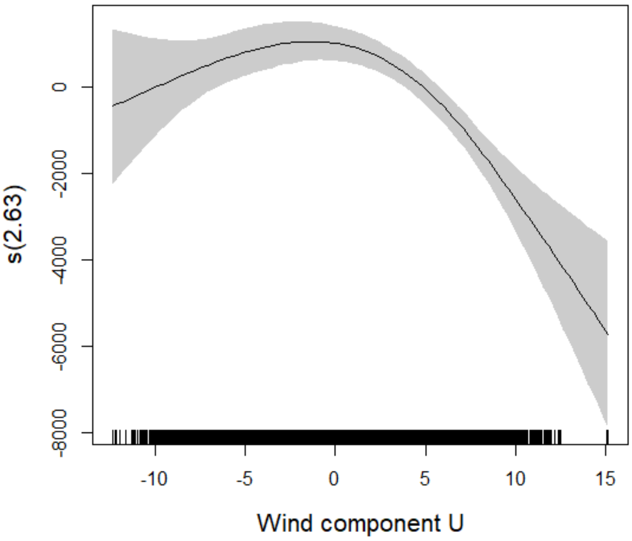


Figure B.11 *GAM response curve indicating that distance between red-throated divers and OWF declines as strength of wind component U increases (F = 16.3, P < 0.001). Higher speed of east-west winds can be linked to stormier sea conditions and subsequently poorer visibility from the perspective of a waterbird sitting low on water surface. The chart shows that positive values characterising winds from the west are more pronounced.*

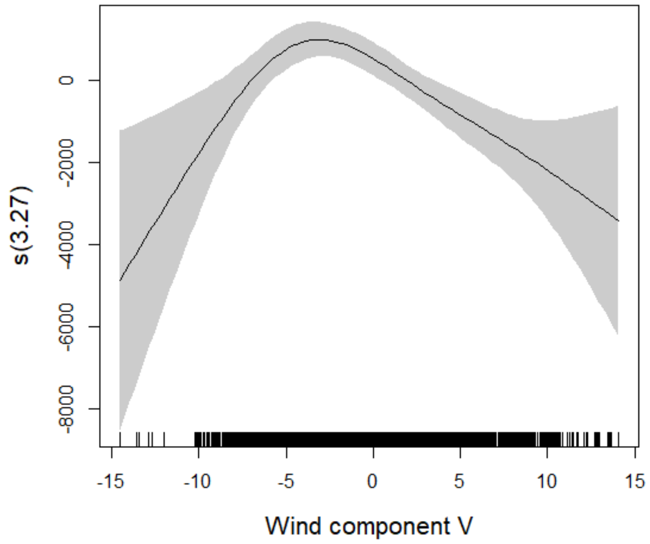


Figure B.12 GAM response curve indicating that distance between red-throated divers and OWF declines as strength of wind component V increases (F = 8.51, P < 0.001). Higher speed of north-south winds can be linked to stormier sea conditions and subsequently poorer visibility from the perspective of a waterbird sitting low on water surface. Positive V wind is from the south and negative from the north.

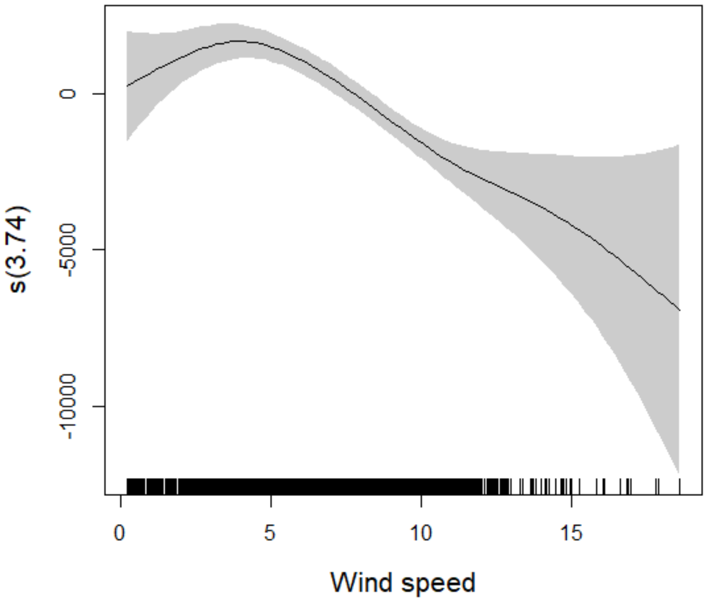


Figure B.13 GAM response curve indicating that distance between red-throated divers and OWF declines as wind speed increases (F = 16.9, P < 0.001). Higher speed winds can be linked to stormier sea conditions and subsequently poorer visibility from the perspective of a waterbird sitting low on water surface.

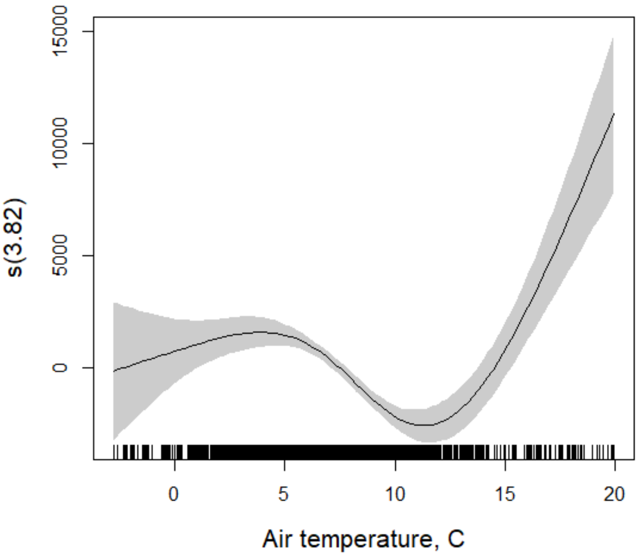


Figure B.14 GAM response curve indicating that distance between red-throated divers and OWF increases when air temperature increases above 12 °C (F = 22.41, P < 0.001). Higher temperature more likely lies above the dew point and is possibly related to favourable and clear meteorological conditions in late spring.

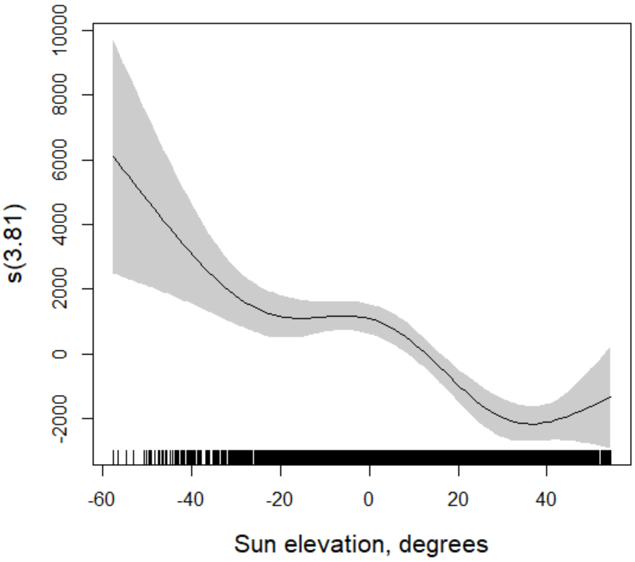


Figure B.15 GAM response curve indicating that distance between red-throated divers and OWF decreases when the Sun angle in relation to the horizon increases (F = 19.43, P < 0.001). Negative values indicate the Sun being below the horizon and positive values – above the horizon.

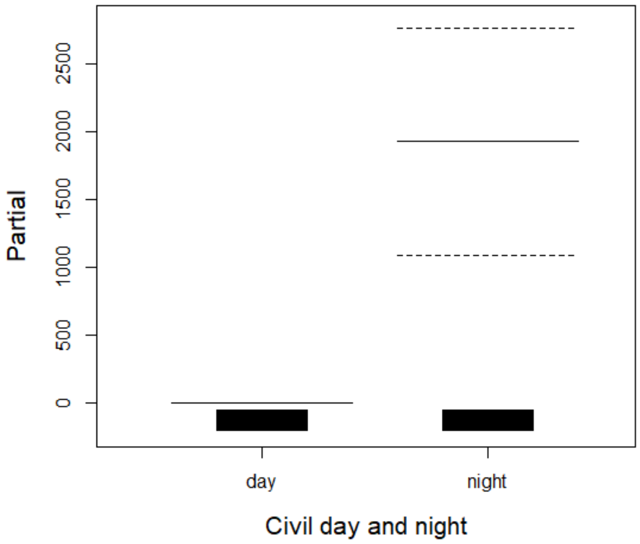


Figure B.16 *Categorical variable distinguishing day and night shows that red-throated divers were staying at greater distances to OWF at night (t = 4.6, P < 0.001). Day was separated from night using Sun elevation of -6 (below the horizon), which defines start/end of civil twilight conditions.*

C APPENDIX TO CHAPTER 7

This appendix contains the supplementary materials for BURGER et al. (2019): A novel approach for assessing effects on distributions and movements of seabirds in relation to shipping traffic (chapter 7).

Table C 1 List of models evaluated during model selection for model 1 (aerial survey data) for radius 1.5 and 3 km. AIC of best model is marked in bold.

Initial model (1.5 & 3 km)	Model formula	AIC (3 km)	AIC (1.5 km)
1	s(N_{ships},by=date) + s(Lon,Lat)+date	**5800.114**	**5860.65**
2	s(N_{ships})+s(Lon,Lat)+date	5861.798	5883.91
3	s(N_{ships}) + s(Lon,Lat)+s(date,bs="re")	5861.932	5884.02
4	s(N_{ships}) + s(Lon,Lat)	6019.534	6026.32

Table C 2 List of models evaluated during initial model selection for model 2 (aerial survey data) and final models for radius 1.5 and 3 km. AIC of best model is marked in bold.

Initial models (1.5 & 3 km)	Model formula	AIC (3 km)	AIC (1.5 km)
1	s(N_{ships})+ te(time,speed)+te(time,length)+s(Lon,Lat)+date	**2646.976**	1508.292
2	s(N_{ships}) + te(time,speed)+te(time,length)+s(Lon,Lat),+s(date,bs="re")	2647.114	**1502.257**
3	s(N_{ships},by=date) + te(time,speed)+te(time,length)+s(Lon,Lat)+date	2647.807	1514.341
4	s(N_{ships})$_s$ + te(time,speed)+te(time,length,by=date)+s(Lon,Lat)+date	2652.231	1507.252
5	s(N_{ships})+ te(time,speed,by=date)+te(time,length)+s(Lon,Lat)+date	2661.170	1522.735
6	s(N_{ships}) + te(time,speed)+te(time,length)+s(Lon,Lat)	2782.214	1562.581
Final model (1.5 km)	s(N_{ships})+ te(time,speed)+s(Lon,Lat)+s(date,bs="re")		**1503.799**
Final model (3 km)	s(N_{ships})+ te(time,speed)+s(Lon,Lat)+date	**2638.994**	

Table C 3 *Aerial survey data: Results of the best fitting GAM (model 1) for data with 1.5 km radius and 7 h time frame (n = 3,388).*

Parametric coefficients	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-0.843	0.083	-10.120	<0.001
Date [10 Apr 2016]	0.293	0.107	2.731	0.006
Date [11 May 2017]	-1.466	0.177	-8.303	<0.001
Date [25 Mar 2017]	-0.486	0.117	-4.160	<0.001
Smooth terms	**edf**	**Ref.df**	**Chi-sq.**	**p-value**
s(N_{Ships}) [01 May 2016]	1.003	1.006	9.580	0.002
s(N_{Ships}) [10 Apr 2016]	1.002	1.005	2.602	0.107
s(N_{Ships}) [11 May 2017]	1.747	2.056	44.234	<0.001
s(N_{Ships}) [25 Mar 2017]	1.327	1.583	13.762	0.002
s(Lon,Lat)	24.523	27.752	682.631	<0.001

Table C 4 *Aerial survey data: Results of the best GAM (model 2) and with 1.5 km radius and 7 h time frame (n = 1,197).*

Parametric coefficients	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-1.812	0.570	-3.18	<0.001
Smooth terms	**edf**	**Ref.df**	**Chi-sq.**	**p-value**
te(Time, Speed)	6.453	8.308	44.21	<0.001
s(Lon, Lat)	16.683	21.391	110.10	<0.001
s(Date, bs = ”re”)[random effect]	2.918	3.000	70.38	<0.001

Table C 5 Bird tracking data: results of the best GAM showing the effect of number of ships on bird relocation distance (n = 170).

Parametric coefficients	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	10,465	1,217	8.598	<0.001
Smooth terms	**edf**	**Ref.df**	**F**	**Pr(>|t|)**
s(N_{Ships})	3.180	3.614	24.174	<0.001
s(Lon, Lat)	12.965	17.273	1.697	<0.001
s(Individual ID, bs = ”re”)[random effect]	0.994	1.000	7.293	0.006

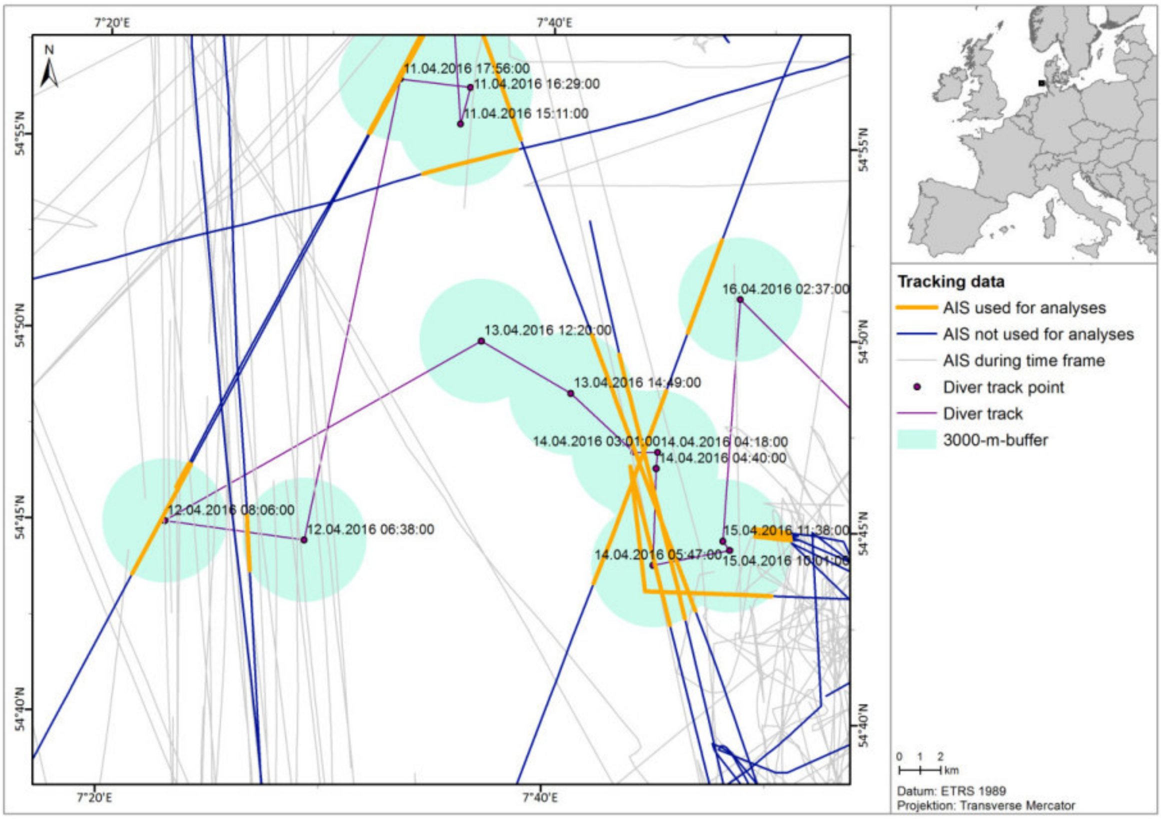


Figure C 1 Analysis of bird tracking data. Example of a bird track with 3 km radius around each position and intersections with AIS tracks. Orange sections indicate ship encounters within the defined radius and timeframe (± 60 min).

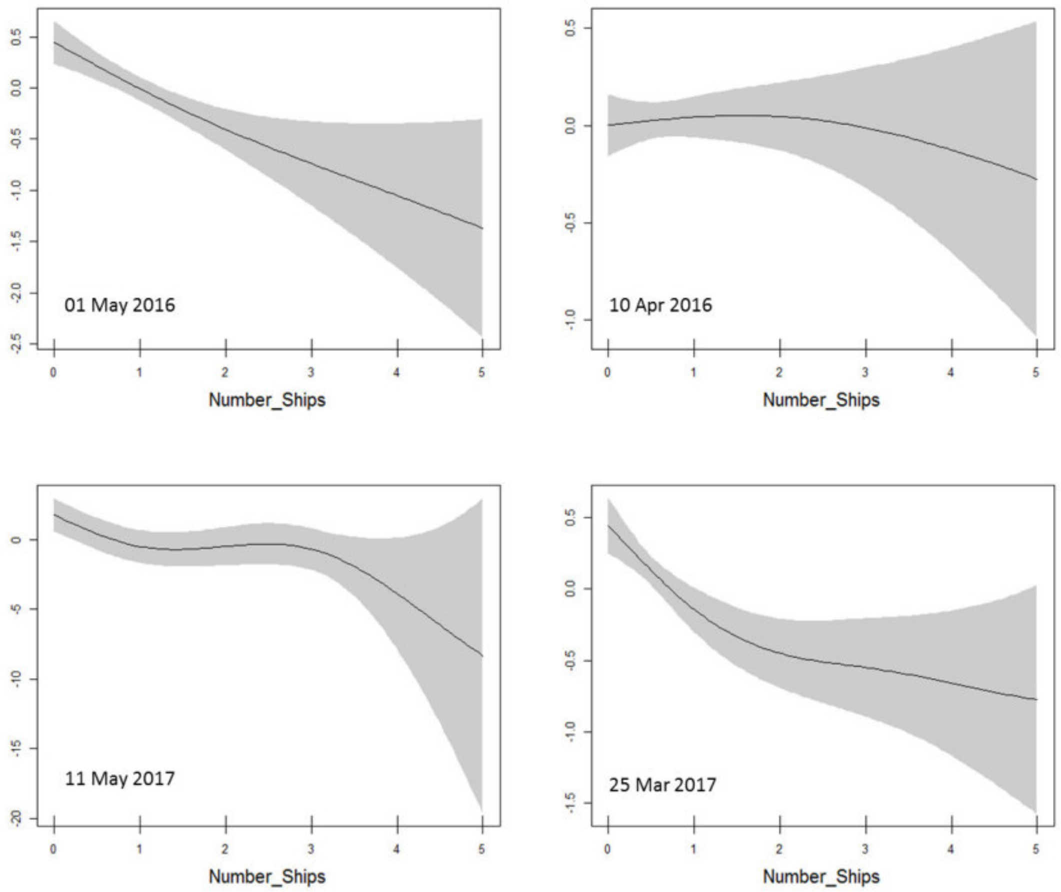


Figure C 2 *Results of model 1 and 3 km radius for number of ships per survey date. For graphical reasons, x-axis was truncated at a ship number of 5. Most data was available for transect segments with 0 or 1 ship, for larger numbers of ships 95 % confidence intervals became very wide.*

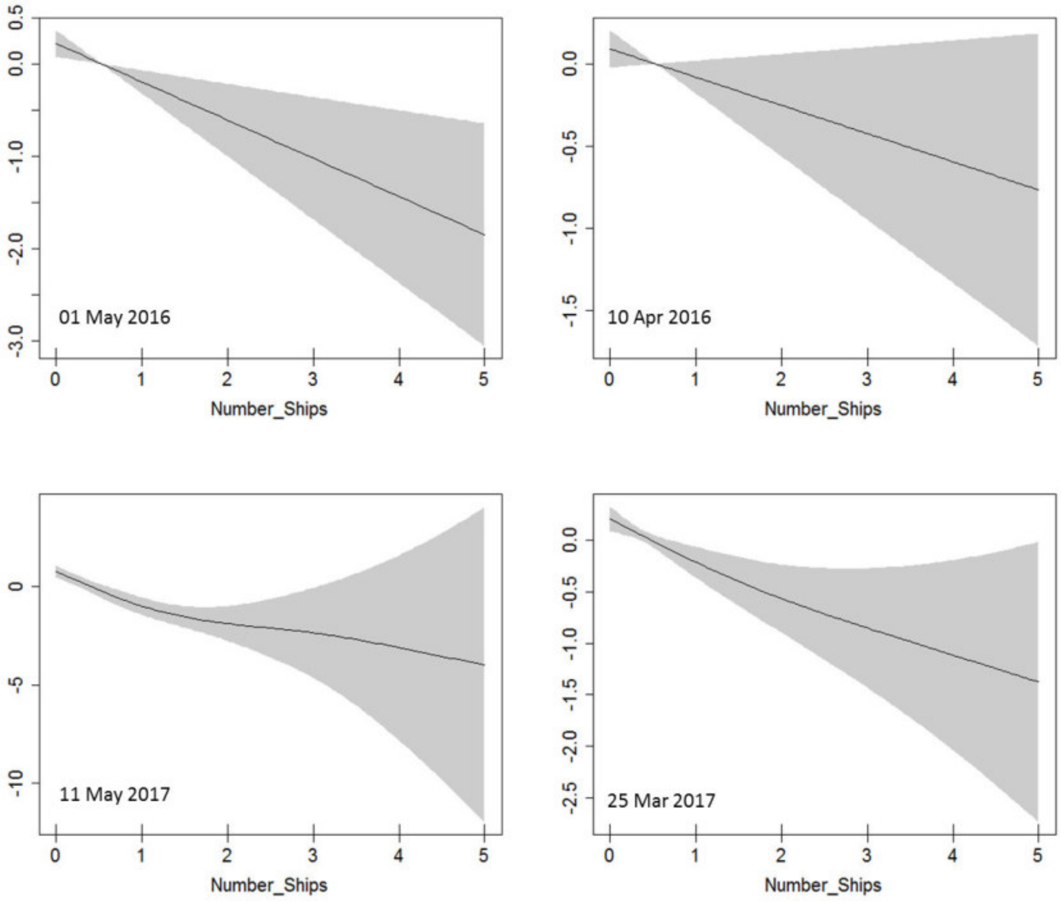


Figure C 3 *Results of model 1 and 1.5 km radius for number of ships per survey date. For graphical reasons, x-axis was truncated at a ship number of 5. Most data was available for transect segments with 0 or 1 ship, for larger numbers of ships 95 % confidence intervals became very wide.*

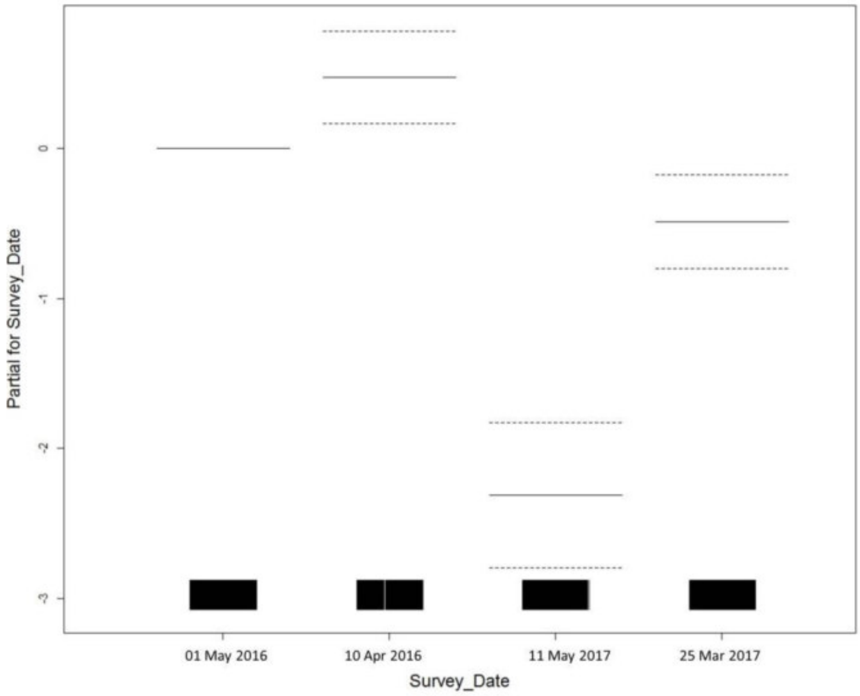


Figure C 4 *Aerial survey data: results of model 2 (aerial survey data) on ship presence data for radius 3 km: effect of survey date*

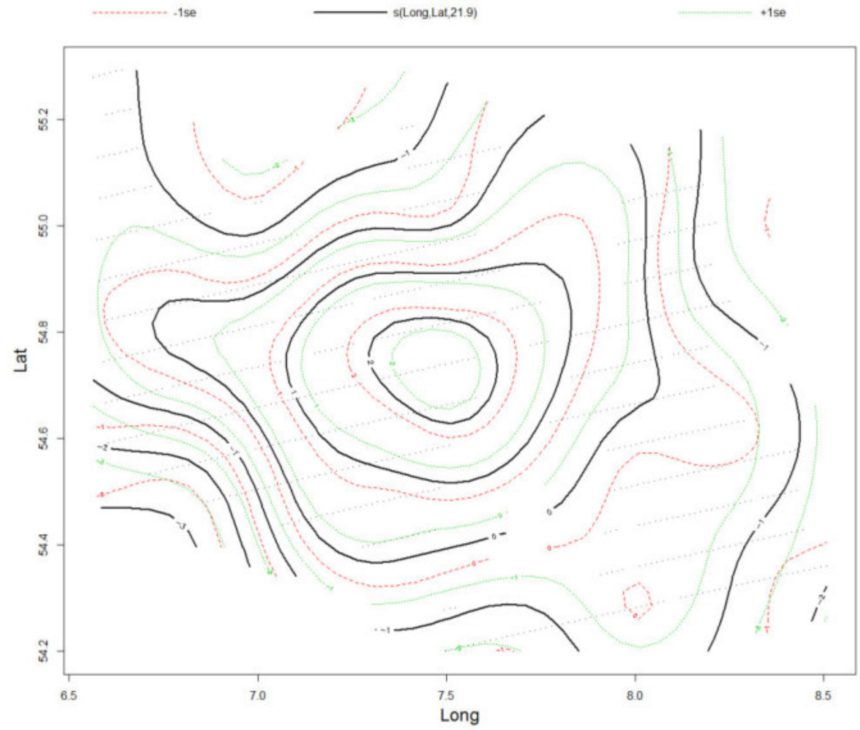


Figure C 5 *Aerial survey data: results of model 2 on ship presence data for radius 3 km: effect of the interaction between latitude and longitude.*

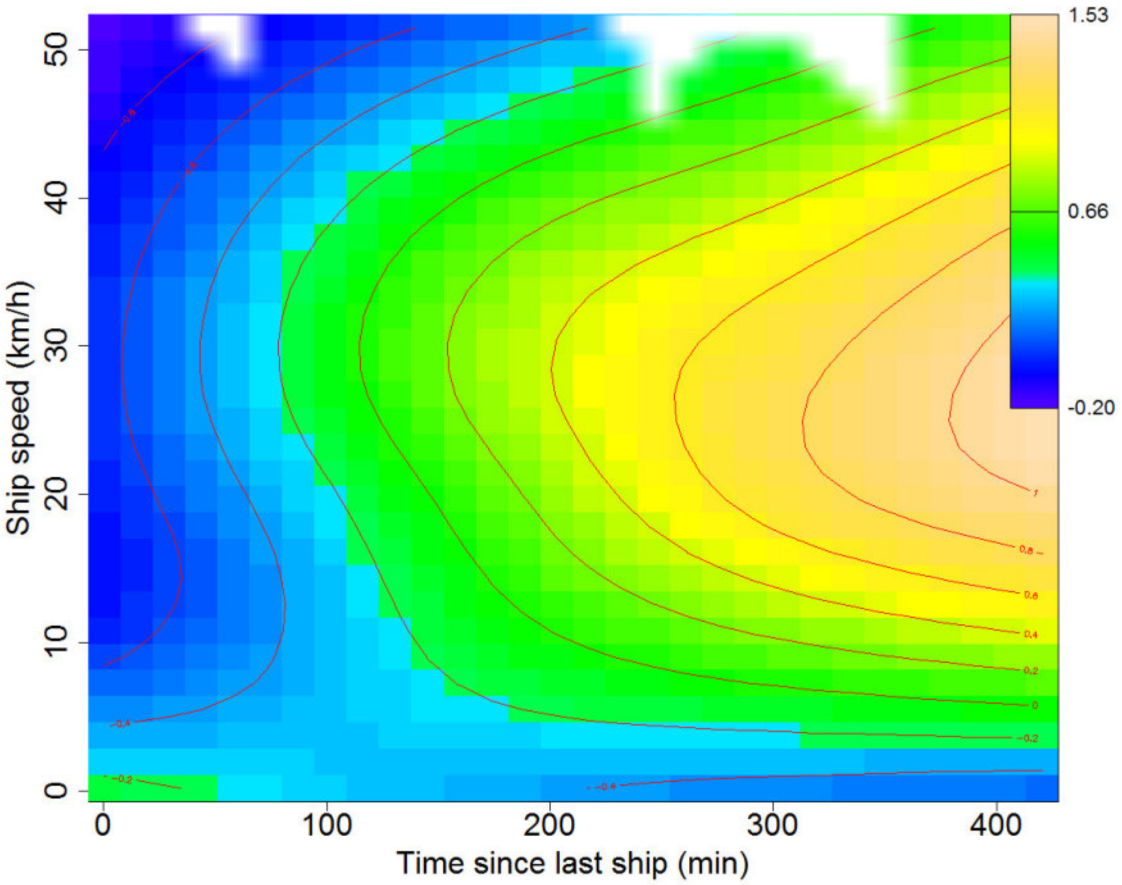


Figure C 6 *Aerial survey data: predicted diver abundance for radius 1.5 km. Red-throated diver abundance for the interaction between time since last ship (in minutes) and ship speed (in km/h). Fitted values are shown for one survey date, 25 March 2017. Transparent areas indicate a lack of data.*

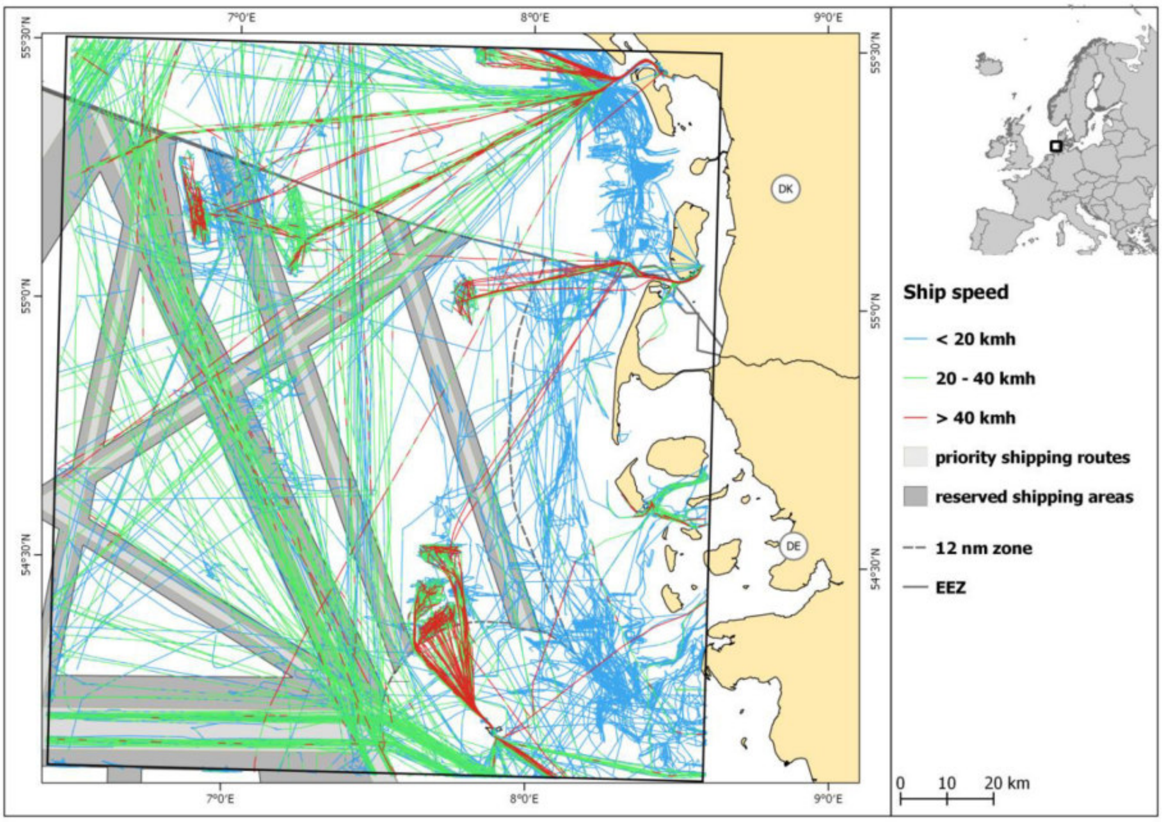


Figure C 7 Study area and ship traffic. Map of ship traffic during four days with HiDef surveys in 2016 and 2017. Colors indicate ship speed.

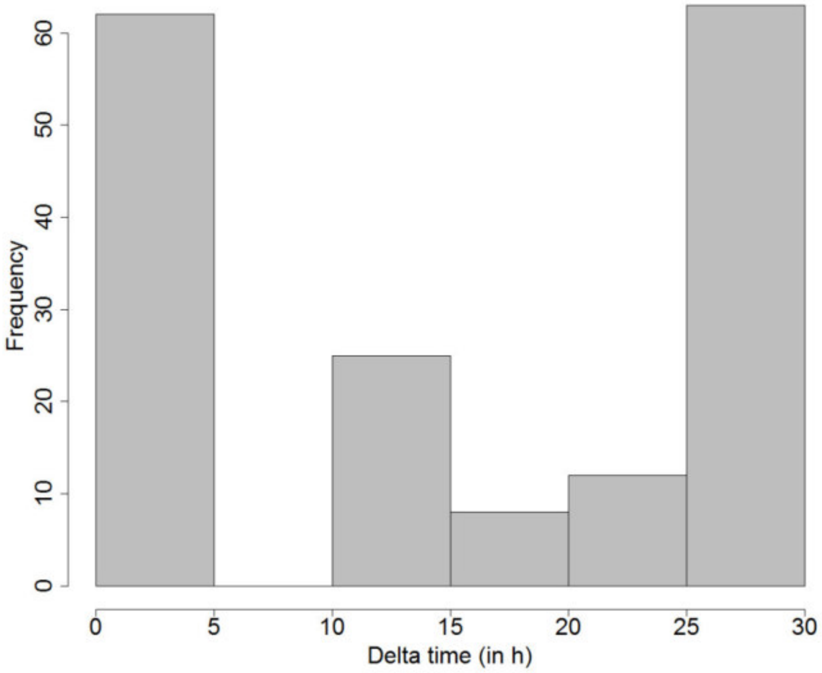


Figure C 8 Bird tracking data: histogram of the time difference between subsequent bird tracking positions.

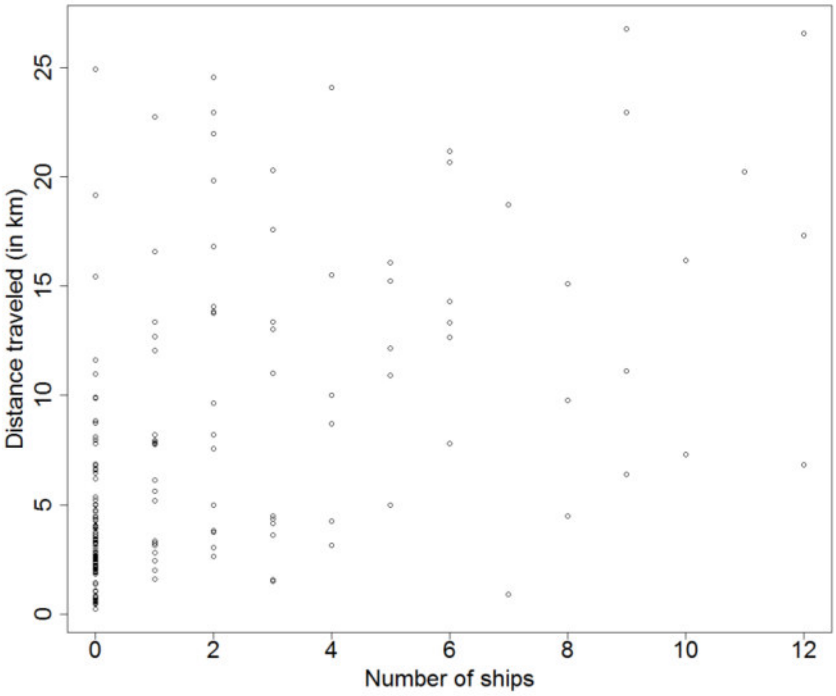


Figure C 9 *Bird tracking data: plot of number of ships in a 3 km radius around the bird tracking position and distance travelled by individuals during the subsequent lag.*

D APPENDIX TO CHAPTER 8

This appendix contains the appendix and supplementary materials for Kleinschmidt et al. (2019): The diet of red-throated divers (*Gavia stellata*) overwintering in the German Bight (North Sea) analysed using molecular diagnostics (chapter 8).

D.1 Appendix

Table D.11.2 Best blast results for each of the 21 detected taxa and corresponding accession number, the identity with the blast reference sequence, the sequence length and the bitscore from data of both sampling years (2015 and 2016) combined.

Order	Family	Genus / species	Common name	Accession number	Ident % (blast)	Sequ. length	E-value	Bit-score
Clupeiformes	Clupeidae	*Clupea harengus*	Atlantic herring	KJ128741	100	210	1.94E-104	388
Clupeiformes	Clupeidae	*Sprattus sprattus*	European sprat	KJ128910	100	210	9.04E-103	388
Clupeiformes	Clupeidae	*Sardina pilchardus*	European pilchard	FR849599	100	205	1.14E-101	379
Clupeiformes	Engraulidae	*Engraulis encrasicolus*	European anchovy	KJ128765	100	211	5.93E-105	390
Pleuronectiformes	Pleuronectidae	-	Right eye flounders	KU936350	99.1	224	7.49E-109	403
Pleuronectiformes	Pleuronectidae	*Limanda limanda*	Common dab	KJ128862	100	224	3.78E-112	414
Pleuronectiformes	Scophthalmidae	*Scophthalmus maximus*	Turbot	EU410416	100	217	2.60E-108	401
Pleuronectiformes	Soleidae	*Solea solea*	Common sole	KJ128906	99.1	224	7.49E-109	403
Salmoniformes	Salmonidae	*Salmo trutta*	Sea/Brown trout	KT633607	100	213	4.25E-106	394
Gadiformes	Merluccidae	*Merluccius merluccius*	European hake	KJ128826	100	208	2.49E-103	385
Gadiformes	Gadidae	*Pollachius pollachius*	European pollock	FR751400	99.5	208	2.50E-98	379
Gadiformes	Gadidae	*Merlangius merlangus*	Whiting	KJ128825	100	208	2.49E-103	363
Gadiformes	Gadidae	*Melanogrammus aeglefinus*	Haddock	KJ128822	100	208	2.49E-103	385
Gadiformes	Gadidae	*Gadus sp.*	Cod	AP017650	99.52	208	1.16E-101	379
Gadiformes	Gadidae	-	Codfishes/True cod	AP017650	99.5	208	2.49E-103	379
Gasterosteiformes	Gasterosteidae	*Gasterosteus sp.*	Stickleback	KJ627974	100	208	1.16E-101	379
Perciformes	Moronidae	*Dicentrarchus labrax*	European bass	KJ168065	99.5	211	2.53E-103	385
Perciformes	Ammodytidae	-	Sand lance	KJ128795	99.1	211	2.53E-103	379
Perciformes	Ammodytidae	*Hyperoplus lanceolatus*	Greater sand eel	KJ128795	100	211	2.53E-103	390
Perciformes	Ammodytidae	*Ammodytes sp.*	Sand eel	AF315121	100	211	1.18E-101	390
Perciformes	Gobiidae	*Pomatoschistus minutus*	Sand goby	KJ128870	100	207	8.89E-103	383

Order	Family	Genus / species	Common name	Accession number	Ident % (blast)	Sequ. length	E-value	Bit-score
Perciformes	Scombridae	*Scomber scombrus*	Atlantic mackerel	KJ128898	100	217	1.21E-106	396

D.2 Supplementary material

Specific information: Primer design

Primer to amplify fish were modified from Chord_16S_F1/ modified Chord_16S_R1 (WAAP et al. unpubl. data) to match the range of potential prey species of red-throated divers occurring in the study site.

Primer to amplify cephalopods were modified from modified Ceph _16S_F1/ modified Ceph _16S_R1 (WAAP et al. unpubl. data) to match the range of potential prey species of red-throated divers occurring in the study site.

PCR amplification of fish and cephalopod prey DNA from faeces

PCR amplifications of fish and cephalopod prey were performed in single reactions using Multiplex PCR Kits (Qiagen). Each 20 µL PCR reaction volume contained 10 µl Multiplex PCR Master Mix, 1.25 µL of each primer (4 µM), 1.25 µL blocking probe (40 µM) if present and 4 µL template DNA. For amplification of fish prey DNA, 2 µL of Q solution per sample were added to the reaction mix and for amplification of cephalopod prey DNA 0.2 µL BSA per sample was added to the reaction mix.

PCR amplification of crustacean prey DNA from faeces

PCR amplifications of crustacean prey DNA were performed in separate reactions, using Multiplex PCR Kits (Qiagen). Each 20 µl PCR reaction volume contained 10 µl Multiplex PCR Master Mix, 2 µL of each primer (2 µM) and 4 µL template DNA. For amplification of crustacean prey DNA 0.2 µL BSA per sample was added to the reaction mix.

Specific information on bioinformatic analyses

We received the sequences in Ilumina 1.8 Phred format + 33 format and for further analysis we processed the data as follows, see also Table 1, 2. First we used Trimmomatic v0.36 (Bolger et al. 2014) to trim out low quality sequences and Illumina adapter sequences in the raw data set. Then we used FLASH v1.2.11 to align paired reads (MAGOC & SALZBERG 2011), and converted the fastq output to fasta format using FASTX Toolkit v0.0.13.2 (GORDON & HANNON 2010). Mothur v1.37.1 (SCHLOSS et al. 2009) was used to identify sequence reads with an exact match to the primers & MID-tags, to avoid any spurious results due to sequencing errors. As the sequencing library was prepared using blunt-end ligation, each primer & MID combination was checked in both possible orientations. Sequencing reads matching with primers and MID-tags were then demultiplexed by pulling out the fasta sequence IDs for each sample from the mothur 'groups' file and using this list to extract the corresponding sequences from the mothur 'trim' file, giving a new fasta file with sequences specific to each sample for each gene. The mothur 'trim' sequences file also has the primer and MID-tag sequences removed from each sequence, as just the amplified gene region is wanted for the following clustering step. To condense large numbers of sequences and therefore to define molecular operational taxonomic units (MOTUs) we first we dereplicated the sequence file to remove identical replicates using usearch v7.0.1090 -derep-fulllength, then removed any potential chimeric sequences using usearch-uchime2_denovo, and finally clustered the sequences based on 97% identity into MOTUs (CLARE et al. 2016; ELBRECHT et al. 2016) using usearch -cluster_fast. Taxonomic information on the sequences was assigned using BLASTN against the nucleotide database and a cut-off of 90% sequence identity and an e value of 1e-10.

Table D.11.3 Working steps, commands and References performed during bioinformatics analysis.

Job to do	Software	Command	Reference
Check and summarise raw data quality	FastQC	fastqc BK-Poolx_R1_trimmed_paired.fq --outdir=./ fastqc BK-Poolx_R2_trimmed_paired.fq --outdir=./	Andrews S (2010) FastQC: a quality control tool for high throughput sequence data. https://www.bioinformatics.babraham.ac.uk/projects/fastqc/
Step1: Trimming raw data of any sequencing adapters and low quality sequence	Trimmomatic	trimmomatic PE -phred33 BK-Poolx_S5_L001_R1_001.fastq.gz BK-Poolx_S5_L001_R2_001.fastq.gz BK-Poolx_R1_trimmed_paired.fq BK-Poolx_R1_trimmed_unpaired.fq BK-Poolx_R2_trimmed_paired.fq BK-Poolx_R2_trimmed_unpaired.fq \ ILLUMINACLIP:TruSeq3-PE-2.fa:2:30:10 LEADING:3 TRAILING:3 SLIDINGWINDOW:4:20 MINLEN:135	Bolger AM, Lohse M, Usadel B (2014): Trimmomatic a flexible trimmer for Illumina sequence data. Bioinformatics, 30, 2114-2120.
Step2: Aligning paired reads and convert fastq to fasta	Flash FASTX-Toolkit	flash BK-Poolx_R1_trimmed_paired.fq BK-Poolx_R2_trimmed_paired.fq -M 250 > flash_out fastq_to_fasta -i out.extendedFrags.fastq -Q 33 > BK-Poolx_aligned.fa	Magoc T & Salzberg SL (2011): FLASH: fast length adjustment of short reads to improve genome assemblies. Bioinformatics, 27 2957-2963. Gordon, A., & Hannon, G. J. (2010). FASTX-Toolkit. Short-reads pre-processing tools. http://hannonlab.cshl.edu/fastx_toolkit/index.html
Step 3a: Identification and selection for sequences with exact matches to oligos & MIDs used, trimming MIDs and primer sequences	Mothur	mothur "#trim.seqs(fasta=BK-Poolx_aligned.fa,oligos=oligos_Poolx.txt,checkorient=T)"	Schloss, P.D., et al., Introducing mothur: Open-source, platform-independent, community-supported software for describing and comparing microbial communities. Appl Environ Microbiol, 2009. 75(23):7537-41.
Step3b:_Demultiplex the sequences into a file for each sample	Deplex – custom perl script	perl deplex_v2.pl SampleList	
		while (<INLIST>) { $lib = $_; chomp($lib);	
		$readids1 = $lib . "_ids.txt"; $fa1 = $lib . ".fasta"; $readidsa = $lib . "a_ids.txt"; $readidsb = $lib . "b_ids.txt"; $readids2 = $lib . "_ab_ids.txt";	
		grep -w $lib $indir/BK-Poolx_aligned.groups | awk	

Job to do	Software	Command	Reference
		'{print \$1}' > $outdir/$readids1"	
		perl deplex_v2b.pl SampleListB	
		while (<INLIST>) {$lib = $_;chomp($lib);	
		$readids1 = $lib . "_ids.txt"; $fa1 = $lib . ".fasta"; $readidsa = $lib . "a_ids.txt"; $readidsb = $lib . "b_ids.txt"; $readids2 = $lib . "_ab_ids.txt";	
		system("cat $outdir/$readidsa $outdir/$readidsb >> $outdir/$readids2");	
		perl -ne'."'".'if(/^>(\S+)/){$c=$i{$1}}$c?print:chomp;$i{$_}=1 if'." @ARGV'"." $outdir/$readids2 $indir/BK-Poolx_aligned.trim.fasta > $outdir/$fa1"	
Step 4:	usearch, custom perl script	perl usearchPoolA.pl SampleListB while (<INLIST>) {$lib = $_;chomp($lib); $fa = $lib . ".fasta"; $usout1 = $lib . "_rc_uniques.fasta"; $usout2 = $lib . "_rc_uniques.out"; $usout3 = $lib . "_rc_uniques_results.uchime"; $usout4 = $lib . "_chimeras.fasta"; $usout5 = $lib . "_nonchimeras.fasta"; $usout6 = $lib . "_uchimealns"; $cent = $lib . "_centroids.fa"; $uc = $lib . "_clusters.uc"; $cons = $lib . "_consout.fa"; $msa = $lib . "_msa.fa";	

Job to do	Software	Command	Reference
Step 4: Removal of identical replicates	usearch v7.0.1090	usearch -derep_fulllength $indir/$fa -output $outdir/$usout1 -sizeout -minseqlength 187 -minuniquesize 5 -strand both -uc $outdir/$usout2	USEARCH and UCLUST algorithms: Edgar,RC (2010) Search and clustering orders of magnitude faster than BLAST, Bioinformatics 26(19), 2460-2461. doi: 10.1093/bioinformatics/btq461
Step 4: Chimera detection		usearch -uchime_denovo $outdir/$usout1 -uchimeout $outdir/$usout3 -uchimealns $outdir/usout6 -chimeras $outdir/$usout4 -nonchimeras $outdir/$usout5	Edgar,RC, Haas,BJ, Clemente,JC, Quince,C, Knight,R (2011) UCHIME improves sensitivity and speed of chimera detection, Bioinformatics doi: 10.1093/bioinformatics/btr381 [PMID 21700674].; UCHIME2 algorithm Edgar, R.C. (2016), UCHIME2: Improved chimera detection for amplicon sequences, http://dx.doi.org/10.1101/074252.
Step 4: Clustering sequences 97%; final dereplication		usearch -cluster_fast $outdir/$usout5 -id 0.97 -centroids $outdir2/$cent -uc $outdir/$uc -sizeout -consout $outdir/$cons -msaout $outdir/$msa");	USEARCH and UCLUST algorithms: Edgar,RC (2010) Search and clustering orders of magnitude faster than BLAST, Bioinformatics 26(19), 2460-2461. doi: 10.1093/bioinformatics/btq461
Step 4b: Connecting each sample to the corresponding sequence/MOTU;		sed 's/^>/>sample_/g' sample_centroids.fa > 146443_centroids_edited.fa cat *_centroids_edited.fa > allsequencesPoolx.fa	
Step 4c: Final dereplication		usearch -derep_fulllength allsequencesPoolx.fa -output allsequencesPoolx_uniques.fasta -sizeout -minseqlength 135 -strand both -uc allseqununences_rc_uniques.out	USEARCH and UCLUST algorithms: Edgar,RC (2010) Search and clustering orders of magnitude faster than BLAST, Bioinformatics 26(19), 2460-2461. doi: 10.1093/bioinformatics/btq461
Step 5: Blast	blastn	export BLASTDB=/usr/local/extras/Genomics/db/ncbi_nt/current blastn -query $outdir/$cent -db nt -num_threads 4 -evalue 1e-10 -outfmt 6 -perc_identity 90 -out Poolx_blast.txt	Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ (1990) Basic local alignment search tool. Journal of Molecular Biology 215:403-410

Table D.11.4 Output of Illumina MiSeq sequencing and bioinformatic analysis.

	PoolA		**PoolB**		**Comment**
	No sequences	Per cent	No sequences	Per cent	
Read pairs MiSeq - paired-end reads	1162800	100%	916245	100%	
Step1: Trimming and quality filtering with Average quality score ≥ 20 over a 4-base sliding window, min length 135 bp					
Dropped	146385	12.59%	105547	11.52%	
Both surviving	897,964	77.22%	724,779	79%	> 70% survived
For only	100633	8.65%	72624	7.93%	
Rev only	17818	1.53%	13295	1.45%	
Step2: Aligning both reads					
Total pairs	897,964	100%	724,779	100%	
Combined pairs/aligned paired reads	864,845	96.31	717,735	99.03	> 90% of pairs aligned
Not combined pairs	33119	3.69	7044	0.97	
Step3: Demultiplexing into a sample specific files and removal of MIDs,primer sequences and sequences without exact match to primer sequence					
Group count_number of sequences assigned to each sample	549,782	63.6% of combined pairs	421,457	58.7% of combined pairs	
Aligned_groups list of sequence names and their assigned sample-ID	549,782	/	421,457	/	
Aligned_scrap sequences without matching primers	315,063	/	296,278	/	
Aligned_trim sequences with matching primers	549,782	63.6% of combined pairs	421,457	58.7% of combined pairs	
Demultiplexed sequences in a file for each sample	549,782	/	421,457	/	
Step 4: Removal of sequences with fewer than 5 copies and chimeric sequences, clustering at 97% and final dereplication					
Unique sequences/MOTU/cluster sequence	392	0.05% of combined pairs	287	0.04% of combined pairs	
Step 5: Blast the representative cluster sequences against NCBI database					
Blast output	386	0.04% of combined pairs	195	0.03% of combined pairs	Loss of 1.5% and 32% respectively due to blast criteria

Table D.11.5 Quality criteria of MOTUs that were used for taxonomic assignment.

No of MOTUs	q-seq-id	S-seq-id	p-ident	length	e-value	Bit-score
1	146437_M00969_273_000000000-AY5TW_1_1102_14305_3883	AF315121	99	211	1.18E-101	379
2	146437_M00969_273_000000000-AY5TW_1_1102_19526_12384	AF315121	100	211	2.53E-103	385
3	146438_M00969_273_000000000-AY5TW_1_1101_27261_9100	EF042208	100	211	2.53E-103	385
4	146438_M00969_273_000000000-AY5TW_1_1101_13444_19038	EF042208	99	211	1.18E-101	379
5	146439_M00969_273_000000000-AY5TW_1_1102_15025_5592	AF315121	100	211	5.43E-105	390
6	146439_M00969_277_000000000-AYLGV_1_1101_12953_5382	KJ128795	100	211	2.76E-103	385
7	146440_M00969_273_000000000-AY5TW_1_1104_23620_22458	KJ128795	100	211	2.53E-103	385
8	146440_M00969_277_000000000-AYLGV_1_1101_19073_27985	AF315121	99	211	1.28E-101	379
9	146441_M00969_273_000000000-AY5TW_1_1102_7930_5591	KJ128795	100	211	5.43E-105	390
10	146441_M00969_277_000000000-AYLGV_1_1102_15894_4292	KJ128795	99	211	1.28E-101	379
11	146449_M00969_277_000000000-AYLGV_1_1101_12703_21299	AF315121	100	211	2.76E-103	385
12	146450_M00969_273_000000000-AY5TW_1_1103_9519_12161	AF315121	100	211	2.53E-103	385
13	146450_M00969_273_000000000-AY5TW_1_1104_24499_8839	KJ128795	100	211	2.53E-103	385
14	146437_2_M00969_277_000000000-AYLGV_1_1101_18349_9237	KJ128795	100	211	5.93E-105	390
15	146437_M00969_273_000000000-AY5TW_1_1103_20135_15217	KJ128826	100	208	2.49E-103	385
16	146438_M00969_273_000000000-AY5TW_1_1102_19858_13124	KJ128826	99.519	208	1.16E-101	379
17	146438_M00969_273_000000000-AY5TW_1_2103_17482_23139	KJ128826	99.519	208	1.16E-101	379
18	146440_M00969_273_000000000-AY5TW_1_1104_19252_3931	KJ128827	100	208	2.49E-103	385
19	146440_M00969_273_000000000-AY5TW_1_1101_8169_10679	KJ128826	100	206	3.22E-102	381
20	146437_M00969_273_000000000-AY5TW_1_1101_9887_10271	AP017650	100	208	2.49E-103	385
21	146437_M00969_273_000000000-AY5TW_1_1101_27425_16396	KJ128822	100	208	2.49E-103	385
22	146437_M00969_273_000000000-AY5TW_1_1103_19670_3702	KJ128822	99.519	208	1.16E-101	379
23	146438_M00969_273_000000000-AY5TW_1_1101_20098_5621	KJ128822	99.519	208	1.16E-101	379
24	146438_M00969_273_000000000-AY5TW_1_1104_6282_12086	KJ128822	98.558	208	2.50E-98	368
25	146438_M00969_273_000000000-AY5TW_1_1104_14160_17658	AP017650	99.519	208	1.16E-101	379

No of MOTUs	q-seq-id	S-seq-id	p-ident	length	e-value	Bit-score
26	146438_M00969_273_000000000-AY5TW_1_1102_15665_10237	AP017650	99.038	208	5.38E-100	374
27	146438_M00969_273_000000000-AY5TW_1_1101_12786_9136	FR751400	98.558	208	2.50E-98	368
28	146440_M00969_273_000000000-AY5TW_1_1106_23026_14975	FR751400	99.519	208	1.16E-101	379
29	146440_M00969_273_000000000-AY5TW_1_1101_16295_9201	AP017650	99.519	208	1.16E-101	379
30	146440_M00969_273_000000000-AY5TW_1_1103_6716_5247	AP017650	99.519	208	1.16E-101	379
31	146444_M00969_273_000000000-AY5TW_1_2102_28368_19489	AP017650	99.519	208	1.16E-101	379
32	146437_2_M00969_277_000000000-AYLGV_1_1102_14038_27379	AP017650	99.038	208	5.87E-100	374
33	146437_M00969_273_000000000-AY5TW_1_1101_24055_10171	FR849599	100	205	1.14E-101	379
34	146437_M00969_273_000000000-AY5TW_1_1101_17362_10139	KJ128741	100	210	1.94E-104	388
35	146437_M00969_273_000000000-AY5TW_1_1102_26108_9370	KJ128910	99.524	210	9.04E-103	383
36	146437_M00969_273_000000000-AY5TW_1_1105_9560_15855	FR849599	97.561	205	2.48E-93	351
37	146437_M00969_273_000000000-AY5TW_1_1101_18313_16770	KC193756	100	210	1.94E-104	388
38	146437_M00969_273_000000000-AY5TW_1_1104_20457_22121	KJ128910	99.048	210	4.21E-101	377
39	146438_M00969_273_000000000-AY5TW_1_1101_4468_10820	KJ128910	99.048	210	4.21E-101	377
40	146438_M00969_273_000000000-AY5TW_1_1101_14598_7864	KJ128740	100	210	1.94E-104	388
41	146438_M00969_273_000000000-AY5TW_1_1104_16340_20725	KJ128741	99.524	210	9.04E-103	383
42	146438_M00969_273_000000000-AY5TW_1_1101_15625_23263	KJ128910	99.524	210	9.04E-103	383
43	146438_M00969_273_000000000-AY5TW_1_1101_14475_25427	DQ912088	99.024	205	2.46E-98	368
44	146438_M00969_273_000000000-AY5TW_1_1101_8549_4540	FR849599	99.512	205	5.29E-100	374
45	146439_M00969_273_000000000-AY5TW_1_1101_15967_4762	FR849561	99.048	210	4.21E-101	377
46	146439_M00969_277_000000000-AYLGV_1_1101_11296_2925	KC193720	98.571	210	2.14E-99	372
47	146440_M00969_273_000000000-AY5TW_1_1101_21176_21035	FR849599	100	202	5.29E-100	374
48	146440_M00969_273_000000000-AY5TW_1_1103_14268_9831	FR849561	98.571	210	1.96E-99	372
49	146440_M00969_273_000000000-AY5TW_1_1101_3603_13495	FR849599	99.024	205	2.46E-98	368
50	146442_M00969_277_000000000-AYLGV_1_1101_19724_5258	KJ128910	99.524	210	9.87E-103	383
51	146442_M00969_273_000000000-AY5TW_1_1101_20475_24539	KJ128740	99.048	210	4.21E-101	377
52	146442_M00969_273_000000000-AY5TW_1_1102_15042_17323	KJ128741	99.048	210	4.21E-101	377

No of MOTUs	q-seq-id	S-seq-id	p-ident	length	e-value	Bit-score
53	146444_M00969_273_000000000-AY5TW_1_1102_13813_8004	KC193777	98.095	210	9.11E-98	366
54	146444_M00969_273_000000000-AY5TW_1_1101_4546_23469	KJ128910	98.095	210	9.11E-98	366
55	146444_M00969_273_000000000-AY5TW_1_1104_13834_23205	FR849561	97.619	210	4.24E-96	361
56	146450_M00969_273_000000000-AY5TW_1_1101_16275_28455	KJ128910	98.571	210	1.96E-99	372
57	146450_M00969_273_000000000-AY5TW_1_1106_16262_11916	FR849561	99.043	209	1.51E-100	375
58	146450_M00969_273_000000000-AY5TW_1_1101_6461_11968	KC193768	98.571	210	1.96E-99	372
59	146450_M00969_273_000000000-AY5TW_1_1106_22895_25788	KJ128910	98.095	210	9.11E-98	366
60	146452_M00969_277_000000000-AYLGV_1_1101_5272_7177	KJ128910	98.571	210	7.59E-99	370
61	146437_2_M00969_277_000000000-AYLGV_1_1101_18100_2367	KJ128910	100	210	2.12E-104	388
62	146437_2_M00969_277_000000000-AYLGV_1_1101_18439_3172	KJ128741	100	210	2.12E-104	388
63	146437_2_M00969_277_000000000-AYLGV_1_1102_5114_15375	KJ128910	99.048	210	4.59E-101	377
64	146439_M00969_277_000000000-AYLGV_1_1101_14720_9732	KJ128765	100	211	5.93E-105	390
65	146437_M00969_277_000000000-AYLGV_1_1101_17036_4544	KJ128862	100	224	3.78E-112	414
66	146438_M00969_273_000000000-AY5TW_1_1102_15507_15905	KJ128862	99.554	224	1.61E-110	409
67	146439_M00969_277_000000000-AYLGV_1_1101_25155_5000	KU510499	100	224	3.78E-112	414
68	146439_M00969_277_000000000-AYLGV_1_1101_9391_7521	FJ870412	99.107	224	8.17E-109	403
69	146439_M00969_277_000000000-AYLGV_1_1103_6393_5494	KJ128862	99.554	224	1.76E-110	409
70	146440_M00969_273_000000000-AY5TW_1_1101_3584_9022	KU936350	99.107	224	7.49E-109	403
71	146440_M00969_277_000000000-AYLGV_1_1102_22459_12199	KJ128862	99.554	224	1.76E-110	409
72	146441_M00969_277_000000000-AYLGV_1_1101_20701_8232	KJ128862	99.554	224	1.76E-110	409
73	146443_M00969_277_000000000-AYLGV_1_1102_5525_24499	KJ128862	98.661	224	3.8E-107	398
74	146445_M00969_277_000000000-AYLGV_1_1101_12011_8918	KJ128862	99.554	224	1.76E-110	409
75	146437_2_M00969_273_000000000-AY5TW_1_1102_24621_21708	KJ128862	100	224	3.46E-112	414
76	146438_M00969_273_000000000-AY5TW_1_1107_19768_20694	AF122825	99.554	224	1.61E-110	409
77	146438_M00969_273_000000000-AY5TW_1_1101_23705_8805	EU410416	100	217	2.60E-108	401
78	146438_M00969_273_000000000-AY5TW_1_1101_9046_9345	KJ128906	99.107	224	7.49E-109	403
79	146438_M00969_273_000000000-	EU419747	98.198	222	2.64E-103	385

No of MOTUs	q-seq-id	S-seq-id	p-ident	length	e-value	Bit-score
	AY5TW_1_1106_5566_12823					
80	146438_M00969_273_000000000-AY5TW_1_1102_14365_5613	KJ168065	99.526	211	2.53E-103	385
81	146438_M00969_273_000000000-AY5TW_1_1101_20270_19169	KJ128870	100	207	8.89E-103	383
82	146437_2_M00969_277_000000000-AYLGV_1_1101_25250_15535	KJ128871	99.034	207	2.1E-99	372
83	146437_M00969_273_000000000-AY5TW_1_1101_15433_7149	KT633607	100	213	4.25E-106	394
84	146438_M00969_273_000000000-AY5TW_1_1102_10784_2931	KT633607	99.531	213	1.98E-104	388
85	146438_M00969_273_000000000-AY5TW_1_1103_11713_13769	KT633607	100	212	1.53E-105	392
86	146439_M00969_273_000000000-AY5TW_1_1101_4637_21155	KT633607	99.531	213	1.98E-104	388
87	146440_M00969_273_000000000-AY5TW_1_1107_19000_23334	KT633607	99.531	213	1.98E-104	388
88	146437_M00969_273_000000000-AY5TW_1_1101_23206_24521	KJ128898	99.539	217	1.21E-106	396
89	146437_M00969_273_000000000-AY5TW_1_1101_19358_7121	KJ128898	99.539	217	1.21E-106	396
90	146438_M00969_273_000000000-AY5TW_1_1106_14903_24911	KJ128898	99.078	217	5.62E-105	390
91	146438_M00969_273_000000000-AY5TW_1_1101_23851_8482	KJ128898	99.539	217	1.21E-106	396
92	146439_M00969_273_000000000-AY5TW_1_1102_21124_23388	KJ128898	100	217	2.60E-108	401
93	146440_M00969_273_000000000-AY5TW_1_1101_11208_7721	KJ128898	99.539	217	4.32E-106	394
94	146444_M00969_273_000000000-AY5TW_1_1101_11268_6586	KJ128898	99.539	217	1.21E-106	396
95	146444_M00969_273_000000000-AY5TW_1_1104_19247_28671	KJ128898	99.539	217	1.21E-106	396
96	146445_M00969_273_000000000-AY5TW_1_1108_18728_21966	KJ128898	99.078	217	5.62E-105	390
97	146437_2_M00969_277_000000000-AYLGV_1_1101_10880_6810	KU510503	100	217	2.83E-108	401
98	146437_2_M00969_277_000000000-AYLGV_1_1101_8190_6848	KU510503	99.539	217	1.32E-106	396
99	146437_M00969_273_000000000-AY5TW_1_1101_6839_6659	KJ627974	99.519	208	1.16E-101	379
100	146437_M00969_273_000000000-AY5TW_1_1109_4238_10131	KJ627974	100	205	1.16E-101	379
101	146438_M00969_273_000000000-AY5TW_1_1101_16501_11424	KJ627974	100	208	2.49E-103	385
102	158316_M00969_273_000000000-AY5TW_1_1101_28507_12328	KC193769	100	210	1.94E-104	388
103	158318_M00969_277_000000000-AYLGV_1_1101_15095_4934	KC193720	99.524	210	9.87E-103	383
104	158326_M00969_273_000000000-AY5TW_1_1101_4831_14636	KC193777	99.048	210	4.21E-101	377
105	158326_M00969_273_000000000-AY5TW_1_1103_2468_15724	KJ128741	99.048	210	4.21E-101	377

No of MOTUs	q-seq-id	S-seq-id	p-ident	length	e-value	Bit-score
106	158327_M00969_273_000000000-AY5TW_1_1101_19137_7485	KC193732	100	210	1.94E-104	388
107	158328_M00969_273_000000000-AY5TW_1_1102_3284_15746	KJ128741	99.524	210	9.04E-103	383
108	158328_M00969_273_000000000-AY5TW_1_1105_10438_14160	KJ128910	97.619	210	4.24E-96	361
109	158328_M00969_273_000000000-AY5TW_1_1107_16399_4897	KJ128741	99.524	210	9.04E-103	383
110	158329_M00969_273_000000000-AY5TW_1_1106_26173_15504	KJ128740	99.524	210	9.04E-103	383
111	158329_M00969_273_000000000-AY5TW_1_1104_21243_11764	KC193720	98.095	210	9.11E-98	366
112	158331_M00969_273_000000000-AY5TW_1_1104_15579_2627	KJ128741	99.524	210	9.04E-103	383
113	158331_M00969_273_000000000-AY5TW_1_1103_14814_8734	KC193777	97.619	210	4.24E-96	361
114	158332_M00969_273_000000000-AY5TW_1_1103_5388_13732	KJ128741	99.048	210	4.21E-101	377
115	158332_M00969_273_000000000-AY5TW_1_1102_24809_24690	KJ128740	97.619	210	4.24E-96	361
116	158333_M00969_273_000000000-AY5TW_1_1101_23775_21597	KC193768	98.571	210	1.96E-99	372
117	158316_M00969_273_000000000-AY5TW_1_1106_3159_18568	KJ128910	99.524	210	9.04E-103	383
118	158317_M00969_277_000000000-AYLGV_1_1101_9295_7591	KJ128910	99.524	210	9.87E-103	383
119	158326_M00969_273_000000000-AY5TW_1_1103_18938_15756	KJ128910	99.524	210	9.04E-103	383
120	158328_M00969_273_000000000-AY5TW_1_1101_21109_18807	KJ128910	99.524	210	9.04E-103	383
121	158328_M00969_273_000000000-AY5TW_1_1105_3153_13664	KJ128910	98.571	210	1.96E-99	372
122	158329_M00969_273_000000000-AY5TW_1_1103_23245_10923	KJ128910	99.524	210	9.04E-103	383
123	158329_M00969_273_000000000-AY5TW_1_1103_11912_22204	KJ128910	99.524	210	9.04E-103	383
124	158331_M00969_273_000000000-AY5TW_1_1101_13010_19728	KJ128910	99.524	210	9.04E-103	383
125	158332_M00969_273_000000000-AY5TW_1_1105_27871_11343	KJ128910	99.524	210	9.04E-103	383
126	158332_M00969_273_000000000-AY5TW_1_1102_23450_20124	KJ128910	99.524	210	9.04E-103	383
127	158333_M00969_273_000000000-AY5TW_1_1107_24795_16622	KJ128910	99.524	210	9.04E-103	383
128	158333_M00969_273_000000000-AY5TW_1_1109_21956_25566	KJ128910	99.524	210	9.04E-103	383
129	158316_M00969_273_000000000-AY5TW_1_1102_17972_18839	FR849599	99.512	205	5.29E-100	374
130	158316_M00969_273_000000000-AY5TW_1_1101_14384_8657	FR849599	99.024	205	2.46E-98	368
131	158327_M00969_273_000000000-AY5TW_1_1101_8872_10503	FR849599	99.512	205	5.29E-100	374
132	158329_M00969_273_000000000-	FR849599	99.512	205	5.29E-100	374

No of MOTUs	q-seq-id	S-seq-id	p-ident	length	e-value	Bit-score
	AY5TW_1_1106_5076_21928					
133	158327_M00969_273_000000000-AY5TW_1_1101_14191_13106	KJ128827	99.038	208	5.38E-100	374
134	158327_M00969_273_000000000-AY5TW_1_1101_18211_28305	KJ128826	99.519	208	1.16E-101	379
135	158333_M00969_273_000000000-AY5TW_1_1102_4609_20805	KJ128795	99.526	211	2.53E-103	385
136	158333_M00969_273_000000000-AY5TW_1_1103_21347_5449	KJ128795	99.052	211	1.18E-101	379
137	158316_M00969_273_000000000-AY5TW_1_1104_8166_5628	AP017650	99.519	208	1.16E-101	379
138	158316_M00969_273_000000000-AY5TW_1_1101_26101_9817	AP017650	99.519	208	1.16E-101	379
139	158318_M00969_277_000000000-AYLGV_1_1101_10887_15643	AP017650	99.519	208	1.26E-101	379
140	158319_M00969_273_000000000-AY5TW_1_1102_15859_8335	AP017650	99.519	208	1.16E-101	379
141	158327_M00969_273_000000000-AY5TW_1_1102_8194_14530	KJ128822	99.519	208	1.16E-101	379
142	158327_M00969_273_000000000-AY5TW_1_1107_25257_10792	AP017650	99.038	208	5.38E-100	374
143	158327_M00969_273_000000000-AY5TW_1_1101_20620_19170	AP017650	99.519	208	1.16E-101	379
144	158333_M00969_273_000000000-AY5TW_1_1103_15530_21664	KJ128825	100	208	2.49E-103	385
145	158317_M00969_277_000000000-AYLGV_1_1101_8195_6365	KJ128862	99.554	224	1.76E-110	409
146	158318_M00969_277_000000000-AYLGV_1_1101_10365_8785	KU510499	99.554	224	1.76E-110	409
147	158321_M00969_277_000000000-AYLGV_1_1101_21608_2864	KJ128862	99.554	224	1.76E-110	409
148	158327_M00969_273_000000000-AY5TW_1_1103_21252_10689	KJ128862	100	223	1.24E-111	412
149	158327_M00969_273_000000000-AY5TW_1_1103_5622_6457	KJ128862	97.788	226	2.12E-104	388
150	158327_M00969_273_000000000-AY5TW_1_1102_6728_13312	KJ128862	99.554	224	1.61E-110	409
151	158328_M00969_277_000000000-AYLGV_1_1101_14974_8593	KJ128862	99.554	224	1.76E-110	409
152	158330_M00969_273_000000000-AY5TW_1_1102_18265_2051	KJ128862	99.554	224	1.61E-110	409
153	158322_M00969_277_000000000-AYLGV_1_1101_23960_7813	KJ128906	99.107	224	8.17E-109	403
154	158322_M00969_277_000000000-AYLGV_1_1101_20149_5105	KJ128906	98.661	224	3.8E-107	398
155	158327_M00969_273_000000000-AY5TW_1_1102_9564_24989	KJ128870	99.517	207	4.14E-101	377
156	158329_M00969_273_000000000-AY5TW_1_1102_20113_13469	KT633607	99.531	213	1.98E-104	388
157	158329_M00969_277_000000000-AYLGV_1_1101_17608_18399	KU510503	99.078	217	6.13E-105	390
158	158317_M00969_277_000000000-AYLGV_1_1101_12124_6581	KU510503	99.539	217	1.32E-106	396

No of MOTUs	q-seq-id	S-seq-id	p-ident	length	e-value	Bit-score
159	158318_M00969_277_000000000-AYLGV_1_1101_24645_12079	KU510503	99.078	217	6.13E-105	390
160	158319_M00969_273_000000000-AY5TW_1_1101_4065_16408	KJ128898	99.078	217	5.62E-105	390
161	158319_M00969_273_000000000-AY5TW_1_1101_27338_12669	KJ128898	99.078	217	5.62E-105	390
162	158322_M00969_277_000000000-AYLGV_1_1101_10398_4334	KU510503	99.539	217	1.32E-106	396
163	158325_M00969_277_000000000-AYLGV_1_1101_25631_15275	KU510503	98.157	217	1.33E-101	379
164	158326_M00969_273_000000000-AY5TW_1_1101_10267_13492	KJ128898	99.539	217	1.21E-106	396
165	158327_M00969_273_000000000-AY5TW_1_1101_17516_21993	KJ128898	99.539	217	1.21E-106	396
166	158332_M00969_273_000000000-AY5TW_1_1101_25351_7734	KJ128898	99.539	217	1.21E-106	396
167	158329_M00969_277_000000000-AYLGV_1_1101_24101_11074	KJ627974	100	208	2.71E-103	385
168	158329_M00969_277_000000000-AYLGV_1_1101_10726_4988	KJ128825	100	208	2.71E-103	385
169	158334_M00969_277_000000000-AYLGV_1_1101_7624_6843	KJ128870	99.517	207	4.51E-101	377

E USE OF TELEMETRY DATA FOR SIMULATION OF DIVER MOVEMENTS

Individual-based modelling (IBM) is considered one of the most advanced tools for assessing and forecasting species responses to changing environmental conditions and anthropogenic pressures (GRIMM et al. 2005; GRIMM & RAILSBACK 2005). In the framework of IBMs, individuals are modelled through a number of time steps, where on every step the modelled individual makes decisions responding to its environment. But as every model, individual-based models are as good as the input data used for parametrisation.

Telemetry data is probably the only source that can provide empirical and unbiased data about bird movements, and advanced telemetry techniques of today can also collect and deliver detailed information about bird foraging ecology and energy budgets. Satellite telemetry, as used in this study, enables to collect rather basic position information, which helps to understand movements of the study species but often lacks details that are important for parametrising IBMs. We nevertheless explored whether information collected when tracking movements of red-throated divers allows to simulate bird movements while on wintering grounds, which is the first step in individual-based modelling.

Movement simulation in IBMs is usually conducted at evenly spaced time steps, with time intervals from minutes to a few hours in order to capture behavioural processes. This also depends on study questions and simulation system setup. Satellite telemetry, however, collects positions at uneven intervals during the data collection bursts with breaks of a day or longer in-between bursts, as was in this study. We thus used information from a few tagged divers that recorded the most temporally frequent information in the first winter of tracking, right after the deployment. Four of the birds recorded positions daily, with average daily relocation distances ranging from 6.6 to 16.2 km (see chapter 5.3.6.2 for details).

Equally distributed steps, turning angles and inspection of diver tracks during the wintering period, suggest that most individuals moved in a correlated random walk pattern with correlation between steps being fairly low (see example in Figure E.1 and Figure E.2). Therefore, we conducted simulations of correlated random walk with low correlation coefficient between steps, ranging from 0.1 to 0.5. Correlation coefficient defined turning angles, making them more likely to be random as correlation coefficient was lower. The simulation was done at a coarse temporal scale with time step duration being 12 hours. For the input on time step length, we divided in half the average daily time step length measured in red-throated divers that were tracked at most intensive schedule. Simulated positions were not allowed to fall on land. Furthermore, the North Sea bathymetry raster was used as environmental preference/resistance dataset, where depth zones between 10 and 30 m were preferred areas and habitat preference was gradually decreasing towards shallower and deeper waters. The movement simulation was implemented in software R (R CORE TEAM 2018) by running custom written code.

Simulations produced movement trajectories that resembled movement patterns and scale of winter area range of actual birds, data from which was used for simulation parametrisation (see examples in Figure E.3 and Figure E.4).

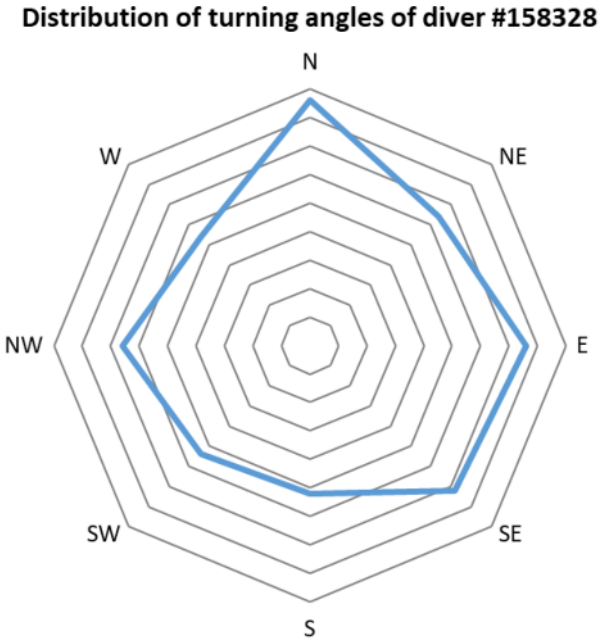


Figure E.1 Example of distribution of turning angles of individual #156328 during the wintering period. The chart shows no particular direction characterising random turns.

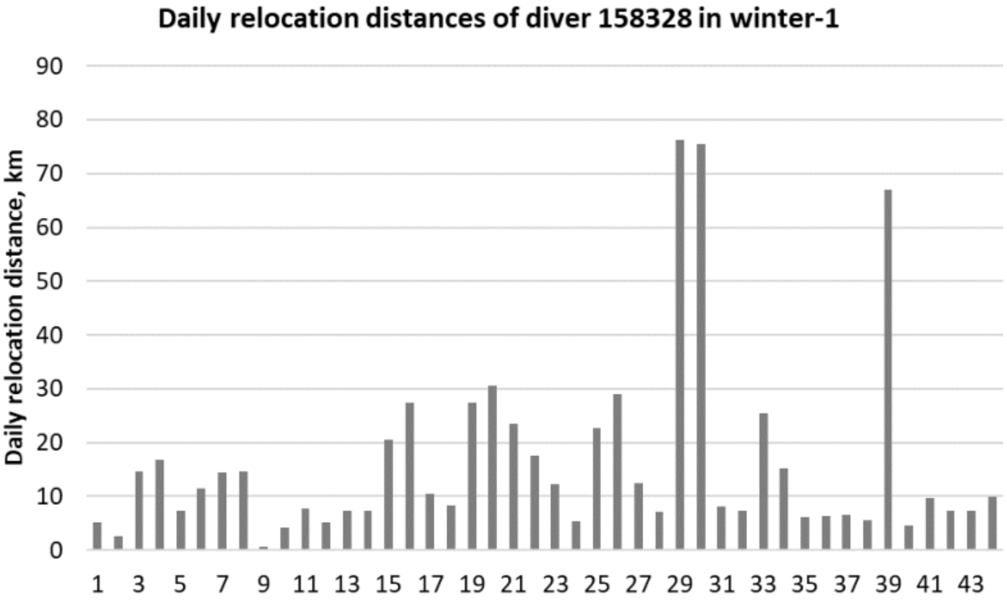


Figure E.2 Example of daily relocation distances of individual #156328 during the wintering period. The chart shows no trend in relocation distances between days characterising random movements.

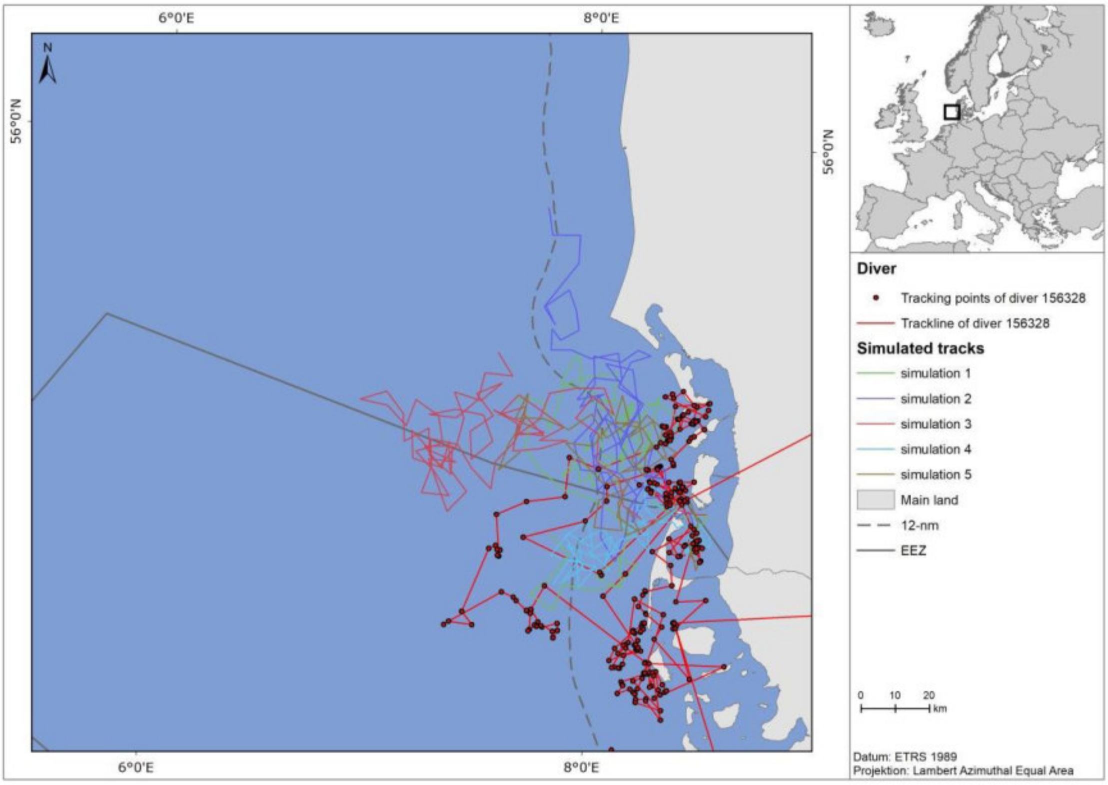


Figure E.3 *Example of 5 simulated tracks of red-throated diver movements on wintering area based on movement parameters of individual #156328. The track of real bird is shown in red line with overlaid points.*

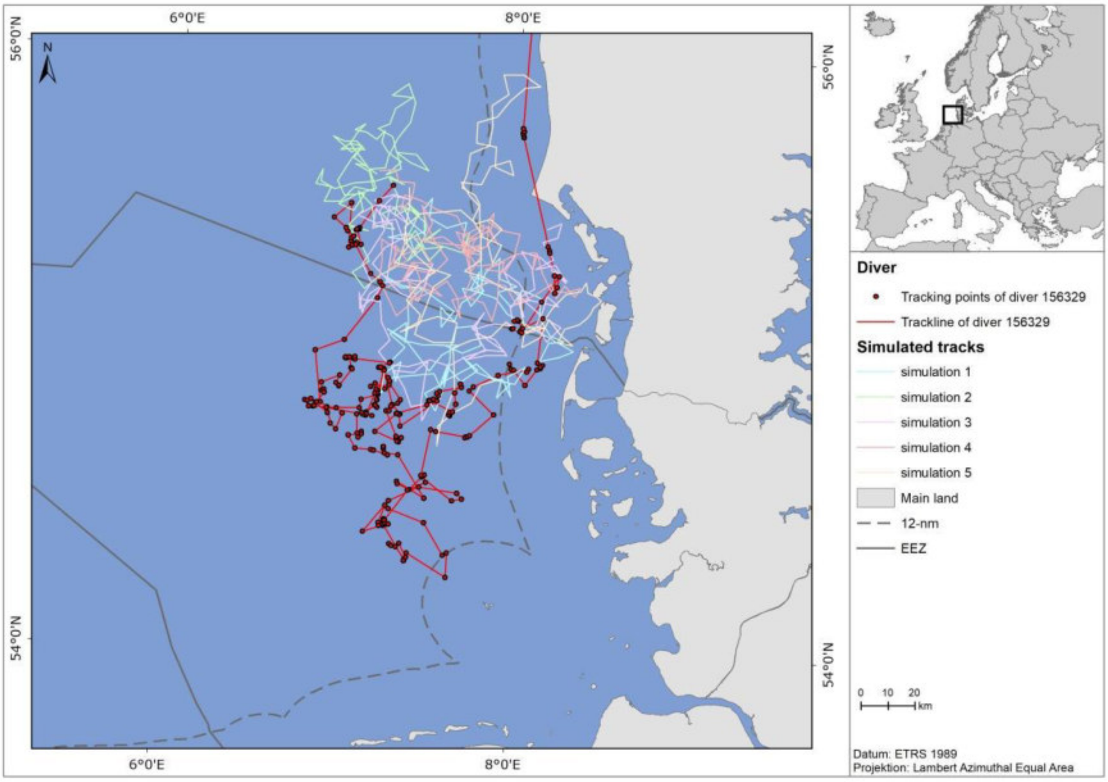


Figure E.4 *Example of 5 simulated tracks of red-throated diver movements on wintering area based on movement parameters of individual #156329. The track of real bird is shown in red line with overlaid points.*

Conclusion

Movement data collected from satellite telemetry suggest that while wintering red-throated divers move in patterns resembling correlated random walk with low correlation coefficient between the steps. The collected data provided information about diver movements at coarse temporal scale and thus allowed to run simulations at daily or 12-hour time steps. In the simulation exercise we accounted for water depth while simulating bird movement, and other variables defining bird preference or resistance to them could be implemented in a similar way (e.g., presence of and distance to offshore wind farms, salinity, meteorological factors).

Future perspective

Diver movement data at finer resolution, e.g. hourly GPS positions, would provide finer temporal resolution that is essential for movement simulations and individual-based modelling with more precision spatially and temporally.

Information about foraging behaviour of the species is of particular importance if we are to assess effects of offshore wind farms and other factors on wintering divers using IBM tools. Novel telemetry techniques allow collecting such information by either deploying transmitting GPS / foraging activity devices, or using data loggers that need to be deployed and recovered by recapturing birds.