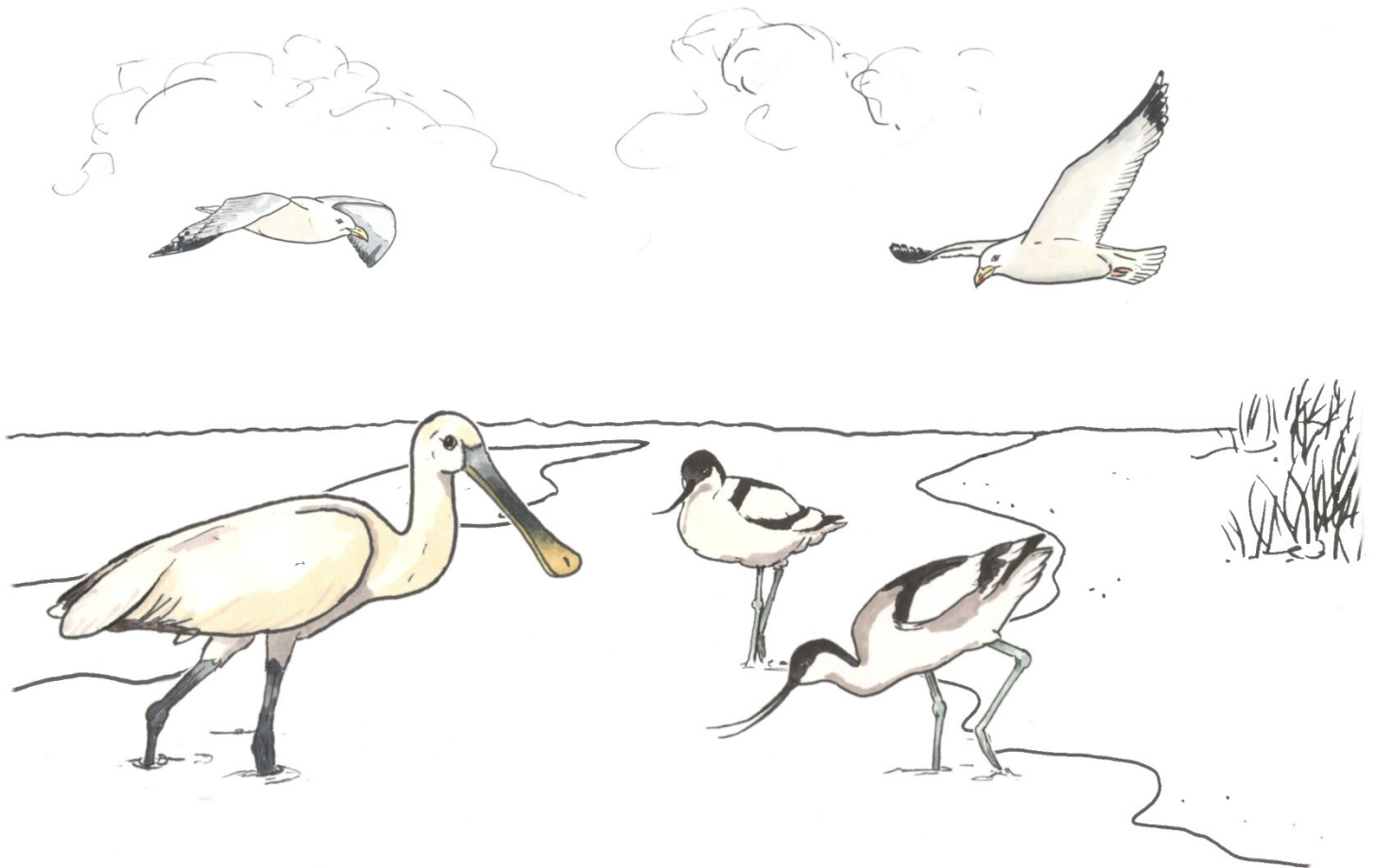


**Follow the birds – Movement ecology and diet composition of coastal birds as indicators for characteristic habitats in the Wadden Sea**



**Dissertation**

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## SUMMARY

The Wadden Sea is a complex mosaic of different habitats, formed by the tidal rhythm. To protect this unique ecosystem, the Wadden Sea has to be monitored and the ecological status assessed. However, due to the high dynamics, the monitoring is difficult. Suitable indicators have to be developed.

This thesis contributes to an ecological assessment of the habitats “intertidal flats” and “shallow waters”, based on the foraging behaviour of coastal birds. While herring gulls (*Larus argentatus*) were chosen for intertidal flats, pied avocets (*Recurvirostra avosetta*) and Eurasian spoonbills (*Platalea leucorodia*) were used as potential bio-indicators for shallow waters. GPS data and diet analyses were combined to investigate the foraging ecology on an individual and colony level, respectively. Both approaches were merged into a holistic assessment of the foraging habitat.

In a multi-colony approach herring gulls demonstrated a dual intertidal-terrestrial foraging strategy. In the intertidal common cockles (*Cerastoderma edule*), blue mussels (*Mytilus edulis*), and especially the invaded American razor clams (*Ensis leei*) were the dominant prey species. Prey depletion close to the breeding site forced herring gulls to use the terrestrial habitat increasingly for foraging. Overall, herring gulls prefer to forage on intertidal bivalve beds in the vicinity of the nesting area during low water levels. This foraging strategy combined with hydrodynamic data have great potential to detect epibenthic as well as endobenthic intertidal bivalve beds and to extend the existing monitoring program.

Pied avocets and Eurasian spoonbills were equipped with GPS devices for the first time in the Wadden Sea and enhance our knowledge on shallow waters. Avocets foraged in intertidal channels in the salt marshes close to the breeding site, performing short foraging trips mainly during daytime. Stable isotope analyses and GPS data indicated that marine fish comprise a greater part in diet composition than previously assumed. Similarly, it was shown that Eurasian spoonbills used the intertidal creek system between the mainland and the islands as foraging habitat. Regurgitates and blood samples reflect the diet composition and revealed an opportunistic foraging strategy. Differences in prey choice between years, colonies, and seasons indicated changes in prey availability. Sticklebacks and flatfish were the dominant prey species in early May (red blood cells), while the diet consisted of smelts, sticklebacks, and gobies end of May (blood serum, regurgitates). Both species prey on marine fish in the shallow waters and indicated the importance of this habitat as nursery area for fish.

This thesis enhances our knowledge on habitat selection and diet composition of characteristic top predators and demonstrates the suitability of herring gulls, Pied avocets, and Eurasian spoonbills as indicator species for intertidal flats and shallow waters. The combination of tracking and diet data provides new findings about the foraging behaviour and reflect the distribution and ecological status

of the associated habitat. Movement data of characteristic shorebirds can improve the monitoring of the Wadden Sea and helps to detect changes in this highly dynamic ecosystem. This strengthens the foundation of scientific conservation management and spatial planning.



## ZUSAMMENFASSUNG

Das Wattenmeer ist ein komplexes Mosaik verschiedener Habitats, das durch den Gezeitenrhythmus gebildet wird. Um dieses einzigartige Ökosystem zu schützen, muss das Wattenmeer überwacht und der ökologische Zustand bewertet werden. Aufgrund der hohen Dynamik ist ein Monitoring jedoch schwierig. Daher müssen geeignete Indikatoren entwickelt werden.

Die vorliegende Arbeit trägt zu einer ökologischen Bewertung der Habitats „Wattflächen“ und „Flachwasser“ bei, basierend auf dem Nahrungsverhalten von Küstenvögeln. Als mögliche Bio-Indikatoren wurden für die Wattflächen Silbermöwen (*Larus argentatus*) und für die Flachwasser Säbelschnäbler (*Recurvirostra avosetta*) und Löffler (*Platalea leucorodia*) ausgewählt. GPS-Daten und Nahrungsanalysen wurden kombiniert, um die Nahrungsökologie auf individueller bzw. Kolonieebene zu untersuchen. Beide Ansätze wurden zu einer ganzheitlichen Bewertung des Nahrungshabitats zusammengeführt.

In einem Ansatz mit mehreren Kolonien zeigten Silbermöwen eine duale Nahrungsstrategie, wobei intertidale und terrestrische Habitats aufgesucht wurden. Auf den Wattflächen waren Herzmuscheln (*Cerastoderma edule*), Miesmuscheln (*Mytilus edulis*) und insbesondere die invasive Schwertmuschel (*Ensis leei*) die dominierenden Beutearten. Nahrungsknappheit in der Nähe des Brutplatzes führte zu einer vermehrten Nutzung terrestrischer Nahrungsquellen. Waren eulitorale Muschelfelder in der Nähe des Brutplatzes vorhanden, wurden diese zu niedrigen Wasserständen von Silbermöwen zur Nahrungssuche präferiert. Das Nahrungsverhalten von Silbermöwen in Kombination mit hydrodynamischen Daten hat damit ein großes Potenzial sowohl epibenthische als auch endobenthische eulitorale Muschelfelder zu finden und das bestehende Muschelmonitoring zu erweitern.

Säbelschnäbler und Löffler wurden zum ersten Mal im Wattenmeer mit GPS-Geräten ausgestattet und erweiterten unser Wissen über die Flachwasserzone. Säbelschnäbler suchten hauptsächlich tagsüber in Salzwiesengraben in der Nähe ihres Brutplatzes nach Nahrung und legten dabei nur kurze Flugdistanzen zurück. Stabile Isotopenanalysen und GPS-Daten zeigten, dass marine Fische einen größeren Anteil an der Nahrung ausmachen als bisher angenommen. Ähnliches gilt für Löffler, die das Prielsystem zwischen dem Festland und den Inseln als Nahrungsgrundlage nutzten. Regurgitationen und Blutproben spiegeln die Zusammensetzung der Nahrung wider und zeigten eine opportunistische Nahrungsstrategie. Unterschiede zwischen Jahren, Kolonien und Jahreszeiten implizierten veränderte Beuteverfügbarkeiten. Anfang Mai dominierten Stichlinge und Plattfische die Nahrung (rote Blutzellen), während sich die Nahrung Ende Mai hauptsächlich aus Stinten, Stichlingen und Grundeln zusammensetzte (Blutserum, Regurgitationen). Beide Vogelarten erbeuten marine Fische in der

Flachwasserzone und zeigen damit die besondere Bedeutung dieses Habitats als Aufzuchtgebiet für Fische auf.

Diese Arbeit erweitert das Wissen über die Habitat- und Nahrungswahl charakteristischer Top-Prädatoren und zeigt die Eignung von Silbermöwen, Säbelschnäblern und Löfflern als Indikatorarten für Wattflächen und Flachwassergebiete. Die Kombination von GPS- und Nahrungsdaten ermöglicht neue Erkenntnisse zum Nahrungsverhalten und spiegelt die Verteilung und den ökologischen Zustand des zugehörigen Lebensraums wider. Bewegungsdaten charakteristischer Watvögel können die Überwachung des Wattenmeeres verbessern und helfen Veränderungen in diesem hochdynamischen Ökosystem zu erkennen. Dies stärkt die Grundlage für ein wissenschaftliches Naturschutzmanagement und marine Raumplanung.







# **GENERAL INTRODUCTION**



## GENERAL INTRODUCTION

The Wadden Sea is one of the largest coherent intertidal wetlands in the world and stretches along the North Sea coast of southern Denmark, Germany, and the northern part of the Netherlands (Kabat et al., 2012; van Roomen et al., 2012; Baptist et al., 2019). It is characterised by a fine spatial mosaic of different habitats, mainly influenced by the tidal rhythm (Yates et al., 1993; Reise et al., 2010). Sediment characteristics as well as benthos composition change within small distances and short time, forming a heterogeneous habitat structure (Beukema et al., 1993; Horn et al., 2017). Intertidal flats, salt marshes, seagrass meadows, bivalve beds, or tidal creeks are only some examples of the large diversity of habitats. Overall, the Wadden Sea is highly dynamic and productive and represents an economically and ecologically important ecosystem (van Roomen et al., 2012; Kabat et al., 2012). Due to its nutrient richness and high biomass, various species use the coastal zone for foraging. They are organised in a complex food web that includes microalgae, benthic fauna, and top predators (Asmus & Asmus, 1985; Beukema, 1976; Waser et al., 2016; Horn et al., 2019).

However, climate change and the cumulative impact of human activities threaten this network of habitats and the integrity of their food webs (Kabat et al., 2012; Emeis et al., 2015; Halpern et al., 2015). To facilitate adequate protection, national and international treaties obligate Germany to monitor and protect its marine environment (e.g., EU Marine Strategy Framework Directive, EU Natura2000 directives, Trilateral Monitoring and Assessment Programme, OSPAR). In this context the knowledge about the distribution and status of marine habitats and their species are important, but the Wadden Sea with its vast intertidal flats and heterogeneous habitat structure is especially difficult to monitor. Suitable indicators are necessary to gain fine-scale information to assess and protect this dynamic ecosystem.

This thesis is focused on the habitat types (1) “mudflats and sandflats not covered by seawater at low tide” (hereafter intertidal flats) and (2) “large shallow inlets and bays” (hereafter shallow waters), both listed in Annex I of the EC Habitats Directive (Naberhaus et al., 2012). The intertidal flats include sandflats, flats of mixed substrate, mudflats, intertidal bivalve beds, and seagrass meadows and are used by various shorebirds for foraging, due to the high biomass of benthic fauna (van Roomen et al., 2012; Horn et al., 2017). The permanently flooded shallow waters represent important nursery areas of invertebrates and fish and form main foraging areas for several species (Reise et al., 2010; Freitas et al., 2016; Couperus et al., 2016). Fishing activities, eutrophication, pollution, or sea-level rise by climate change threaten these habitats (Naberhaus et al., 2012; Kabat et al., 2012).

The present study investigates the habitat use of characteristic coastal bird species in intertidal flats and shallow waters. As top predators, birds react to changes in their environment, and are important bio-indicators for the status of the ecosystem (Furness & Greenwood, 1993; Parsons et al., 2008;

Dänhardt & Becker, 2011; Courtens et al., 2017). About 10 to 12 million shorebirds use the Wadden Sea as breeding, resting, and foraging area during their annual cycle (Reise et al., 2010; van Roomen et al., 2012; Blew et al., 2016). Distinct ecological niches minimize the competition and enable coexistence (Beukema et al., 1993; Goss-Custard, 1980; Kubetzki & Garthe, 2003; El-Hacen et al., 2014). Coastal bird species are usually adapted to specific intertidal habitats with specific sediment characteristics and benthos composition. Most coastal birds breeding in the Wadden Sea are central-place foragers and depend on the tidal rhythm (Ashmole, 1963; Monaghan, 1996; Schwemmer & Garthe, 2011). Therefore, prey of high quality and quantity in the vicinity of the breeding place is a main factor shaping their foraging ranges (Boersma & Rebstock, 2009; Isaksson et al., 2016; Schwemmer et al., 2017).

Knowledge about the habitat use and behaviour of top-predators is crucial for conservation management and spatial planning. Previous studies analysed the habitat selection and diet composition of coastal birds mainly based on visual observations (Nehls & Tiedemann, 1993; Hötker, 1999; Garthe et al., 2007). However, there are still gaps in knowledge on individual spatial-temporal movement patterns and diet composition, because visual observations are limited by weather, daylight, and accessibility of the terrain. The main aim of the present study was to investigate the habitat selection and foraging behaviour of three coastal bird species in the German Wadden Sea during the breeding season and to gain information about the used habitat types.

## **1 Species studied**

European herring gulls (*Larus argentatus*), pied avocets (*Recurvirostra avosetta*), and Eurasian spoonbills (*Platalea leucorodia*) were chosen as characteristic species of intertidal flats and shallow waters in the Wadden Sea. These species breed in colonies and prefer to forage close to their nesting sites (van Donk et al., 2017; Oudman et al., 2017). While herring gulls are linked to intertidal flats, pied avocets and Eurasian spoonbills require shallow waters for foraging. They are widely distributed and the status according to the IUCN Red List is 'least concern' (BirdLife International, 2020). As abundant and long-lived top predators they are well-suited model species. Changes in their distribution or behaviour indicate changes in the lower trophic levels and reflect the status of their characteristic habitat (Parsons et al., 2008; Courtens et al., 2017).



### 1.1 Herring gull (*Larus argentatus*)

In 2016 about 51,000 pairs of herring gulls bred in the Wadden Sea (Joint Monitoring Group for Breeding birds/TMAP; Koffijberg et al., 2017) with approximately 7,200 breeding pairs in Schleswig-Holstein in 2017 (TMAP/Nationalparkverwaltung Schleswig-Holsteinisches Wattenmeer). In coastal areas herring gulls usually nest on the ground and prefer salt marshes and dunes as breeding sites (Gedeon et al., 2014).

Herring gulls usually forage in the intertidal zone, where they feed on bivalves and crustaceans (Dernedde, 1993; Kubetzki & Garthe, 2003; Camphuysen, 2013). Therefore, herring gulls are an important keystone compartment in the intertidal food web (Horn et al., 2019). During the breeding season they prefer bivalve beds near their colony as foraging habitats and show a tide-dependent foraging strategy (Spaans, 1971; Garthe et al., 1999a; van Donk et al., 2017). They mainly forage by walking, trampling, or shallow plunge-diving (Glutz von Blotzheim et al., 1982; Mendel et al., 2008). Nevertheless, as opportunistic and omnivorous top predators, herring gulls adapt to changes in their environment and can switch to terrestrial or anthropogenic prey source (Sibly & McCleery, 1983; Kim & Monaghan, 2006; van Donk et al., 2017). But there is still a gap in knowledge which parameters affect these habitat switches, and if information on the foraging strategy can be used to indicate the distribution of the associated foraging habitat.

### 1.2 Pied avocet (*Recurvirostra avosetta*)

The Wadden Sea is the most important area for pied avocets in Western Europe. It contains almost 60% of the flyway population during summer and autumn (Kleefstra et al., 2019). About 5,800 breeding pairs in the entire Wadden Sea in 2016 (Joint Monitoring Group for Breeding birds/TMAP; Koffijberg et al., 2017) and 2,440 breeding pairs in Schleswig-Holstein in 2017 (TMAP/Nationalparkverwaltung Schleswig-Holsteinisches Wattenmeer) indicate a high degree of responsibility of Germany for this species. For a long time, the breeding numbers in Schleswig-Holstein were stable, but started decreasing in 2008 (Hötker & West, 2005; Koffijberg et al., 2015; Hötker et al., 2017). Predation events, and nest losses due to flooding are the main reasons for a low reproductive success (Hötker and West, 2006; Hötker & Segebade, 2010; Thorup & Koffijberg, 2016).

Pied avocets in the Wadden Sea breed in salt marshes and use their typical upward-curved bill to forage in shallow waters with muddy sediments, close to the coast (Quammen, 1982; Moreira, 1995a). They mainly use a scything movement to feed on small prey items in the water column and in the uppermost centimetre of fine sediment (Moreira, 1995b; Quammen, 1982). Previous studies were based on visual observations and dropping analyses and determined crustaceans, molluscs, ragworms, insect larvae, and small fish as prey source (Moreira, 1995b; Hötker, 1999). Hötker (1999) showed that the time-

activity budgets of avocets are influenced by the tide, type of prey, and the weather conditions. Nevertheless, information on individual foraging ecology is still scarce and knowledge on diet composition over longer time scales are missing.

### **1.3 Eurasian spoonbill (*Platalea leucorodia*)**

Eurasian spoonbills have an extremely large range and breed in several disjunct areas in Eurasia and North Africa. In the Wadden Sea this species extended its range in the last few decades and has its northern distribution limit in Denmark (approximately 2,700 breeding pairs in the Wadden Sea in 2016; Joint Monitoring Group for Breeding birds/TMAP; Koffijberg et al., 2017). Germany was first colonised by spoonbills in 1995 and since then the breeding numbers have increased (Krüger et al., 2010). Schleswig-Holstein had 390 breeding pairs in 2019 (Günther, K.; pers. comm.).

In the German Wadden Sea, spoonbills only breed on islands, and use salt marshes and dunes as nesting sites (Gedeon et al., 2014). For protection against flooding events some nest piles are up to one meter high.

Spoonbills forage between the subtidal and the intertidal zone by wading through shallow waters. They sieve the water for prey items with sideward-sweeping movements of their head (van Wetten & Wintermans, 1986; Veen et al., 2012). A previous study demonstrated that spoonbills breeding in the Dutch Wadden Sea mainly prey on small flatfish and gobies (Jouta et al., 2018). For the German Wadden Sea knowledge about habitat selection and food choice is lacking.

## **2. Methods**

In the recent years, the foraging ecology of birds is usually investigated by telemetry data or diet analyses. Both approaches provide important information about the habitat selection or diet composition, respectively. For bird species foraging in the intertidal or marine habitat it is difficult to identify important foraging habitats and prey items, due to the inaccessibility of the wide-stretched intertidal flats. Information about the foraging ecology on an individual and colony level are essential for monitoring and assessing the foraging habitat.

## 2.1 Telemetry data

The ongoing development of ever smaller GPS devices enables to analyse the habitat selection and foraging strategy on a fine-scale (Wilson et al., 2002; Garthe et al., 2016). In this study, different logger types and attachment methods were applied, depending on the research objective, as well as on the body mass and behaviour of the bird species.

Telemetry data provide information about trip characteristics (e.g., maximum trip distance, total trip distance, trip duration) and individual habitat selection. Longer trip distances imply higher energetic costs and may indicate prey depletion close to the breeding site (Morris and Black, 1980; Pierotti and Annett, 1991). Statistical approaches can detect the influence of different biotic and abiotic factors on the habitat choice. Particularly for tide-dependent bird species, tracking data provide important information on the habitat selection and foraging behaviour that can hardly be collected with other methods. Furthermore, birds can act as indicators for the distribution and status of characteristic habitats. So far, only few studies used tracking data to predict the distribution of specific habitats.

## 2.2 Diet analyses

To assess the diet composition, a combination of direct and indirect methods was applied. Samples from different colonies were used for an inter-colony comparison of diet choice.

Direct methods, like the analysis of regurgitates, pellets, and droppings, reflect the short-term diet over the preceding hours to few days before collection (Barrett et al., 2007). Prey items can usually be identified to species level. Depending on the degree of digestion information about prey size and mass can be inferred (e.g., Guse et al., 2009; Leopold and van Damme, 2003). However, direct diet methods are biased by the different digestibility of different food items (González-Solís et al., 1997; Barrett et al., 2007).

In contrast, indirect methods, in this case stable isotope analyses, are less susceptible to under- or overestimate different types of prey, but limited in terms of species determination. They generate information about the diet composition up to several weeks preceding the sampling event (Hobson & Clark, 1992; Phillips et al., 2014; Inger & Bearhop, 2008). Serum provides information on the diet composition over the past week, whole blood samples and red blood cells provide information on the preceding 3 weeks (Barrett et al., 2007; Veen et al., 2012). To assess the diet composition of the selected bird species, blood samples were collected and the predominant foraging habitat (terrestrial vs. marine; represented by the  $\delta^{13}\text{C}$  value) and the trophic level of diet (represented by the  $\delta^{15}\text{N}$  value) were analysed (Barrett et al., 2007; Inger & Bearhop, 2008). To determine the relative contributions of potential prey species to the diet, Bayesian mixing models were conducted.

### **3 Objectives and chapter outline**

This thesis is focused on the habitat selection and diet composition of several coastal bird species in the German Wadden Sea. The state of knowledge differed for the studied species. Therefore, we generated basic information on foraging ecology by a combination of methods in multi-colony approaches. This knowledge on abiotic and biotic influences on habitat selection was then used to gain information on distribution and status of characteristic intertidal habitats.

The following questions were addressed:

- **Herring gull**
  - Which abiotic and biotic parameters influence the habitat selection of herring gulls during the breeding season?
  - Do herring gull foraging trip characteristics and geographic patterns differ between colonies?
  - What is the proportion of terrestrial, intertidal or marine prey and which are the preferred prey species?
  - Can herring gulls act as bio-indicator for detecting the position of intertidal bivalve beds?
- **Pied avocet**
  - Which habitats do breeding avocets select for foraging?
  - What are their main prey species?
  - Do results of direct and indirect diet analyses differ, and if so, why?
- **Eurasian spoonbill**
  - Which habitats do spoonbills use for foraging?
  - What is the distribution of prey size and what proportion of biomass do different prey species represent?
  - Does diet composition differ between seasons, years, or colonies?

The thesis is composed of four chapters to answer these questions. **Chapters I to III** examine the habitat selection and diet composition of the different bird species. **Chapter IV** focuses on habitat modelling, based on tracking and hydrodynamic data.

More specifically **Chapter I** analyses individual habitat and prey use by herring gulls during incubation season in a multi-colony approach. Pellets and blood samples, as well as fine-scale telemetry data provide new information about the foraging strategy.

**Chapter II** combines different methods to assess the foraging ecology of breeding avocets. Important foraging habitats are identified by using telemetry data. Diet composition is investigated by analysing droppings and blood samples.

**Chapter III** determines foraging hotspots of spoonbills, based on tracking data. The variations in diet composition are analysed on different time scales (regurgitates, blood samples).

**Chapter IV** predicts the occurrence of intertidal bivalve beds by applying a habitat model, based on the results of Chapter I. Herring gull tracking data, as well as biotic and abiotic parameters are used to detect bivalve beds in the intertidal area.





## CHAPTER I

### **Intercolony variations in movement patterns and foraging behaviours among herring gulls (*Larus argentatus*) breeding in the eastern Wadden Sea**

Enners L, Schwemmer P, Corman A-M, Voigt CC, Garthe S (2018) Intercolony variations in movement patterns and foraging behaviours among herring gulls (*Larus argentatus*) breeding in the eastern Wadden Sea. *Ecology and Evolution* 8(15):7529–7542.





**CHAPTER I: INTERCOLONY VARIATIONS IN MOVEMENT PATTERNS AND FORAGING BEHAVIOURS AMONG HERRING GULLS (*LARUS ARGENTATUS*) BREEDING IN THE EASTERN WADDEN SEA**

Leonie Enners, Philipp Schwemmer, Anna-Marie Corman, Christian C. Voigt, Stefan Garthe

**Abstract**

Herring gulls (*Larus argentatus*) are opportunistic predators that prefer to forage in the intertidal zone, but an increasing degree of terrestrial foraging has recently been observed. We therefore aimed to analyse the factors influencing foraging behaviour and diet composition in the German Wadden Sea. Gulls from three breeding colonies on islands at different distances from the mainland were equipped with GPS data loggers during the incubation seasons in 2012–2015. Logger data were analysed for 37 individuals, including 1,115 foraging trips. Herring gulls breeding on the island furthest from the mainland had shorter trips (mean total distance = 12.3 km; mean maximum distance = 4.2 km) and preferred to feed on the tidal flats close to the colony, mainly feeding on common cockles (*Cerastoderma edule*) and shore crabs (*Carcinus maenas*). In contrast, herring gulls breeding close to the mainland carried out trips with a mean total distance of 26.7 km (mean maximum distance = 9.2 km). These gulls fed on the neobiotic razor clams (*Ensis leei*) in the intertidal zone, and a larger proportion of time was spent in distant terrestrial habitats on the mainland, feeding on earthworms.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were higher at the colony furthest from the mainland and confirmed a geographical gradient in foraging strategy. Analyses of logger data, pellets, and stable isotopes revealed that herring gulls preferred to forage in intertidal habitats close to the breeding colony, but shifted to terrestrial habitats on the mainland as the tide rose and during the daytime. Reduced prey availability in the vicinity of the breeding colony might force herring gulls to switch to feed on razor clams in the intertidal zone or to use distant terrestrial habitats. Herring gulls may thus act as an indicator for the state of the intertidal system close their breeding colony.

**Keywords:** foraging strategy, GPS tracking, *Larus argentatus*, pellet, stable isotope analysis

## 1 Introduction

Spatial movements and the foraging ecology of seabirds provide important information on food availability and potential habitat changes. Herring gulls (*Larus argentatus*), Pontoppidan 1763, are flexible and opportunistic top predators (Figure 1). In the Wadden Sea World Heritage Site, they mainly forage on intertidal flats, feeding on bivalves and crustaceans (Dernedde, 1993; Kubetzki and Garthe, 2003; Camphuysen and Gronert, 2012; Camphuysen, 2013). Breeding herring gulls at the coast thus showed tide-dependent foraging patterns (Sibly and McCleery, 1983; Mendel, 2008).

Individuals from some colonies also spend a large amount of time foraging in terrestrial habitats on earthworms or anthropogenic refuse (Sibly and McCleery, 1983; Kim and Monaghan, 2006; van Donk et al., 2017). Similar observations have been made for lesser black-backed gulls (*Larus fuscus*), previously known as a predominantly marine species, but which is increasingly adopting a dual foraging strategy utilising both marine and terrestrial habitats (Isaksson et al., 2016), possibly as a result of food depletion at sea (Votier et al., 2004; Garthe et al., 2016). Furthermore, a multi-colony study of lesser black-backed gulls based on individual movement patterns revealed that foraging behaviours also differed between neighbouring colonies (Corman et al., 2016).

Former studies of foraging behaviour and food composition in herring gulls were mainly based on visual observations and pellet analysis (e.g., Pierotti and Annett, 1991; Kubetzki and Garthe, 2003; Kim and Monaghan, 2006; Steenweg et al., 2011), but GPS data loggers and stable isotope analysis now allow the collection of information on individual movement patterns and foraging behaviours (e.g., Wilson et al., 2002; Votier et al., 2010; Shamoun-Baranes et al., 2011). Within-colony variation in individual movement patterns was recently demonstrated for roof-nesting herring gulls, based on GPS data (Rock et al., 2016). A multi-colony approach, based on pellets and stable isotope data of chicks, showed that the breeding success of herring gulls in Scotland depended on the foraging habitat. A higher proportion of intertidal prey sources led to a higher breeding success (O’Hanlon et al., 2017).

Herring gulls are central-place foragers (Steenweg et al., 2011; Isaksson et al., 2016) that depend on profitable foraging habitats near their breeding grounds. Prey depletion may imply long flight distances with higher trip costs and an increased risk of nest predation (Morris and Black, 1980; Pierotti and Annett, 1991). Prey availability in the vicinity of the breeding place is thus a “key” factor determining foraging success (Rogers et al., 2006; Boersma and Rebstock, 2009; Isaksson et al., 2016). Tidal flats are visited by herring gulls, as well as by other gull species and a variety of waders, but are only temporarily available for foraging because of tidal water coverage, and previous studies demonstrated both inter- and intraspecific competition on tidal flats (Tiedemann and Nehls, 1997).

The German Wadden Sea is characterised by a fine spatial mosaic of different intertidal habitats (e.g., mud flats, sand flats, tidal creeks), with resulting changes in benthos composition and sediment

characteristics within small distances. We carried out a multi-colony approach to compare individual movement patterns and foraging behaviours of herring gulls from neighbouring breeding colonies within this highly dynamic system.

The aim of this study was to determine the relationships among individual habitat and prey use by herring gulls and the colony's distance from the mainland, tidal stage, time of day, and sex. We combined data of the diet of gulls at the colony level (stable isotope and pellet analyses) with information on the individual level (GPS loggers) to provide a comprehensive assessment of inter-colony differences in individual foraging behaviours during incubation.



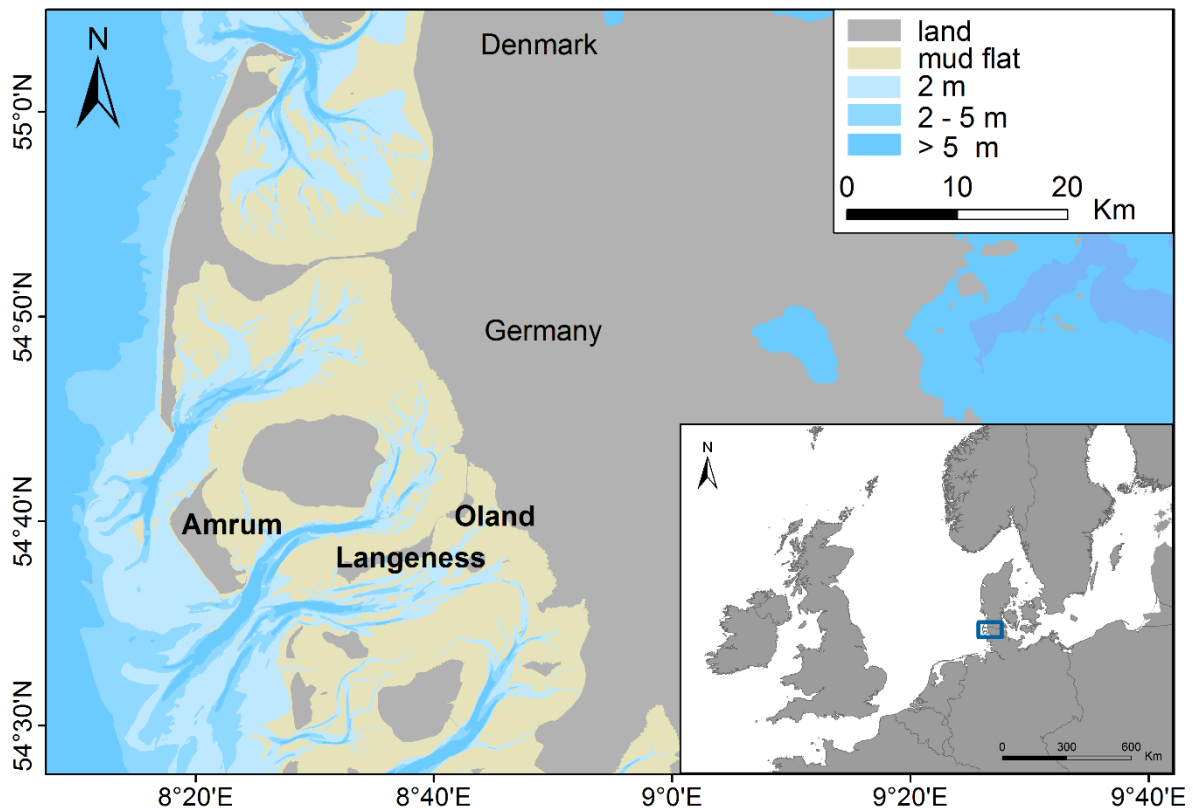
**Figure 1:** Adult herring gull with prey. Photograph credit: Sven Sturm

## 2 Materials and methods

### 2.1 Study area

The study was conducted on the islands of Oland (54°40'39"N, 8°42'14"E; 2 km<sup>2</sup> total area), Langeness (54°38'26"N, 8°37'2"O; 11.5 km<sup>2</sup>), and Amrum (54°39'6"N, 8°20'11"E; 20.5 km<sup>2</sup>) in the German North Sea, from 2012 to 2015 (Figure 2). All these islands are located in the Wadden Sea World Heritage Site and are surrounded by tidal flats. The islands host breeding colonies of herring gulls (breeding pairs: Oland, n = 300; Langeness, n = 640; Amrum, n = 700) and represent a geographic gradient from close to the mainland to the outermost intertidal flats adjacent to the open sea. Oland is located closest to

the mainland (2.5 km), followed by Langeness (9 km) and Amrum (23 km) (Figure 2). Oland and Langeness are connected to the mainland by an artificial dam.



**Figure 2:** Study area—Oland, Langeness, Amrum. Inserted map: location of the study area within northern Europe.

## 2.2 Experimental setup

Sixty-three herring gulls were caught on their nests during incubation using walk-in traps (Oland,  $n = 27$ ; Langeness,  $n = 9$ ; Amrum,  $n = 27$ ). Each bird was ringed, weighed, and equipped with a GPS data logger. Two different types of devices were used. (a) The CatLog-S (Catnip Technologies, Hong Kong SAR, China;  $n = 47$ ) was attached to the bases of the four innermost tail feathers using textile adhesive TESA tape (Wilson et al., 1997), and birds equipped with these devices were recaptured at the end of the incubation period to remove the devices and download the data. The loggers recorded the date, time, geographical position, and velocity every 2 min. (b) E-obs Bird Solar 28 g loggers (e-obs GmbH, München, Germany;  $n = 16$ ) were solar powered and were attached to the back of the gulls using a body harness. Two straps were passed in front of and behind the wings and connected in the middle of the sternum, similar to Thaxter et al. (2014). The data could be downloaded via an ultra-high frequency connection, and the birds therefore did not need to be recaptured. Date, time, geographical position, velocity, and accelerometer data were recorded at different intervals, depending on the battery status; the devices recorded data every 2–3 min when optimally charged, and at a maximum

of every 30 min at lower battery levels. The total masses of the CatLog-S and e-obs devices, including the tape or harness, were 28.1 and 39.8 g, respectively, accounting for 3.0 % and 3.9 %, respectively, of the average body mass of all equipped herring gulls (mean body mass  $\pm$  standard deviation [SD], CatLog-S: 941 g [ $\pm$  135 g]; e-obs: 1,017 g [ $\pm$  105 g]), which was within the commonly tolerable limits of 3 %–5 % of additional body mass (Kenward, 2001; Barron et al., 2010) that can be attached to birds. Possible device effects were assessed by monitoring the behaviour of the tagged gulls throughout the study period using telescopes.

Blood samples (maximum 0.3 ml) from the ulnar vein were taken from 22 individuals during recapture of the equipped birds and from an additional 20 herring gulls for stable isotope analysis. Furthermore, pellets were collected in the studied colonies.

To analyse the prey availability benthos and sediment samples were taken at foraging hotspots identified from the logger data and at control areas (hotspots:  $n = 322$  replicates; control:  $n = 297$  replicates).

### 2.3 Dietary analysis

Prey composition was compared among the three colonies by analysing the collected pellets and blood stable isotope levels. The predominant foraging habitat used by the gulls ( $\delta^{13}\text{C}$ , marine vs. terrestrial) and the trophic level of the prey ( $\delta^{15}\text{N}$ ) were determined by analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in the blood (Hobson and Clark, 1993; Barrett et al., 2007; Inger and Bearhop, 2008). The blood samples were centrifuged to separate serum and red blood cells, and the diet during the active logger period was determined based on red blood cell isotope levels. The samples were freeze-dried, and 0.3–0.5 mg of each sample was burned under chemically pure helium gas in an elemental analyser (FlashEA, ThermoFisher Scientific Bremen, Germany). The resulting gases were then routed via a ConFlo III (ThermoFisher Scientific, Bremen, Germany) to a stable isotope ratio mass spectrometer (Delta V Advantage mass spectrometer; ThermoFisher Scientific) to measure the ratios of light to heavy stable nitrogen and carbon isotopes. Stable isotope values were expressed in delta ( $\delta$ ) notation as the deviation from international standards in ‰ (air nitrogen for N and V-PDB for carbon), according to the following equation:  $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$ ; where X is  $^{13}\text{C}$  or  $^{15}\text{N}$  and R is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . The analytical precision was  $> 0.3$  ‰ (1 SD) for stable carbon and 0.2 ‰ for nitrogen isotopes. Stable isotope analysis of blood samples was conducted at the Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany.

A total of 461 fresh pellets were collected during the incubation periods, and prey items were identified visually to the lowest possible taxon following the method described by Duffy and Jackson (1986). The pellets represented the diet over the preceding 2–3 days. Pellet analysis is known to be biased due to

the different digestibilities of different prey items (González-Solís et al., 1997; Kubetzki and Garthe, 2003; Barrett et al., 2007). We therefore also examined the pellets for shell fragments, earthworm and polychaete bristles, polychaete jaws, fish otoliths and vertebrae, and mammal bones and jaws. To avoid a bias by comparing presence and absence of prey items only, the frequencies of each dietary component were analysed semi-quantitatively, as described in Garthe and Scherp (2003) and Schwemmer et al. (2013). Based on a value of 1 for each pellet, we estimated the main prey items for each pellet considering their digestibility, energy content, and biomass (data on energy content were used from literature, e.g., Cummins and Wuycheck, 1971; own unpublished data). Furthermore, prey items were also classified into three categories: sea, mud flat, and land, according to their origin.

We took benthos and sediment core samples at foraging hotspots identified from the logger data and at control areas, for subsequent habitat analysis. Important foraging sites were selected according to the frequency of visits and duration of time (> 30 min) spent within the site. Control areas were sampled randomly at a distance of 300–500 m from the identified hotspots. A total of 200 stations with usually three replicates each (hotspots:  $n = 322$  replicates; control:  $n = 297$  replicates) were sampled using a corer (diameter: 11.7 cm; depth: 20 cm), and the samples were washed through a 2-mm mesh sieve in the field. Bivalves were stored frozen in plastic bags and polychaetes were preserved in 70 % ethanol until laboratory analysis. All organisms were identified, counted, measured (bivalves: length, height, width; polychaetes: length) and the ash-free dry weight was determined as a measure of biomass (Beukema, 1974; Choi et al., 2017).

Sediments were sampled once at each station and the grain-size fractions were analysed.

Benthos and sediment data were used to interpret foraging patterns, but were not used for a detailed habitat modelling approach. For clarity, only the most abundant bivalves (length  $\geq 20$  mm) of foraging hotspots of herring gulls were shown.

## **2.4 Statistical analysis**

All statistical analyses were performed using the open-source software R 3.4.2 (R Development Core Team, 2017).

#### **2.4.1 Habitat choice based on GPS data**

In this study, we only analysed foraging-trip data, that is all breeding positions on the nest and all trips targeting roosts were excluded from the analysis. The GPS fixes were classified as flying, roosting, breeding, or feeding behaviour based on an analysis of the frequency distribution of the movement speeds of the birds (Shamoun-Baranes et al., 2011; Yoda et al., 2012), as well as the geographical position (Schwemmer et al., 2016). All fixes with a speed > 7 km/hr were defined as flying behaviour. The start of a foraging trip was identified by an increase in speed and a subsequent change in geographical position. The first and last positions of each trip were either at the colony or at a resting site.

Trips with large gaps ( $\geq 30$  min;  $n = 3$ ) between consecutive positions were excluded from the analysis. Small gaps (< 30 min) were interpolated linearly (R package `data.table` 1.10.4) to an interval of 2 min to allow comparisons of data collected using different logger types. Maximum trip distance (direct maximum distance), total trip distance (total distance flown per trip), and trip duration of foraging flights were calculated.

In addition to the trip characteristics, we also analysed the foraging patterns in detail. To achieve this, GPS positions during flight were excluded from the dataset and the remaining GPS fixes were classified as land, mud flat, or sea, according to their geographical position. Visualisation was performed using ArcGIS 10.1 (ESRI, 2011). Herring gulls from all three colonies foraged mainly on mud flats or on land, and only a few trips targeted the sea. Shamoun-Baranes et al. (2011) demonstrated that birds could rest at sea for several hours, passively drifting with the tide. However, it is difficult to differentiate between resting and foraging at sea in the absence of accelerometer data, and because only a few positions targeted the sea, we excluded these positions and tested the differences in utilisation of the two main habitats among the colonies.

Trip characteristics were analysed using linear mixed-effect models (LMM, R package `lme4` 1.1-12) based on the restricted maximum likelihood estimation (Korner-Nievergelt, 2015). To assess the effect of the geographical gradient on the foraging behaviour of the herring gulls, we used each of the three trip parameters (total distance, maximum distance, and trip duration log-transformed to achieve a normal distribution of the residuals) as dependent variables in separate LMMs, with colony as the only predictor. Bird ID was treated as a random factor in all LMMs, to account for pseudoreplication. For each model, we performed an analogue model including only the random factor and tested for differences between both models using a likelihood ratio test (ANOVA; Faraway, 2006).

The influences of different predictors (colony location, water level, time of day, sex) on habitat choice (terrestrial vs. mud flat) were tested using binomial generalised linear mixed models with appropriate autoregression structures, using all available raw data.

Water level was measured every minute at stationary positions and obtained by Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein. Every GPS logger fix was assigned to the water level of the next measurement station (“Hilligenley”: 54°37’6.6’’N, 8°32’50.424’’E; “Langeness Kirchwarf”: 54°38’25.2096’’N, 8°36’49.8528’’E; “Pellworm Hafen”: 54°31’15.6144’’N, 8°41’6.468’’E; “Schluett”: 54°39’8.9748’’N, 8°42’49.3272’’E; “Wyk”: 54°41’36.4488’’N, 8°34’34.5468’’E <http://www.umweltdaten.landsh.de/atlas/script/>).

According to the averaged sunrise and sunset times of the study days and region, hours from 22:00 to 04:49 Central European Summer Time (CEST) were classified as “night”, and hours from 05:00 to 21:59 CEST as “day”. To differentiate between the sexes, a breast feather was taken of the equipped birds for DNA analysis (females,  $n = 16$ ; males,  $n = 17$ ; unknown,  $n = 4$ ). Laboratory work was conducted by Tauros Diagnostik GbR, Bielefeld, Germany.

The GPS-tracking data were nested (especially trips within individuals) and highly temporally autocorrelated. To handle this extreme temporal autocorrelation, the raw data were thinned out using only every  $N$ -th entry, starting at entry number  $M$  for every trip ID. Testing different values for  $N$  revealed that  $N = 15$  led to an autoregression-order of approximately 2. However, the choice of  $M$  slightly influenced the final results due to stochasticity, and only part of the raw data were used for analysis. To address these problems, we fitted the final regression model separately to 14 different datasets ( $M = 1, \dots, 14$ ) and calculated the average values for the resulting regression coefficients, standard errors, degrees of freedom ( $df$ ), and  $t$ -values. The final  $p$  values were calculated based on these averages. To obtain and validate the optimal model, predictor selection was performed using the best-subset method and based on the Akaike information criterion (AIC) value. A reasonable definition of the AIC based on mixed models is problematic (Zuur et al., 2009; Korner-Nievergelt, 2015), and we therefore neglected the random effects solely for this predictor selection process, thus reducing the models to fixed effects. Model selection revealed that all the proposed predictors should be used as predictors within the final regression model. The final mixed-effect model is thus given by the following equation:

$$\begin{aligned} \text{logit}(y_{ijk}) = & \beta_0 + u_i + v_j + (\text{colony})_k \\ & + (\text{water\_level})_k + (\text{day\_night})_k \\ & + (\text{sex})_k + \epsilon_{ijk}, \end{aligned} \quad (1)$$

with  $\epsilon_{ijk} \sim N(0, \sigma^2)$ ,  $u_i \sim N(0, \sigma_u^2)$  and  $v_j \sim N(0, \sigma_v^2)$ . Here,  $y_{ijk}$  is the binary outcome,  $i$  and  $j$  refer to trip and bird ID, respectively,  $k$  refers to the observation number, and  $u$  and  $v$  represent the random intercepts related to trip and bird ID, respectively. Furthermore,  $N(x,y)$  indicates a normal distribution



with mean  $x$  and variance  $y$ . Finally, model validation was performed by graphical analysis via various residual plots (Zuur et al., 2010; Zuur, 2012; Field et al., 2012).

Odds ratios are given by the exponential of regression coefficients and indicate the change in odds of the binomial outcome variable resulting from a unit change in the predictor (Field et al., 2012). If the predictor is categorical, the corresponding odds ratio represents the change in odds of the considered factor level compared to the baseline level.

### **2.4.2 Dietary analysis**

Ratios of carbon and nitrogen isotopes were compared among colonies using a linear model. We applied Tukey's post hoc test to detect significant differences in stable isotope ratios among all colonies (Faraway, 2006; Korner-Nievergelt, 2015).

## **3 Results**

### **3.1 Potential device effects and datasets**

Thirty-seven datasets from the 63 deployed loggers were available for analysis during incubation (Oland,  $n = 15$ ; Langeness,  $n = 3$ ; Amrum,  $n = 19$ , Table 1).

Most of the datasets covered  $> 20$  days, but three only covered 3–5 days because of battery problems. Data from 26 deployed loggers were not available for analysis: Five tagged individuals could not be recaptured, one had lost its device, five devices did not record any data, ten nests were predated by foxes, and five nests were destroyed by grazing cows, making it impossible to retrap the equipped birds. The predations by foxes and trampling of nests by cows led to a low breeding success of the whole colony, which included the tagged birds. This high rate of clutch loss meant that only three datasets were recorded for Langeness, demonstrating high individual variability in foraging patterns, and indicating that the results for this colony should be interpreted with caution.

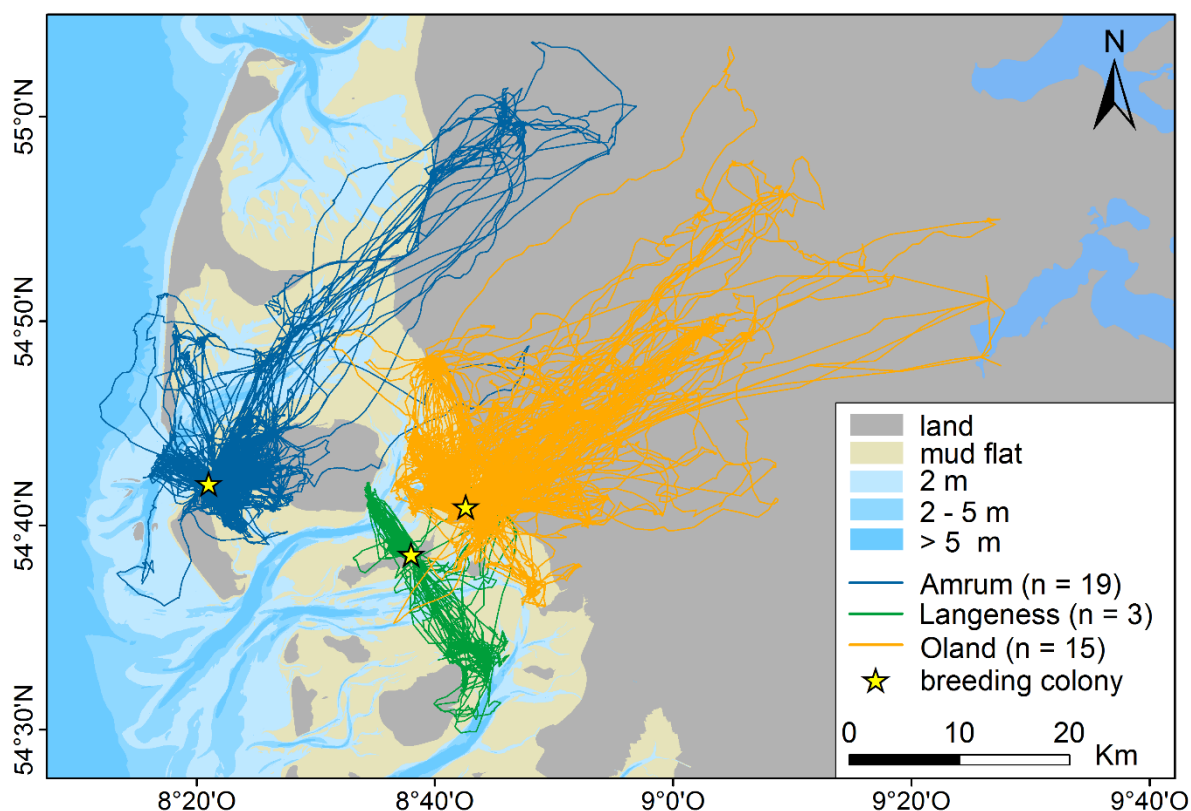
Herring gulls equipped with CatLog-S loggers had to be recaptured, and comparisons of the body mass at capture (mean  $\pm$  *SD*:  $982 \pm 114$ ) and recapture (mean  $\pm$  *SD*:  $987 \pm 94$ ) indicated an increase in average body mass. This indicated that the gulls were behaving and feeding normally. Individuals tagged with e-obs loggers did not have to be recaptured. However, we observed five of these tagged birds and found no differences in behaviours (e.g., increasing preening activity or aggression against the attachments) compared with four control (untagged) birds (Schäfer-Nolte, 2014).

**Table 1:** Study location, study periods, logger type, and sample size of tagged herring gulls.

Colony	Study period	No. of birds (available datasets)	No. of loggers from type “CatLog-S”	No. of loggers from type “E-obs”
<b>Oland</b>	07-25 May 2012	8	8	0
	07-20 May 2013	2	2	0
	14 May-01 June 2015	5	0	5
<b>Langeness</b>	11-28 May 2014	3	2	1
<b>Amrum</b>	14 May-04 June 2013	8	8	0
	07 May-01 June 2014	8	4	4
	16 May-03 June 2015	3	0	3

### 3.2 Trip characteristics

Foraging trips ( $n = 1,115$ ) differed substantially among the colonies (Oland:  $n = 407$ ; Langeness:  $n = 80$ ; Amrum:  $n = 628$ ; Figure 3). Herring gulls from Amrum preferred to forage on tidal flats near the breeding colony, while relatively fewer trips were directed to the mainland or to terrestrial areas on the adjacent island of Föhr (67.5 % exclusively targeted the tidal flats, 3.7 % solely to terrestrial habitats, 28.8 % mixed). Gulls from Langeness showed high individual variability and utilised both mud flats and terrestrial habitats on different Wadden Sea islands. For herring gulls breeding on Oland (the colony closest to the mainland), 37.1 % of the foraging trips targeted the tidal flats, 20.6 % targeted solely terrestrial habitats, and 42.3 % were mixed. Foraging trips often extended far inland (maximum distance from the nest = 54.6 km; Table 2) and also reached the coast of the Baltic Sea. The total and maximum distances of the foraging trips reflected the geographic gradient and differed significantly among the colonies (Table 2). Trips by Amrum individuals were shorter (mean = 12.3 km  $\pm$  8.4 km) compared with trips from Oland (mean = 26.7 km  $\pm$  26.1 km). The maximum distance travelled was higher for birds breeding at Oland than at Amrum, but the trip duration did not differ significantly among birds from the three colonies (Table 2). There were no sex differences in flight patterns.



**Figure 3:** Foraging trips of tracked *Larus argentatus* ( $n=37$ ) breeding at three different colonies in the German North Sea (2012-2015).

**Table 2:** Total distance, maximum distance, and trip duration for herring gulls from different breeding colonies. Influence of colony on trip parameters was tested using likelihood ratio tests.

	Total distance (km)	Maximum distance (km)	Trip duration (h)
<b>Oland</b>	Mean = 26.7 $SD \pm 26.1$ Min = 0.3 Max = 148.8	Mean = 9.2 $SD \pm 9.4$ Min = 0.1 Max = 54.6	Mean = 5.22 $SD \pm 5.26$ Min = 0.21 Max = 37.30
<b>Langeness</b>	Mean = 21.6 $SD \pm 18.2$ Min = 1.9 Max = 83.8	Mean = 6.8 $SD \pm 4.1$ Min = 1.0 Max = 16.6	Mean = 5.09 $SD \pm 3.38$ Min = 0.16 Max = 190.26
<b>Amrum</b>	Mean = 12.3 $SD \pm 18.4$ Min = 0.2 Max = 190.3	Mean = 4.2 $SD \pm 6.0$ Min = 0.1 Max = 51.6	Mean = 3.32 $SD \pm 4.17$ Min = 0.14 Max = 45.27
<b>Model</b>	$\chi^2 = 7.6$ $df = 2$ $p = 0.022$	$\chi^2 = 7.7$ $df = 2$ $p = 0.022$	$\chi^2 = 3.9$ $df = 2$ $p = 0.143$

### 3.3 Foraging patterns

The geographic position of the breeding colonies had a highly significant effect on the foraging habitat utilised; gulls breeding on the farthest offshore island, Amrum, foraged on the tidal flats five times more often than gulls breeding on Langeness (odds ratio [OR] = 0.2,  $p < 0.001$ ) and Oland (OR = 0.17,  $p < 0.001$ ), which were located closer to the mainland (Table 3).

Presence at tidal flats was highly significantly associated with the tide, and herring gulls foraged in terrestrial areas more frequently in line with increasing water levels (OR = 0.67,  $p < 0.001$ ). Herring gulls also foraged more intensively on tidal flats at night (OR = 1.8,  $p < 0.001$ ) than during the day. There was no significant difference in the use of mud flats between females and males.

**Table 3:** Averaged regression results for relative use of mud flats by herring gulls compared with Amrum, sex\_female, and daytime. Final generalised linear mixed models applied to 14 datasets with different starting values  $M = 1, \dots, 14$  for data thinning.

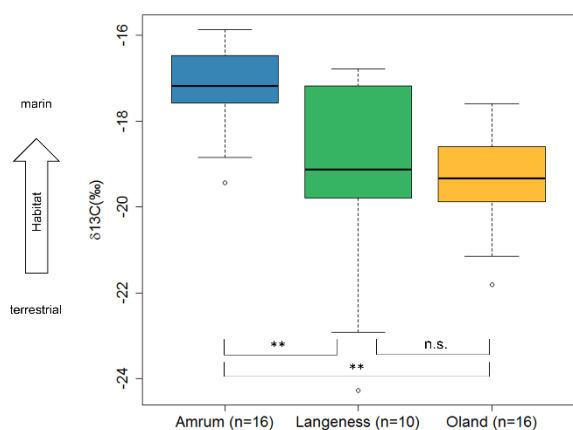
For example, herring gulls breeding on Amrum foraged on the tidal flats five times more frequently than herring gulls from Langeness (=0.2 odds ratio).

	Beta	SE	$p$	Odds ratio
Langeness	-1.61	0.28	< 0.001	0.20
Oland	-1.76	0.16	< 0.001	0.17
Water level	-0.40	0.04	< 0.001	0.67
Sex_male	-0.32	0.17	0.06	0.73
Night	0.59	0.08	< 0.001	1.80

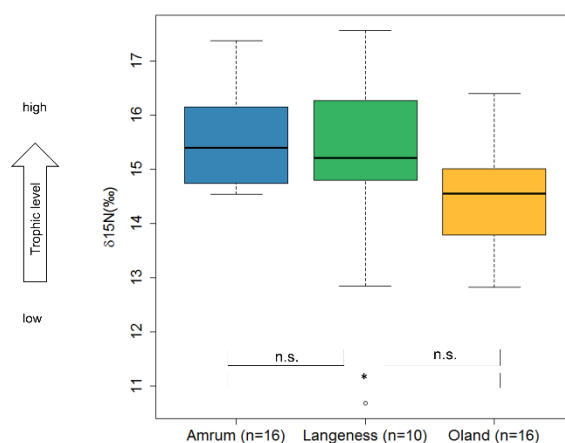
### 3.4 Dietary analysis

Stable isotope analysis of red blood cell samples showed a clear relationship between  $\delta^{13}\text{C}$  and colony ( $f = 8.72$ ,  $df = 2$ ,  $p = 0.0007$ ; Figure 4). Gulls breeding on Amrum had significantly higher  $\delta^{13}\text{C}$  values than those from Oland (Tukey's test,  $p = 0.0016$ , 95 % confidence interval [CI] = -3.4, -0.7) and Langeness (Tukey's test,  $p = 0.0058$ , 95 % CI = -3.6, -0.5). There were no differences in  $\delta^{13}\text{C}$  values between gulls from Oland and Langeness (Tukey's test,  $p > 0.95$ , 95 % CI = -1.5, -0.5; Figure 4).

$\delta^{15}\text{N}$  values also differed among all three colonies, but not significantly ( $f = 3.147$ ,  $df = 2$ ,  $p = 0.0541$ ; Figure 5). Individuals from Amrum and Oland had different  $\delta^{15}\text{N}$  values (Tukey's test,  $p = 0.04$ , 95 % CI = -2.3, -0.03), but there was no difference in  $\delta^{15}\text{N}$  values between gulls from Langeness and Amrum (Tukey's test,  $p = 0.62$ , 95 % CI = -1.8, -0.8) or between Langeness and Oland (Tukey's test,  $p = 0.42$ , 95 % CI = -1.98, -0.6; Figure 5). Compared with the other islands, birds from Langeness showed a higher variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values.



**Figure 4:** Carbon isotope ratios in red blood cells of herring gulls from breeding colonies on Amrum, Langeness, and Oland. Boxes represent 50 % of the data between the first (25 %) and the third (75 %) quartile. Upper and lower whiskers represent maximum and minimum, respectively. Horizontal line marks the median. Level of significance: \*\*\* < 0.001; \*\* < 0.01; \* < 0.05; n.s.: not significant.



**Figure 5:** Nitrogen isotope ratios in red blood cells of herring gulls from breeding colonies on Amrum, Langeness, and Oland. For explanation of box plot, see Figure 4. Level of significance: \*\*\* < 0.001; \*\* < 0.01; \* < 0.05; n.s.: not significant.

The mean numbers of food items per pellet were between one and two, and the maximum number of food items per pellet was five (Table 4). Herring gulls had a variable diet composition, ranging from earthworms and insects to bivalves, fish, and mammals. Herring gulls from Oland fed mostly terrestrially, while those from Amrum consumed prey originating from the intertidal flats (Table 4). The most important terrestrial prey items were earthworms (Table 4), while common cockles (*Cerastoderma edule*), razor clams (*Ensis leei*), and shore crabs (*Carcinus maenas*) were the most frequent prey items from mud flats, and swimming crabs (*Liocarcinus holsatus*) probably originating from the farthest offshore (habitat) zone were captured more frequently than fish. While diet composition of pellets from Amrum was similar over the years, herring gulls from Oland and Langeness showed a slightly more variable foraging behaviour. The sample sizes were small for Oland and Langeness 2014 and should be interpreted with caution. Common cockles were mostly consumed and resulted in a higher proportion of intertidal prey items in 2012 of Oland gulls. Herring gulls from Langeness fed mostly in intertidal habitats, where razor clams, common cockles and shore crabs were the most frequent prey items. In this colony, the proportion of swimming crabs was highest, and the proportion of prey items originating from the terrestrial habitat smallest in 2015 (Table 4).

**Table 4:** Semi-quantitative frequency of each dietary component in pellets from herring gulls at different colonies during incubation. Sums of all prey items deviate from 100 % due to rounding errors.

	Oland (2012)	Oland (2013)	Langeness (2014)	Langeness (2015)	Amrum (2013)	Amrum (2014)	Amrum (2015)
<b>n Pellets</b>	<b>22</b>	<b>35</b>	<b>26</b>	<b>114</b>	<b>56</b>	<b>123</b>	<b>85</b>
<b>Mean number of prey items</b>	<b>2</b>	<b>1</b>	<b>1</b>	<b>2</b>	<b>1</b>	<b>1</b>	<b>1</b>
<b>Max. number of prey items</b>	<b>5</b>	<b>5</b>	<b>3</b>	<b>5</b>	<b>4</b>	<b>5</b>	<b>4</b>
<b>Sea</b>	<b>4.5</b>	<b>12.9</b>	<b>7.7</b>	<b>17.4</b>	<b>17.5</b>	<b>11.1</b>	<b>9.6</b>
Crustaceans ( <i>Liocarcinus holsatus</i> )	0.9	11.7	6.5	12.8	15.2	10.9	8.6
Fish	3.6	1.1	1.2	4.6	2.3	0.2	1.1
<b>Mud flat</b>	<b>55.5</b>	<b>33.4</b>	<b>50.0</b>	<b>59.4</b>	<b>74.5</b>	<b>78.0</b>	<b>79.2</b>
Bivalves ( <i>Mytilus edulis</i> )	3.6	4.0	0.0	3.9	5.2	2.4	0.0
Bivalves ( <i>Ensis leei</i> )	12.3	11.4	11.5	17.5	18.2	11.8	3.9
Bivalves ( <i>Limecola balthica</i> )	0.0	2.0	0.0	3.8	0.4	1.1	0.0
Bivalves ( <i>Cerastoderma edule</i> )	22.7	0.3	22.7	12.8	19.3	32.6	47.3
Bivalves	0.0	1.4	0.0	0.3	0.4	0.0	0.0
Gastropods	0.0	0.0	0.0	1.5	0.0	0.0	0.0
Annelids ( <i>Hediste diversicolor</i> )	0.0	0.0	0.0	0.0	0.5	0.1	0.7
Crustaceans ( <i>Carcinus maenas</i> )	15.9	11.1	15.8	17.5	27.9	27.7	27.3
Crustaceans	0.9	3.1	0.0	2.0	2.7	2.3	0.0
<b>Land</b>	<b>40.0</b>	<b>53.7</b>	<b>42.3</b>	<b>23.2</b>	<b>8.0</b>	<b>10.9</b>	<b>10.0</b>
Earthworms	10.5	19.4	15.0	11.8	2.5	1.3	4.1
Insects	7.3	3.4	2.3	2.3	0.4	0.8	1.3
Birds	0.0	0.0	0.0	0.9	0.0	2.6	0.4
Eggs	4.5	14.3	15.4	2.6	0.0	0.8	2.4
Mammals	0.0	0.0	9.6	2.5	1.8	1.8	0.0
Plant material – crop/seed	17.7	16.6	0.0	2.2	3.4	2.0	1.9
Waste	0.0	0.0	0.0	0.9	0.0	1.6	0.0

### **3.5 Prey availability**

Foraging hotspots of herring gulls breeding on Amrum had very high abundances (mean = 90.08) and biomass values (mean = 9.49 g) of common cockles, both in comparison with other bivalve species investigated and when compared to the other colonies. In the vicinity of Oland, only a small number of blue mussels and common cockles were available at the targeted hotspots. There, the dominant prey species was the razor clam with a mean abundance of 4.95 and a mean biomass of 13.03 g. In relation to their abundance, razor clams showed a high biomass. (Table 5). Due to the small sample of logger data from herring gulls breeding on Langeness, only a few foraging hotspots could be identified for the tagged birds, with common cockle being the dominant bivalve species.

Overall blue mussels were rarely found at the foraging hotspots.

The mud content of Langeness (26.38 %) differed from Amrum (8.38 %) and Oland (8.95 %).

**Table 5:** Mean abundance ( $n/m^2$ ) and mean biomass (AFDW  $g/m^2$ ) of benthic prey as well as the mean mud content ( $63 \mu m$ ) of sediment at foraging sites selected by herring gulls. For clarity, only the most abundant bivalves (length  $\geq 20$  mm) are shown.

	Oland (n = 169 replicats)		Langeness (n = 9 replicats)		Amrum (n = 144 replicats)	
	$n/m^2$ (SD $\pm$ )	AFDW $g/m^2$ (SD $\pm$ )	$n/m^2$ (SD $\pm$ )	AFDW $g/m^2$ (SD $\pm$ )	$n/m^2$ (SD $\pm$ )	AFDW $g/m^2$ (SD $\pm$ )
<b>Blue mussel</b> <i>(Mytilus edulis)</i>	1.10 ( $\pm$ 0.06)	0.10 ( $\pm$ 0.01)			1.29 ( $\pm$ 0.08)	0.42 ( $\pm$ 0.03)
<b>Razor clam</b> <i>(Ensis leei)</i>	4.95 ( $\pm$ 0.12)	13.03 ( $\pm$ 0.39)			0.80 ( $\pm$ 0.07)	0.03 ( $\pm$ 0.00)
<b>Baltic tellin</b> <i>(Limecola balthica)</i>	2.20 ( $\pm$ 0.08)	0.31 ( $\pm$ 0.01)			5.32 ( $\pm$ 0.17)	0.79 ( $\pm$ 0.03)
<b>Common cockle</b> <i>(Cerastoderma edule)</i>	2.20 ( $\pm$ 0.10)	0.80 ( $\pm$ 0.04)	20.67 ( $\pm$ 4.30)	1.58 ( $\pm$ 0.34)	90.08 ( $\pm$ 1.41)	9.49 ( $\pm$ 0.15)
<b>Mud content* (%)</b>	8.95 ( $\pm$ 9.75)		26.38 ( $\pm$ 31.27)		8.38 ( $\pm$ 9.95)	

\* Sediment was sampled per station: Oland n = 50; Langeness n = 3; Amrum n = 48.



## 4 Discussion

### 4.1 General foraging strategies

Both, isotopic ratios and pellet data consistently supported the results from the loggers and indicated that herring gulls from Amrum, Oland, and Langeness had significantly different foraging patterns during incubation season.

The carbon signals in particular were significantly correlated with the distance of the breeding location from the mainland, such that gulls breeding farther offshore had a higher carbon and nitrogen signal (indicating a more intensive use of marine/intertidal prey) than birds breeding closer to the coast.

Goss-Custard (1977) and van Gils et al. (2006) showed that birds adapted their foraging strategies according to the energy-intake rate at the foraging site and the distance between the foraging and roosting areas. Gulls from Amrum, the colony farthest from the mainland, made the shortest foraging trips and spent the highest proportion of time feeding in intertidal areas, relative to gulls from the other colonies. Observations and benthos sampling revealed that the birds from Amrum visited a large cockle bed close to the breeding colony as a feeding habitat. This area was exposed for a long time during low tide and had a high biomass of potential prey. Pellets from herring gulls from Amrum included the highest proportion of intertidal prey, relative to gulls from other colonies. Similar to the 1990s (Garthe et al., 1999a; Kubetzki and Garthe, 2003), common cockles and shore crabs were the dominant prey items, although razor clams were more frequent in 2013–2015. Terrestrial prey items were the least common in the pellets.

The location of Amrum close to the open sea suggested that herring gulls might follow fishing vessels to obtain easily accessible prey, but data from loggers and pellets did not support this idea, given that only a few trips targeted the sea.

Pelagic prey is energetically rich but unpredictable, due to its patchy distribution (Garthe and Hüppop, 1994; Weimerskirch, 2007; van Donk et al., 2017), while terrestrial and intertidal habitats are characterised by more stable feeding conditions (reliability, low handling and flight costs). The logger data implied that predictable and productive intertidal habitats, such as the cockle bed, were well known to the breeding herring gulls and were thus used intensively for foraging.

In contrast, herring gulls breeding on Oland, closest to the mainland, carried out the longest foraging trips and spent more time in terrestrial habitats compared with birds from the other colonies. Only a few trips targeted defined intertidal areas near the breeding colony.

Previous studies demonstrated that flights over land consumed less energy than expected, and flight costs were reduced by using fine-scale structures (e.g., dykes) to increase orographic lift (Shepard et

al., 2016; Shamoun-Baranes et al., 2016). Furthermore, birds prefer foraging habitats with predictable prey distributions during the breeding season (Weimerskirch, 2007; Camphuysen, 2013), as expected in terrestrial habitats (Sibly and McCleery, 1983; Gorke and Brandl, 1986; Palm et al., 2013). The energetic contents of terrestrial and intertidal prey items have been shown to be comparable (Cummins and Wuycheck, 1971), which suggest that terrestrial foraging should be as beneficial as marine foraging, particularly for gulls breeding in a colony close to the mainland. However, herring gulls foraging at higher trophic levels have demonstrated better body conditions and a higher breeding success (O'Hanlon et al., 2017), as well as a higher lifetime reproductive success (van Donk et al., 2017). Although no breeding success data were measured in our own study, the results of these previous studies suggest that terrestrial food resources may not be particularly disadvantageous as often assumed. However, this depends much on the type of terrestrial food and apparently intertidal habitats remain more important for foraging and reproductive success.

#### **4.2 Influence of tide, time of day and density dependence**

Intertidal systems are characterised by their elevation and their inundation time (Evans, 1976), which influence the biomass and species richness of suitable prey (Beukema, 1976; Yates et al., 1993; Waser et al., 2016). Prey depletion close to the breeding colony may be counteracted by a habitat switch (Schwemmer and Garthe, 2008) or a change in the diet (O'Connor and Brown, 1977; Zwarts and Wanink, 1993; Goss-Custard et al., 2006). A previous study on the food choice of oystercatchers noted a shortage of suitable prey in the vicinity of Oland (Schwemmer et al. 2016). In our study, benthos samples at foraging hotspots confirmed this shortage, especially of common cockles. Herring gulls may thus have switched their foraging strategy to a mainly terrestrial one, in addition to learning to utilise newly introduced species in the intertidal zone as a novel prey resource. Inspection of important spots used by the tagged birds revealed that herring gulls from Oland visited razor clam beds in the intertidal zone, although these were only available to herring gulls for a short time during low tide. Razor clams were accidentally introduced to the Wadden Sea with ballast water in 1978 (von Cosel et al., 1982; Freudendahl et al., 2010; Dannheim and Rumohr, 2012), and the species has since extended its range substantially over the last three decades (Dekker and Beukema, 2012). Common eiders, common scoters, and various shorebird and gull species regularly use this new source of food (Swennen et al., 1985; Tulp et al., 2010). Compared with other bivalve species, razor clams represent an energy-rich prey organism with a good shell–flesh-ratio (own unpublished data).

We regularly recorded herring gulls feeding at razor clam beds, with some individuals transporting razor clams to their breeding colony, but most birds opening the shells and only consuming the flesh, suggesting that razor clams are likely to be underrepresented in pellets.

However, razor clams and other bivalve beds are only available for foraging for a short time during the lowest part of the tide, and herring gulls were forced to use the mainland as a feeding habitat at other times. Logger data for herring gulls breeding on, for example, Oland showed a high proportion of mixed foraging trips, suggesting that individuals from this colony might be forced to forage on the mainland after the razor clam beds become inundated by the tide. Herring gulls are flexible and opportunistic predators that can adapt their diet to the habitat (Sibly and McCleery, 1983; Pierotti and Annett, 1991; Schwemmer and Garthe, 2008) and might act as an indicator for changes in prey availability (Courten et al., 2017) close to their breeding colony during incubation.

In addition to the tidal cycle, the foraging strategy is also strongly influenced by the time of day. The relative use of mud flats highly significantly increased at night compared to the daylight period. Herring gulls are both visual and tactile foragers, and they may optimize their food intake (Yoda et al., 2012) by avoiding terrestrial habitats at night to minimize the risk of predation by foxes and other mammalian predators, while it might be equally feasible to search for food in the dark on mud flats as compared to daylight.

#### **4.3 Competition and influence of sex**

Pellet analysis revealed a wide spectrum of prey items. Although the logger data showed that different habitat types were often visited in the same foraging trip, the prey diversity within a single pellet was relatively small. Overall, the dietary niche of herring gulls overlaps with that of other gull species, such as common and black-headed gulls, both of which are also concentrated in coastal areas and forage in intertidal and terrestrial habitats (Kubetzki and Garthe, 2003). Earthworms have also been shown to be an important food source for lesser black-backed gulls breeding inland and at the coast, which also forage on the mainland (Coulson and Coulson, 2008; Garthe et al., 2016).

Inter- and/or intraspecific competition (Hamilton et al., 1967; Corman et al., 2016) may thus be an important factor driving decisions on where to forage. Corman et al. (2016) demonstrated low inter- and intracolony overlaps in foraging behaviour in lesser black-backed gulls. In our study, gulls from Langeness were the most flexible in terms of habitat choice although the sample size of tagged birds from this colony was very low. Both terrestrial and intertidal areas were easily accessible to these birds because of the central location of the breeding colony. However, this colony location could also imply greater intra- and interspecific competition with other colonies. Herring gulls from Langeness might thus choose flexible foraging sites to avoid intraspecific competition from neighbouring colonies (e.g., Oland, Amrum, Föhr), as well as intraspecific competition from within the same colony. Although only three datasets were available for Langeness, 80 foraging trips from these three individuals were included in the analysis. Nevertheless, the high individuality of herring gulls breeding on Langeness

might lead to different results with a higher sample size. Although the logger dataset for Langeness was small, stable isotope and pellet analyses supported a flexible foraging strategy for birds from this colony. The same could be supposed for herring gulls breeding closer to the coast. Foraging trips heading to the west might not be an option for gulls from Oland, because of intraspecific competition from neighbouring colonies (Corman et al., 2016).

We found no sex-related differences in foraging-trip characteristics during incubation. However, lesser black-backed gulls have demonstrated sexual segregation in foraging patterns throughout incubation and chick rearing (Camphuysen et al., 2015), with males travelling longer distances from the colony and feeding mostly on fisheries discards. Camphuysen et al. (2015) suspected that the marginally larger males foraged more successfully behind fishing vessels compared with the smaller females. In contrast, herring gulls in the current study predominantly targeted the vast intertidal and terrestrial habitats for foraging, where sexual dimorphism is less likely to confer any advantage because prey is usually distributed much more evenly over a wide area.

## **5 Conclusions**

Herring gulls in our study showed a wide range of foraging behaviours, from intertidal to combined intertidal–terrestrial strategies. This switch was driven by the distance between the colony and the mainland, the level of the tide, the time of day, and the food availability near the breeding colony.

Logger data, as well as stable isotope and pellet analyses, confirmed a geographical gradient in terms of foraging behaviours during incubation; gulls breeding close to the mainland mainly used terrestrial habitats as foraging grounds, while gulls breeding farther offshore preferred intertidal areas close to the breeding colony. Behavioural observations, and analyses of pellet and logger data demonstrated that herring gulls utilised the non-indigenous species *Ensis leei* as new prey source. The logger data also implied that predictable and productive intertidal habitats, such as cockle beds and razor clam fields, were well known to the breeding herring gulls and were utilised for foraging, although the birds were forced to feed in terrestrial areas at high tide. Furthermore, herring gulls preferred to forage on mud flats at night and in terrestrial habitats during the day (and interestingly very similar to lesser black-backed gulls which also use terrestrial habitats during the daylight but often switch to pelagic habitats at night (Garthe et al. 2016)). Prey depletion during incubation near the breeding colony might have increased the degree of foraging in terrestrial habitats. Given that herring gulls prefer to forage on bivalve beds, these gulls can be used to assess the status of the intertidal system close to their breeding colonies and may thus act as indicators of changes in the food web during incubation.

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**Data Accessibility**

Tracking data are archived at Movebank (<https://www.movebank.org>). Bird-ringing data are archived at the Beringungszentrale Vogelwarte Helgoland (Institute for Avian Research, Wilhelmshaven).





## CHAPTER II

### **Foraging patterns and diet composition of breeding Pied avocets (*Recurvirostra avosetta*) in the German Wadden Sea**

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**CHAPTER II: FORAGING PATTERNS AND DIET COMPOSITION OF BREEDING PIED AVOCETS (*RECURVIROSTRA AVOSETTA*) IN THE GERMAN WADDEN SEA**

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**Abstract**

Pied avocets (*Recurvirostra avosetta*) breeding in the Wadden Sea typically forage in shallow water, using their characteristic upward-curved bill to feed on macrozooplankton in the water column and prey items in the uppermost centimetre of the sediment. Former studies on prey choice based on droppings and visual observations of feeding behaviour suggested that ragworms were the main prey items of avocets. The present study combined different methods to assess the foraging ecology of breeding avocets in the eastern Wadden Sea. Important foraging grounds were identified using GPS telemetry. Diet was analysed from droppings and stable isotope signatures of whole blood samples from breeding avocets at two different colonies in April–June 2014 and 2015. Analysis of droppings confirmed the former results, but stable isotope analysis suggested that marine fish comprised the highest proportion of the avocet diet by mass. Telemetry data indicated that intertidal channels close to the breeding areas were used as the main foraging grounds. Avocets performed short foraging trips (maximum distance: 0.3–5.9 km) mainly during the daytime. Logger data and diet analysis thus implied the existence of high fish densities in intertidal channels, underlining the importance of this salt marsh habitat as foraging areas for breeding avocets.

**Keywords:** GPS tracking, foraging strategy, stable isotope analysis, droppings, shorebird

## 1 Introduction

Coastal regions are important and productive transition zones between terrestrial and marine habitats (Reise et al., 2010). A variety of shorebirds use intertidal flats and creeks as well as marshes as breeding grounds or as resting and foraging areas along their annual cycle (Sonntag et al., 2009; Reise et al., 2010). Many of these show significant decreasing population trends and low breeding success (e.g., Trilateral Monitoring and Assessment Program, TMAP; Koffijberg et al., 2015; Thorup and Koffijberg, 2016). For conservation, knowledge about important foraging areas is essential, but the detection of these areas is difficult. Foraging ecology of shorebirds is mainly investigated by visual observations (Nehls and Tiedemann, 1993; Hötker, 1999) or diet analyses (Veen et al., 2012; Scheiffarth, 2001), but there is still a lack of information on individual habitat choice and foraging strategies.

The Wadden Sea is one of the largest intertidal wetlands stretching along the North Sea coast, shared by the Netherlands, Germany, and Denmark (Reise et al., 2010; van Roomen et al., 2012; Blew et al., 2016). Together with Spain it hosts the largest numbers of Pied avocets (*Recurvirostra avosetta*) in western Europe, with the Wadden Sea containing almost 60 % of the flyway population during summer and autumn (Kleefstra et al., 2019). The overall avocet population across the Wadden Sea has been in decline since 1999. The regional breeding population of avocets in the federal state of Schleswig-Holstein (northern Germany) was stable for a long time, but started decreasing in 2008 (Hötker and West, 2005; Hötker and West 2006; Koffijberg et al., 2015; Hötker et al., 2017). This decline has been mainly attributed to low reproductive success caused by colder June temperatures, predation events, and nest losses due to flooding (Hötker and Segebade, 2010; Thorup and Koffijberg, 2016).

Low-altitude salt marshes are at increased risk of flooding, while higher-level salt marshes on the mainland are mostly overgrown and vulnerable to predation by foxes and other mammalian predators (van de Pol et al., 2010; Hötker and Segebade, 2010; Thorup and Bregnballe, 2015). Avocets therefore need to balance their foraging activities during the breeding season with the risks of predation and flooding (Hötker, 1999; Thorup and Koffijberg, 2016). Foraging grounds with good prey quality and quantity in the vicinity of the breeding site are thus basic factors determining foraging success during the breeding period (Boersma and Rebstock, 2009). Shorter foraging trips imply lower trip costs and a decreased risk of nest predation (Morris and Black, 1980; Pierotti and Annett, 1991). Information on habitat selection and diet composition are therefore important for understanding the population dynamics and optimizing conservation management efforts for avocets. However, information on the foraging patterns and diet composition of avocets breeding in the Wadden Sea is currently lacking.

Avocets use their typical upward-curved bill to forage in the top 20 mm of muddy sediments, mainly using a scything action (Quammen, 1982; Moreira, 1995b). It is difficult to record avocet diet visually because prey items are ingested very quickly and the items taken up are usually very small.

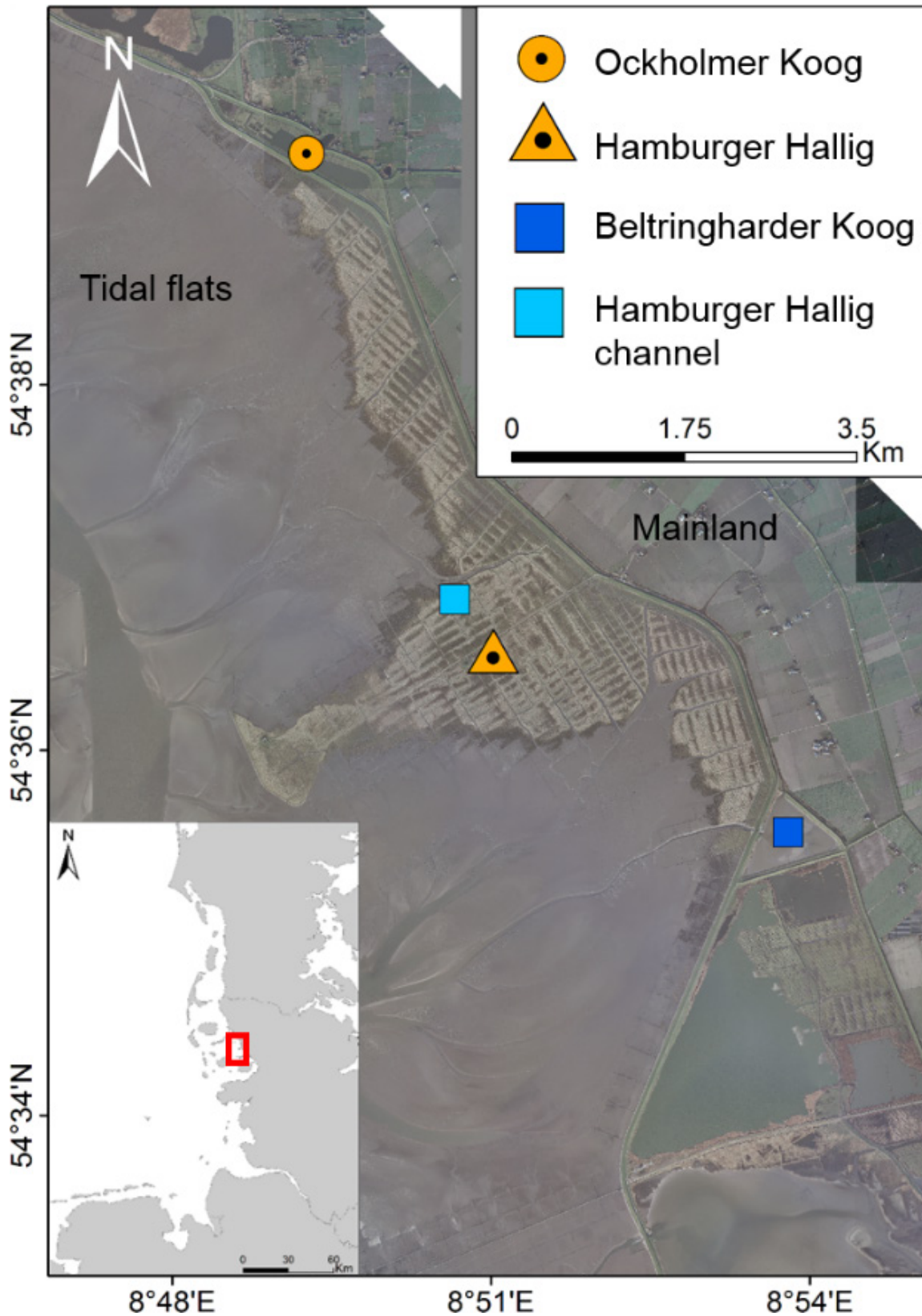
Nevertheless, previous studies on the prey choice of avocets were based on droppings and visual observations, and concluded that small crustaceans, molluscs, ragworms, insect larvae, and small fish were utilised as prey sources (Moreira, 1995b; Hötker, 1999), with ragworms being the dominant prey (Moreira, 1995b; Hötker, 1999). However, Moreira (1995b) investigated the prey choice by observations and droppings in Portugal, where avocets may use different prey species as compared to the Wadden Sea, due to the different climate and food availability.

We aimed to gather more information on the foraging ecology of breeding avocets in the German Wadden Sea by equipping adult avocets with GPS loggers to identify important foraging areas, and by studying their diet composition based on analyses of droppings and blood samples.

## **2 Materials and methods**

### **2.1 Study area**

The study was conducted at two breeding colonies in the German Wadden Sea in April–June 2014 and 2015: Hamburger Hallig (54°36'N, 8°50'E) and Ockholmer Koog (54°39'N, 8°49'E) (Figure 1). Hamburger Hallig is a holm surrounded by tidal flats and connected to the mainland. The study site is a nature reserve and an important breeding area for several coastal species. Avocets breed on small artificial islets in the salt marshes of the holm (76 breeding pairs in 2014 and 26 in 2015). Ockholmer Koog is a freshwater wetland located between two dykes with no connection to the North Sea. Avocets here breed in a small area almost completely surrounded by shallow water (26 breeding pairs in 2015).



**Figure 1:** Study area in the northern German Wadden Sea. Four sites (orange, blue) were sampled in terms of abiotic and biotic parameters. Breeding colonies are located in orange. Inserted map: location of the study area within Germany. Aerial photographs obtained by the National Park Administration of the Wadden Sea of Schleswig-Holstein.

## 2.2 Study design

Foraging patterns were analysed based on telemetry data and the diet composition by droppings and blood samples of breeding avocets (Table 1). Avocets on Hamburger Hallig were caught during incubation and equipped with GPS devices. During capture blood samples were taken and droppings collected.

At Ockholmer Koog, only blood samples and droppings were collected (Table 1). Footprints of foxes were observed during capture and therefore no birds were equipped with GPS loggers, as we feared severe clutch losses due to predation which would have prevented a recapture of equipped individuals.

A breast feather was taken from each bird for DNA analysis to differentiate between the sexes. Laboratory work was conducted by Tauros Diagnostik GbR, Bielefeld, Germany.

Based on GPS tracking (see 2.3) important sites were identified and abiotic (i.a. temperature, salinity) and biotic (macrozooplankton, macrobenthos) parameters were sampled and analysed.

**Table 1:** Number of recaptured birds equipped with GPS devices, number of droppings collected, and number of blood samples taken during the study period in the two breeding colonies.

	GPS 2014	GPS 2015	Droppings 2015	Blood 2014	Blood 2015
Hamburger Hallig	3	1	10	7	7
Ockholmer Koog	0	0	10	0	9

## 2.3 GPS tracking

Breeding avocets on Hamburger Hallig were caught on their nests during incubation using walk-in traps (2014: n = 5; 2015: n = 6). Each bird was ringed, weighed, measured (wing, tarsus), and equipped with a GPS data logger (mGPS-2, Earth & Ocean Technologies, Kiel, Germany; mass: 6 g). The device was attached to the bases of the four innermost tail feathers using textile adhesive TESA tape (Wilson et al., 1997). The total mass of the logger, including the tape, was 8.5 g, equivalent to 2.1 % (range: 1.6–2.6 %) of the average body mass of all equipped avocets (mean body mass  $\pm$  standard deviation (SD), 401  $\pm$  58 g). This ratio was within the commonly tolerable limits of 3–5 % of additional body mass (Kenward, 2001; Barron et al., 2010). Equipped birds were recaptured at the end of the incubation period to remove the devices and download the data. The loggers recorded the date, time, geographical position (< 10 m), and velocity every 10 min.

## 2.4 Environmental factors

Based on visual observations and logger data, four sites were chosen to analyse environmental parameters in June 2015 (Figure 1). The analysed abiotic and biotic characteristics indicate the state of the habitat and display present species communities (Reise et al., 2010).

Salinity and temperature were measured using a sensor (Cond 3210, WTW GmbH, Weilheim, Germany) attached to a portable conductivity meter (TetraCon 325, WTW GmbH). Water samples were collected from each site (replicates:  $n = 3$ ) using a sample bottle attached to a sampling rod, filtered with a syringe filter (0.22  $\mu\text{m}$ , Rotilab, Carl Roth GmbH, Karlsruhe, Germany), and frozen for laboratory analysis. Nitrite, nitrate, ammonia, silicate, and phosphate were analysed according to Grasshoff et al. (1999).

A total of five replicate sediment samples were collected from each site using a corer (diameter: 11.7 cm, depth: 10 cm) and the grain-size fractions were determined (Störtenbecker, 1997).

We designed a sampling device to analyse prey availability, comprising a net (300  $\mu\text{m}$  mesh size) attached to a metal frame opening (length: 25 cm, height: 21 cm). The net was placed on the bottom of the foraging habitat and then dragged using a rope (length: 200 cm) connected to the opening of the device. This method allowed sampling of macrozooplankton from the water column and prey items from the uppermost centimetre of the substrate. The samples were fixed in ethanol (70 %) until further analysis.

A total of ten subsamples (1  $\mu\text{l}$  each) were taken using a pipette and placed in quad petri dishes. Prey items were counted and identified visually under a stereomicroscope to the lowest possible taxon, according to Hayward and Ryland (1990-1994) and Hartmann-Schröder (1996).

## **2.5 Dietary analysis**

Droppings and blood samples were used to compare the diet composition between the two breeding colonies. Droppings reflect the short-term diet over the preceding 2–3 days before collection and enable the identification of prey items up to species level. However, dropping analysis is known to be biased due to the different digestibility of different prey species (González-Solís et al., 1997; Barrett et al., 2007). In contrast to analysis of droppings, stable isotope analysis of blood samples provides information about the diet composition up to 3 weeks prior to sampling (Phillips et al., 2014), and is less susceptible to under- or overestimate different types of prey. But this method is limited in terms of determining single prey species (Barrett et al., 2007; Inger and Bearhop, 2008; Phillips et al., 2014).

### **2.5.1 Dietary analysis – droppings**

A total of 10 droppings were collected from each breeding colony in 2015. Only complete and fresh droppings were sampled around avocet nests to avoid confusion with other species. Droppings were kept frozen at  $-20^{\circ}\text{C}$  until laboratory work. For analyses, samples were dissolved in ethanol (70 %) and ten subsamples (1  $\mu\text{l}$ ) were taken from each sample using a pipette. The prey remains were identified

for each dropping separately under a stereomicroscope to the highest possible taxonomic resolution and the presence or absence of each prey item was determined.

### **2.5.2 Dietary analysis – stable isotope analysis**

We analysed  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in whole blood samples to investigate the predominant foraging habitats used by the avocets ( $\delta^{13}\text{C}$ , marine vs. terrestrial) and the trophic level of the prey ( $\delta^{15}\text{N}$ ) (Hobson and Clark, 1993; Barrett et al., 2007; Inger and Bearhop, 2008). Blood samples (max. 0.2 ml) were taken from the ulnar vein from 14 birds from Hamburger Hallig (2014:  $n = 7$ ; 2015:  $n = 7$ ) and from an additional 9 avocets from Ockholmer Koog in 2015 for stable isotope analysis (Table 1).

Whole blood samples were dried and prepared as described by Ismar et al. (2017), and 30–50  $\mu\text{g}$  of each sample was placed into a tin cup, and analysed in triplicate. Stable isotope analysis was conducted at the Geomar Helmholtz Centre for Ocean Research Kiel, Germany.

After identification, the sampled prey items (macrozooplankton, macrobenthos) from each site were dried for 24 h ( $\sim 60^\circ\text{C}$ ) and weighed to calculate the biomass. The samples were then ground using a pestle and mortar. Up to five replicates of each prey item were used for subsequent analysis, according to Mittermayr et al. (2014).

$\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopes in the samples were analysed using an NA 110, Thermo elemental analyser connected to a mass spectrometer (Delta<sup>plus</sup> Advantage, Thermo Fisher Scientific, Bremen, Germany).  $\text{CO}_2$  and  $\text{N}_2$  gases were used as working standards, as described by Hansen et al. (2009), and calibrated against solid standards (IAEA-N1, -N2, -N3, USGS24, NBS22). Caffeine and acetanilide were used for internal calibration on every sixth run. The stable isotope values were calculated as follows:  $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ ; where X is  $^{13}\text{C}$  or  $^{15}\text{N}$  and  $R$  is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ .

## **2.6 Statistical analysis**

All statistical analyses were performed using the open-source software R 3.4.2, assuming significance thresholds of  $\alpha = 0.05$  (R Development Core Team, 2017).

### **2.6.1 Telemetry data**

Four GPS datasets (2014:  $n = 3$ ; 2015:  $n = 1$ ) were available for analysis from avocets breeding on Hamburger Hallig, including 39 foraging trips. The remaining loggers did not record data or the nests were predated by common gulls (*Larus canus*). One logger only recorded data for 1 day (2015 dataset) before it stopped recording (Table 2). Equipped avocets were observed after catching and showed no

differences in behaviours compared to unequipped birds. No nest desertions following the catching were observed.

Important foraging hotspots were identified from GPS logger data and visual observations (Figure 1). The GPS fixes were classified as flying, roosting, breeding, or feeding behaviour, based on the velocity and geographical position, according to Enners et al. (2018). We defined foraging trips from the GPS data: each trip started with the last GPS position at the nest and ended with the first GPS position at the breeding colony after the return of the bird. Maximum trip distance (linear maximum distance from the nest), total trip distance (total distance flown per trip), and trip duration of foraging flights were calculated. The proportions of foraging fixes during the day and at night were also analysed. According to the average sunrise and sunset times for the study days and region, the hours from 22:00 to 04:59 Central European Summer Time (CEST) were classified as “night”, and the hours from 05:00 to 21:59 CEST as “day”. Visualisation was performed using ArcGIS 10.1 (ESRI, 2011).



**Table 2:** GPS logger data for equipped breeding avocets.

Bird ID	Study period	Trip (n)	Total distance (km)	Maximum distance (km)	Trip duration (h)	Time of day (number of foraging fixes)	Sex
SSHH1_2014	06/05/2014-10/05/2014	18	mean = 3.4 SD ± 3.5 min = 0.6 max = 13.6	mean = 1.5 SD ± 1.4 min = 0.3 max = 5.5	mean = 1.6 SD ± 1.1 min = 0.5 max = 4.6	day = 89 night = 23	male
SSHH2_2014	06/05/2014-10/05/2014	16	mean = 2.8 SD ± 2.8 min = 0.9 max = 9.1	mean = 1.3 SD ± 1.2 min = 0.5 max = 3.9	mean = 1.0 SD ± 0.5 min = 0.5 max = 2.1	day = 60 night = 0	male
SSHH3_2014	23/05/2014-27/05/2014	4	mean = 9.8 SD ± 1.6 min = 8.7 max = 12.6	mean = 4.7 SD ± 0.7 min = 3.9 max = 5.9	mean = 1.7 SD ± 0.7 min = 0.7 max = 2.5	day = 23 night = 0	male
SSHH1_2015	01/05/2015	1	mean = 11.1	mean = 4.4	mean = 2.4	day = 6 night = 0	female

### 2.6.2 Hotspot sites

Several indicators were analysed to specify the differences between the foraging areas: biomass and abundance of prey items as well as prey richness, which is giving information on the number of different species. In addition, we analysed diversity and evenness, which both take abundance for each different species into account. Measuring the evenness allows for drawing conclusions on the similarity of frequencies of prey items in the different samples. Richness and diversity were calculated at higher taxonomic levels (order and subclass) because not all prey items could be identified to species level.

Differences in biomass and abundance were analysed with a Kruskal-Wallis-Test. Diversity was compared between the sites using the Shannon index, calculated as follows:  $H' = -\sum_{i=1}^S p_i \ln p_i$ , where  $p_i$  is the proportion of biomass of a particular group, divided by the overall biomass and  $S$  is the number of groups found at the site. Pielou's evenness index was calculated as followed:  $J' = \frac{H'}{\ln(S)}$ , where  $H'$  is the Shannon index value, and  $S$  is the number of groups found at the specific site.

### 2.6.3 Isotopic signatures

There was no significant correlation between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for prey items (Pearson's test,  $t_{(170)} = 0.09$ ,  $p > 0.05$ ,  $R^2 = 0.01$ ) or blood samples from breeding avocets ( $t_{(22)} = -1.47$ ,  $p > 0.05$ ,  $R^2 = 0.09$ ). Carbon and nitrogen isotopes were therefore subsequently analysed separately using univariate analysis.

The assumption of normality was checked by Shapiro's test, and differences in isotopic signatures between the two breeding colonies, two breeding years, and between sexes were analysed using Mann-Whitney-Wilcoxon tests.

The relative contributions of several potential prey species to the avocet diet were determined using a Bayesian mixing model (R package *simmr*, Parnell et al., 2013; Parnell, 2016). The package *simmr* represents an upgrade to the SIAR package and contains similar features (Parnell, 2016). Given the generalist feeding behaviour of the species, this model allows the incorporation of any number of prey items and allows accounting for uncertainty from different sources (Parnell et al., 2010; Phillips, 2012).

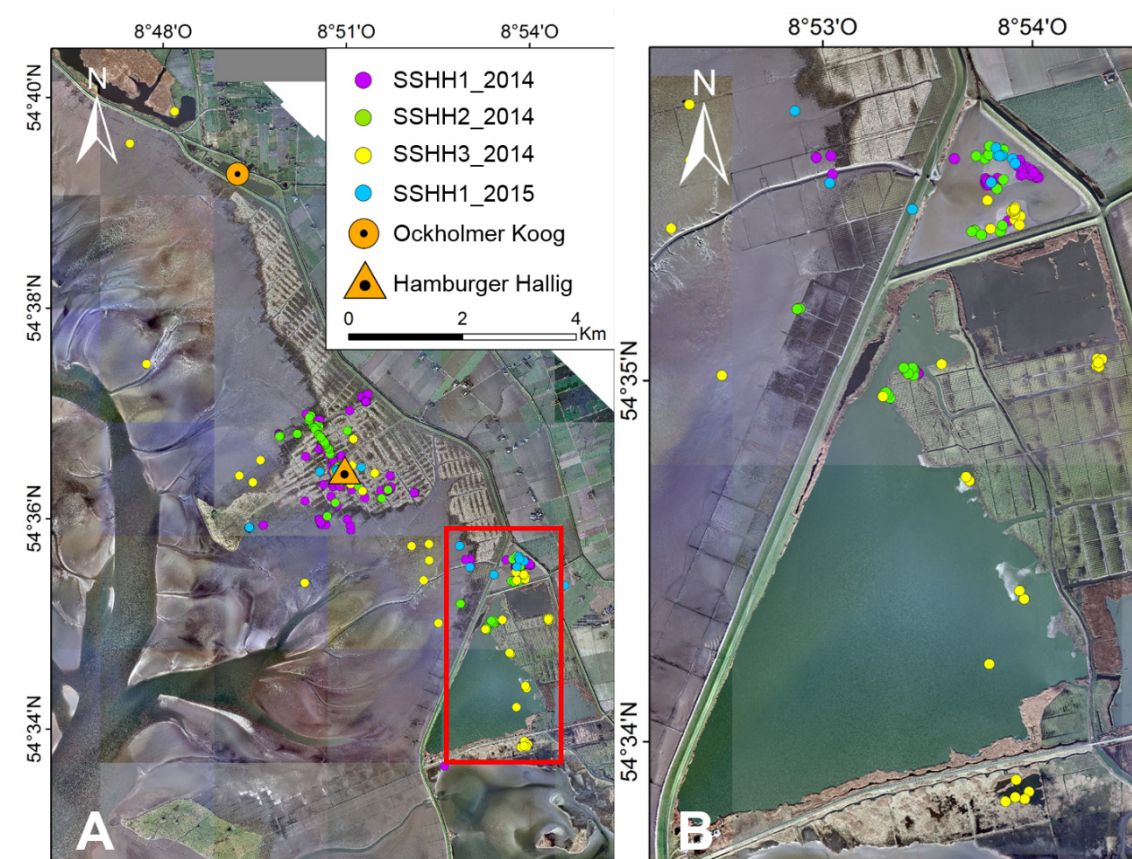
We included three data sets (consumer data, trophic enrichment data, sources data) to the mixing model. Consumer data (biotracer data:  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) were based on the mean values of

three replicates obtained from stable isotope analysis of the blood samples. No trophic enrichment data were available for avocets, and we therefore used trophic enrichment factors for dunlins (*Calidris alpina*; i.e. 1.3 ‰ for  $^{13}\text{C}$  and 2.9 ‰ for  $^{15}\text{N}$ ; Ogden et al., 2004). These factors were required to account for the trophic enrichment between prey and bird blood (Phillips et al., 2014). Sources were included in three models to accommodate the large set of prey items. The first model only used prey components found in droppings. The second model included potential prey sources grouped into three categories according to the different foraging habitats: brackish, marine, and terrestrial. The third model analysed the diet composition based on the prey species that occurred in the most important habitat.

### **3 Results**

#### **3.1 Foraging patterns**

Foraging trips were mainly directed to an intertidal channel in the lower salt marsh at Hamburger Hallig or to a brackish lagoon on the mainland (Figure 2). The foraging ranges of the breeding avocets were within a few kilometres of the respective breeding sites (maximum distance of foraging trips: 0.3–5.9 km, Table 2), but the total distances travelled were higher and differed between individuals in 2014 (total distance: 0.6–13.6 km). Avocets foraged mainly during the daytime. The mean trip duration was 1.4 h (Table 2).



**Figure 2:** All GPS fixes of tracked avocets ( $n = 4$ ) breeding at Hamburger Hallig in 2014 and 2015. B: GPS fixes at Beltringharder Koog lagoon. Aerial photographs obtained by the National Park Administration of the Wadden Sea of Schleswig-Holstein.

### 3.2 Quality of hotspot sites

Visual observations in the two breeding areas assumed intensive feeding in the direct vicinity of the breeding areas. Two additional sites were identified as important foraging grounds based on telemetry data. The characteristics of the four identified areas are described in more detail below.

According to tracking data, avocets frequently foraged in a channel close to the breeding islets on Hamburger Hallig. The channel had a direct connection to the Wadden Sea (mean salinity: 26.8‰, Table 3) and was influenced by the tide. The concentrations of the measured parameters, except phosphate, were higher at low tide than at high tide. This site showed the highest species richness among the feeding sites ( $n = 15$ , Table 4) and a high biomass ( $0.74 \text{ g/m}^2$ , Appendix 1), largely due to the high biomass and abundance of gastropods. This was the only one of the four sites where marine fish were detected.

According to the tracking data, avocets also regularly used a shallow, brackish lagoon at Beltringharder Koog on the mainland (salinity: 4.44 ‰, Table 3). This area was subject to local coastal protection and the inflow of seawater was controlled. Crustaceans were the dominant group by both biomass (0.267 g/m<sup>2</sup>, Appendix 1) and numbers (2921.6 individuals/m<sup>2</sup>, Appendix 1). Among crustaceans, ostracods and mysids were the main available groups.

The breeding area on Hamburger Hallig was surrounded by shallow seawater (mean salinity: 26.9 ‰) with soft muddy ground (Table 3). The highest Shannon–Wiener index ( $n = 1.41$ ) and Pielou’s index ( $n = 0.61$ ) were found at this site (Table 4). Crustaceans and molluscs were the main available prey items. However, this breeding area contained the lowest biomass (Appendix 1). Copepods were very abundant but contributed the smallest proportion of biomass.

The second breeding colony of avocets in Ockholmer Koog was surrounded by shallow, brackish water (salinity: 1 ‰) with the highest variability of sediment types, ranging from completely sandy to very muddy. This site also had the highest silicate and phosphate levels (Table 3), and the lowest Pielou’s evenness value ( $n = 0.18$ , Table 4).

Overall, there was no significant difference in available prey biomass among the foraging areas (Kruskal–Wallis test ( $\chi^2_3 = 7.64$ ,  $p > 0.05$ )).

**Table 3:** Environmental factors in sampled areas (mean ( $\pm$ SD)).

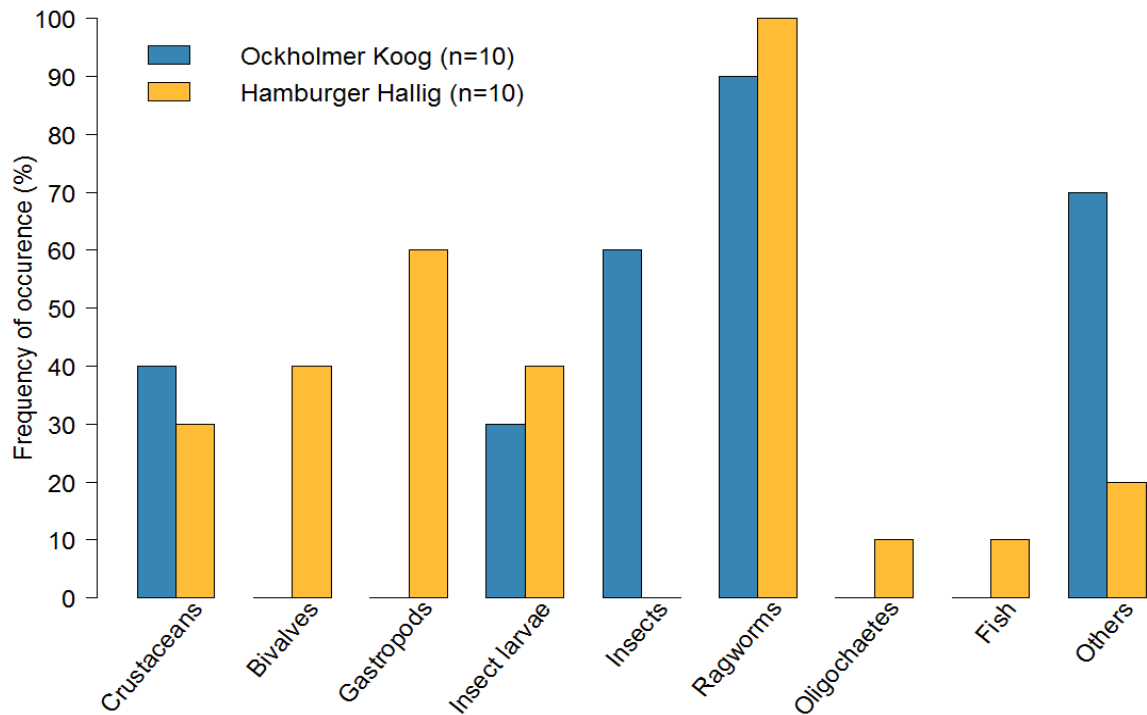
Site	Mud content ( $< 63 \mu\text{m}$ in %)	Temperature ( $^{\circ}\text{C}$ )	Salinity (‰)	Water depth (cm)	Nitrate ( $\mu\text{mol/l}$ )	Nitrite ( $\mu\text{mol/l}$ )	Silicate ( $\mu\text{mol/l}$ )	Phosphate ( $\mu\text{mol/l}$ )	Ammonia ( $\mu\text{mol/l}$ )
Hamburger Hallig	87.7 ( $\pm 4.3$ )	13.00 (0.0)	26.90 ( $\pm 0.35$ )	11.20 ( $\pm 2.59$ )	0.24 ( $\pm 0.08$ )	0.12 (0.00)	56.80 ( $\pm 0.74$ )	16.87 ( $\pm 2.65$ )	0.42 ( $\pm 0.08$ )
Hamburger Hallig channel	91.1 ( $\pm 4.7$ )	15.23 ( $\pm 1.96$ )	26.80 ( $\pm 2.12$ )	28.4 ( $\pm 15.6$ )	2.02 ( $\pm 3.44$ )	0.25 ( $\pm 0.12$ )	26.44 ( $\pm 14.16$ )	1.33 ( $\pm 0.97$ )	6.72 ( $\pm 5.61$ )
Beltringharder Koog	72.0 ( $\pm 8.3$ )	13.78 ( $\pm 0.19$ )	4.44 ( $\pm 0.05$ )	14.3 ( $\pm 2.82$ )	0.00	0.07 ( $\pm 0.05$ )	0.59 ( $\pm 3.75$ )	3.79 ( $\pm 0.49$ )	2.19 ( $\pm 0.06$ )
Ockholmer Koog	31.2 ( $\pm 31.2$ )	16.43 ( $\pm 0.91$ )	1.00 (0.0)	26.0 ( $\pm 8.80$ )	0.00	0.04 (0.00)	172.07 ( $\pm 11.77$ )	24.51 ( $\pm 1.28$ )	1.19 ( $\pm 0.08$ )

**Table 4:** Richness, Shannon–Wiener index ( $H'$ ), and Pielou's evenness ( $J'$ ) for each sampled site.

Area	Richness	Shannon–Wiener index ( $H'$ )	Pielou's evenness ( $J'$ )
Hamburger Hallig	10	1.41	0.61
Hamburger Hallig channel	15	0.65	0.24
Beltringharder Koog	10	0.60	0.26
Ockholmer Koog	9	0.39	0.18

### 3.3 Diet analysis – dropping analysis

The diet composition of breeding avocets determined by dropping analysis ranged from insects and crustaceans to fish and varied slightly between the two studied breeding colonies. Ragworms were the most frequent prey items found in the droppings, appearing in all samples collected at Hamburger Hallig and 90 % of samples from Ockholmer Koog (Figure 3). However, in contrast to avocets breeding in Ockholmer Koog, droppings from Hamburger Hallig also contained bivalves, gastropods, oligochaetes, and fish.



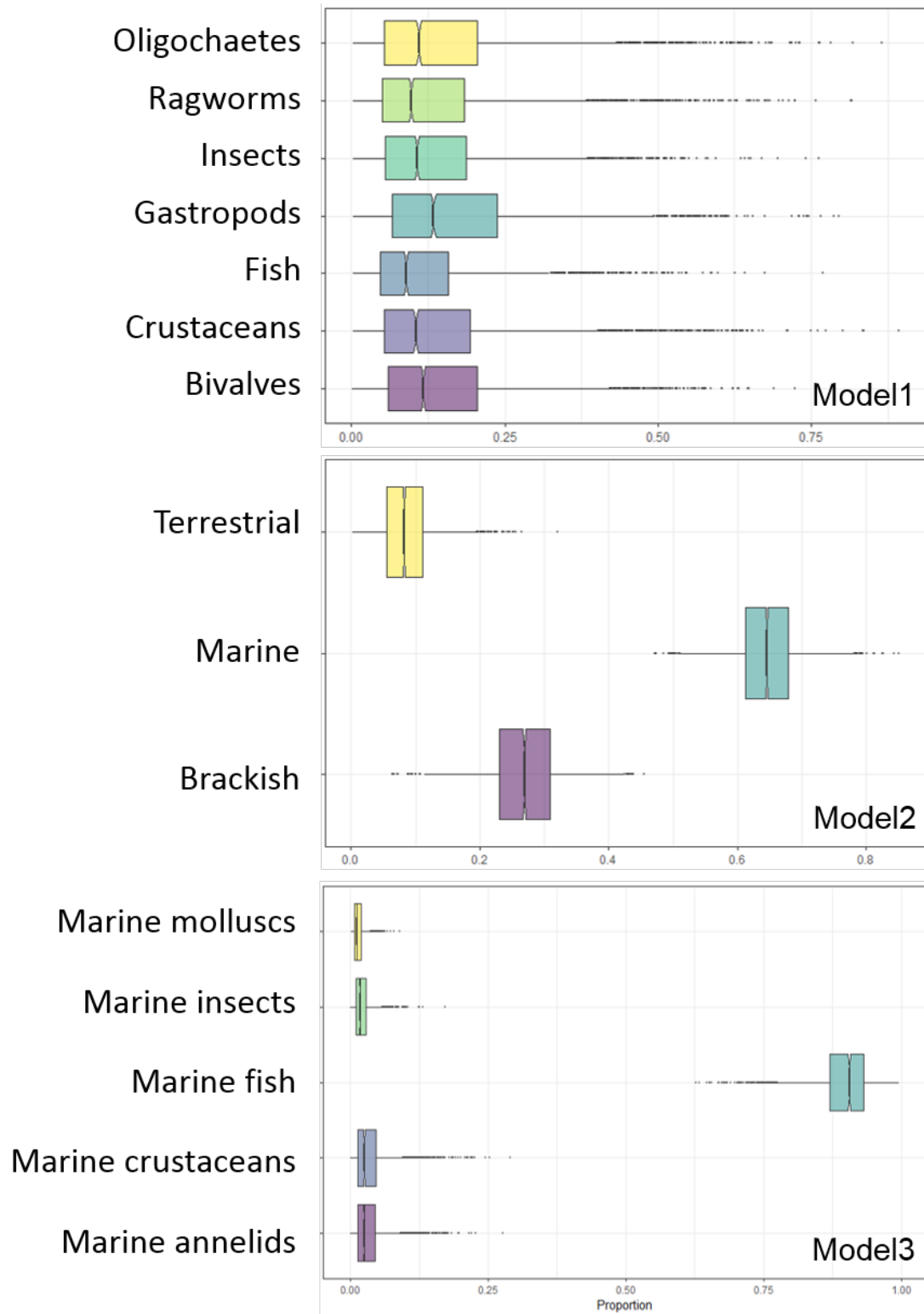
**Figure 3:** Frequency of dietary components in droppings from breeding avocets at Hamburger Hallig and Ockholmer Koog, based on presence/absence.

### 3.4 Diet analysis – stable isotope analysis

There were no differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between breeding years ( $\delta^{13}\text{C}$ :  $W = 59$ ,  $p > 0.05$ ;  $\delta^{15}\text{N}$ :  $W = 58$ ,  $p > 0.05$ ; Mann-Whitney-Wilcoxon test), between sexes ( $\delta^{13}\text{C}$ :  $W = 50.5$ ,  $p > 0.05$ ;  $\delta^{15}\text{N}$ :  $W = 78$ ,  $p > 0.05$ ; Mann-Whitney-Wilcoxon test), or between the two colonies ( $\delta^{13}\text{C}$ :  $W = 54$ ,  $p > 0.05$ ;  $\delta^{15}\text{N}$ :  $W = 95.5$ ,  $p = 0.04$ ; Mann-Whitney-Wilcoxon test). Avocets breeding on Hamburger Hallig appeared to feed at a wider range of trophic levels than those from Ockholmer Koog. Because there were no significant differences between breeding seasons, sexes, or breeding colonies, these data were pooled in the following analyses.

The first model included only prey species that were found in droppings, with no information about the habitat they originated from. All prey species showed similar contributions to the avocet diet, but with very wide confidence intervals (Model 1, Figure 4, Appendixes 2 and 3). The second model pooled different prey species according to their habitat. Marine species were the main prey items of breeding avocets in the German Wadden Sea, with an average mass contribution of 64 %, followed by brackish prey items with an average contribution of 27 % (Model 2, Figure 4, Appendixes 2 and 3). The third model, based on only marine prey sources, demonstrated that fish made the highest contribution to the avocet diet, ranging from 77 % to 97 %, with a mean contribution of 90 % (Figure 4, Appendixes 2 and 3).





**Figure 4:** Outcomes of three models showing contribution of each prey source. Model 1: prey components found in droppings; Model 2: prey species grouped according to habitat origin; Model 3: marine prey components.

#### 4 Discussion

The results of stable isotope analysis suggested that avocets breeding at the coast of Schleswig-Holstein foraged in the marine habitat and consumed marine fish as their main prey source during the incubation period.

Previous studies based on visual observations and analysis of droppings identified ragworms as the dominant prey species (Moreira, 1995b; Hötter, 1999), which was supported by the dropping analysis in the current study. However, dropping analysis is known to be biased because of the different digestibility of different prey items (González-Solís et al., 1997; Barrett et al., 2007). The incidence of ragworms in the diet of avocets may thus have been overestimated as a result of the slow digestion of the jaws. Furthermore, the remains of small fish could be missed by using a stereomicroscope. In addition, droppings represent the short-term diet and thus only provide a snapshot of the available prey.

In contrast, stable isotope analysis enabled us to identify the preferred foraging habitat and trophic level used by the birds up to 3 weeks before blood sampling (Hobson and Clark, 1993; Barrett et al., 2007; Inger and Bearhop, 2008). This method identified marine fish as the dominant prey species. Although ragworms and crustaceans were also used as prey sources, they were of minor importance and only accounted for a small proportion of the assimilated prey items. Analyses of stable isotopes are less susceptible to under- or overestimate different prey species, but limited in terms of species determination. Isotopic signatures showed no significant differences between years, sexes, and colonies; however, this should be confirmed by analysis of a larger dataset. Preconditions of the current analyses were the inclusion of all relevant prey species and of a species-specific discrimination factor (Phillips et al., 2014). Although no discrimination factor was available for avocets, the values for dunlin were expected to provide a good approach. We analysed prey species/prey groups in detail, using a large dataset originating from the same area as the blood-sampled avocets. The sampled areas were identified by telemetry data and visual observations. The use of GPS loggers identified intertidal channels as a foraging habitat, though other foraging sites may have been missed because of the small logger data set.

Nevertheless, this stable isotope analysis together with telemetry data have provided new information on the foraging ecology of avocets. Our results of stable isotopes and droppings were contradicting with respect to the relevance of fish. Droppings may underestimated the importance of marine fish in avocet diet, due the fast digestion. Similar results were shown for spoonbill diet, where results of visual examinations of digested food items and stable isotope analyses differed (Jouta et al., 2018; Enners et al., 2020). Therefore, a combination of different methods showed the diet in detail and suggested that the marine habitat in general might be more important for avocets than previously assumed. Although

the data set was small, results of telemetry data, stable isotope analyses and prey sampling supported each other.

Hötker (1999) observed no differences between activity patterns of avocets during the day and night, and assumed that the active time depended on the prey choice. Avocets feeding on fish needed to forage for a shorter time and preferred the daytime, while birds consuming chironomid larvae foraged at day and night (Hötker, 1999). Although the logger data set was small, the foraging patterns indicated that avocets foraged within 6 km of their breeding colony, and foraged mainly during the day. These patterns suggested that they were feeding on fish, which was clearly supported by the results of the stable isotope analysis.

Based on the assumption that bird densities are positively correlated with prey densities (Goss-Custard et al., 1991; Zwarts and Wanink, 1993), fish may be expected to be available in high numbers in our study area, thus helping avocets to reduce their foraging times.

It is difficult to quantify the occurrence of prey in a dynamic area, and we could not record the actual fish abundance using the current recording methods. However, we did sample the macrozooplankton and the benthos, and detected crustaceans most frequently in terms of numbers and mass. Fish were only available in the channel close to the breeding islets on Hamburger Hallig. This area showed the greatest richness and variability in terms of available prey species, indicating a patchy biomass distribution. The spatio-temporal patterns revealed by the logger data demonstrated that avocets regularly used the channel as a foraging habitat.

Habitat structure and prey density are mainly influenced by abiotic parameters including sediment, salinity, and water input (Goss-Custard et al., 1991). Breeding avocets were shown to prefer areas with finer grain sizes, which facilitate their foraging mode of scything (Quammen, 1982; Moreira, 1995b). The highest mud content in the current study area was in the channel near Hamburger Hallig, while the breeding area Ockholmer Koog consisted mainly of coarse grain sizes. In addition, the channel was connected to the sea, with fluctuating nutrient concentrations between low and high tide, indicating dilution of the nutrients by the incoming water. Although our sample size of tagged individuals was small, the data indicated the importance of tidal channels in the salt marsh as important foraging habitats for avocets. This importance was underlined by the high prey abundance and fish presence. Tidal channels act as nurseries for small fish, which become concentrated in this habitat during low water levels (Colclough et al., 2005; El-Hacen et al., 2013).

Analyses of logger data, droppings, and stable isotopes, as well as area sampling, revealed spatial segregation among avocets' activities within the areas. Some sites were used mainly for foraging (channel close to the breeding area Hamburger Hallig), while other areas were used for

resting/breeding activities. Logger data and prey availability suggested that both breeding areas were used exclusively for breeding and not for foraging by the avocets, while the brackish lagoon of Beltringharder Koog might be an important resting area. Prey depletion in the breeding habitat might have forced the avocets to select these areas for breeding because of their better protection against mammalian predators. The creation of such small islets offers the possibility of increasing the breeding success of avocets and other coastal birds (Thorup and Bregnballe, 2015). However, it would be necessary to locate such newly created breeding areas near good foraging grounds, and to manage the vegetation appropriately (grazing, mowing) (Lengyel, 2006; Thorup and Bregnballe, 2015).

Predator-free breeding sites with nearby foraging grounds with good prey quality and quantity are fundamental to counteracting the population decline of avocets. The current study demonstrated the importance of the marine habitat, particularly intertidal channels in the salt marshes, as foraging habitats for breeding avocets, because of their high fish density. Feeding on energy-rich fish thus enabled the avocets to minimize their foraging time and decrease the risk of nest predation.

Although the Wadden Sea hosts very high breeding numbers of avocets, the studied colonies represent only a small part of the western avocet population. Further studies are needed to compare the results with other coastal areas. Different climate and prey availability may affect the avocet foraging strategy. However, the combination of stable isotope analysis, common dropping analysis in combination with tracking data can be regarded as a useful methodological approach which could be extended to other study systems.

## **5 Conclusions**

Overall, the results of this study demonstrated that marine fish make up a greater proportion of the diet of breeding avocets than previously assumed. Ragworms and crustaceans were also used as prey sources, but stable isotope signatures indicated that these were of relatively minor importance. Marine fish as the main prey were caught in intertidal channels in the salt marshes, close to the breeding areas. The fact that the avocets only made short foraging trips and only during the day implied a high fish density in the intertidal channels, underlining the importance of this habitat. Furthermore, most avocets were breeding, resting, and foraging in protected areas, also demonstrating the importance of these habitats for the conservation and management of avocet populations.

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**Data Accessibility**

Tracking data are archived at Movebank (<https://www.movebank.org>). Bird-ringing data are archived at the Beringungszentrale Vogelwarte Helgoland (Institute for Avian Research, Wilhelmshaven).

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**Appendix 1:** Summary of prey items with their respective  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values (mean ( $\pm$ SD)), abundance, and biomass.

Habitat	Site	Prey item	Mean $\delta^{15}\text{N}$	Mean $\delta^{13}\text{C}$	Abundance (individuals/m <sup>2</sup> )	Biomass (g/m <sup>2</sup> )
Marine	Hamburger Hallig	<b>Crustacea</b>				
		Copepoda (Subclass)	12.59 ( $\pm$ 1.01)	-18.70 ( $\pm$ 3.03)	3356	0.069
		Decapoda (Order)				
		<i>Crangon crangon</i>	12.89 ( $\pm$ 0.34)	-16.71 ( $\pm$ 0.37)	2.8	0.004
		Mysida (Order)				
		<i>Neomysis integer</i>	13.86 (0.00)	-18.69 ( $\pm$ 0.00)	0.4	0.001
		Ostracoda (Class)	12.03 ( $\pm$ 0.37)	-13.18 ( $\pm$ 1.25)	394.4	0.035
		<b>Insecta</b>				
		Diptera (Order)				
		Chironomidae larvae	10.28 ( $\pm$ 0.27)	-15.17 ( $\pm$ 0.54)	7.2	0.002
		<b>Mollusca</b>				
		Gastropoda (Class)	-	-	6.8	0.023
		<b>Annelida</b>				
Sabellida (Order)						
<i>Manayunkia</i> sp	13.38 ( $\pm$ 0.58)	-20.10 ( $\pm$ 0.64)	18.8	0.001		
Phyllodocida (Order)						
<i>Nereis</i> sp	11.61 ( $\pm$ 0.37)	-15.26 ( $\pm$ 0.61)	10.4	0.001		
Spionidae (Order)						
<i>Streblospio benedicti</i>	12.54 ( $\pm$ 0.83)	-17.70 ( $\pm$ 0.40)	6.4	0.000		
Oligochaeta (Subclass)	12.11 ( $\pm$ 0.59)	-15.53 ( $\pm$ 0.75)	298	0.011		
Marine	Hamburger Hallig Channel	<b>Crustacea</b>				
		Amphipoda (Order)	12.27 (0.00)	-14.19 (0.00)	0.4	0.000
		Decapoda (Order)				
		<i>Carcinus</i> sp	13.34 (0.00)	-17.91 (0.00)	0.2	0.023
		<i>Crangon crangon</i>	11.66 ( $\pm$ 0.48)	-15.75 ( $\pm$ 0.48)	6.8	0.003
Copepoda (Subclass)	14.33 ( $\pm$ 0.75)	-18.28 ( $\pm$ 2.68)	5.8	0.000		

Habitat	Site	Prey item	Mean $\delta^{15}\text{N}$	Mean $\delta^{13}\text{C}$	Abundance (individuals/m <sup>2</sup> )	Biomass (g/m <sup>2</sup> )
		Mysida (Order)				
		<i>Neomysis integer</i>	15.49 ( $\pm 1.28$ )	-20.52 ( $\pm 3.70$ )	2	0.001
		<i>Praunus flexuosus</i>	15.13 ( $\pm 0.19$ )	15.02 ( $\pm 0.27$ )	3.6	0.019
		Ostracoda (Class)	15.09 ( $\pm 0.52$ )	-15.67 ( $\pm 1.69$ )	33.8	0.003
		<b>Insecta</b>				
		Diptera (Order)				
		Diptera larvae	14.42 ( $\pm 0.53$ )	-14.53 ( $\pm 0.12$ )	0.8	0.000
		Hymenoptera (Order) (terrestrial)	12.87 ( $\pm 0.56$ )	-23.71 ( $\pm 0.02$ )	0.4	0.000
		Coleoptera (Order) (terrestrial)	5.21 (0.00)	-21.30 (0.00)	0.2	0.000
		<b>Mollusca</b>				
		Bivalvia (Class)	11.35 ( $\pm 0.32$ )	11.55 ( $\pm 0.25$ )	47	0.014
		Gastropoda (Class)	9.37 ( $\pm 1.51$ )	-9.96 ( $\pm 1.43$ )	93.8	0.637
		<b>Annelida</b>				
		Phyllodocida (Order)				
		<i>Eulalia viridis</i>	14.41 (0.00)	-14.45 (0.00)	0.2	0.001
		<i>Nereis</i> sp	15.20 ( $\pm 0.79$ )	-14.58 ( $\pm 1.04$ )	156.2	0.004
		Sabellida (Order)				
		<i>Manayunkia</i> sp	13.11 ( $\pm 0.26$ )	-15.65 ( $\pm 0.60$ )	56	0.001
		Spionidae (Order)				
		<i>Streblospio benedicti</i>	12.76 ( $\pm 0.53$ )	-16.37 ( $\pm 0.29$ )	4.2	0.001
		Oligochaeta (Subclass)	14.19 ( $\pm 0.34$ )	-16.54 ( $\pm 0.27$ )	580	0.035
		<b>Fish</b>				
		Pleuronectiformes (Order)	13.74 ( $\pm 0.86$ )	-18.31 ( $\pm 1.16$ )	0.6	0.001

Habitat	Site	Prey item	Mean $\delta^{15}\text{N}$	Mean $\delta^{13}\text{C}$	Abundance (individuals/m <sup>2</sup> )	Biomass (g/m <sup>2</sup> )
Brackish	Beltring-harder Koog	<b>Crustacea</b>				
		Copepoda (Subclass)	15.96 ( $\pm 0.41$ )	-29.49 ( $\pm 1.06$ )	9.2	0.000
		Decapoda (Order)				
		<i>Crangon crangon</i>	14.78 (0.00)	-21.17 (0.00)	0.4	0.001
		Mysida (Order)				
		<i>Neomysis integer</i>	15.85 ( $\pm 0.43$ )	-23.38 ( $\pm 0.62$ )	76.2	0.013
		Ostracoda (Class)	14.38 ( $\pm 1.19$ )	-16.00 ( $\pm 2.00$ )	2835.8	0.253
		<b>Insecta</b>				
		Hymenoptera (Order) (terrestrial)	11.62 (0.00)	-25.32 (0.00)	0.2	0.000
		<b>Mollusca</b>				
		Gastropoda (Class)	13.99 ( $\pm 0.11$ )	-18.63 ( $\pm 2.99$ )	24.2	0.040
		<b>Annelida</b>				
Phyllodocida (Order)						
<i>Nereis</i> sp	17.63 ( $\pm 0.56$ )	-21.80 ( $\pm 2.73$ )	5.8	0.001		
Sabellida (Order)						
<i>Manayunkia</i> sp	16.13 ( $\pm 0.63$ )	-23.01 ( $\pm 0.55$ )	0.6	0.000		
Oligochaeta (Subclass)	15.53 (0.00)	-21.86 (0.00)	3.6	0.000		
Brackish	Ockolmer Koog	<b>Crustacea</b>				
		Amphipoda (Order)	9.90 ( $\pm 1.32$ )	-23.27 ( $\pm 0.82$ )	0.8	0.001
		Diplostraca (Order)				
		Cladocerans	8.26 ( $\pm 0.21$ )	-27.16 ( $\pm 2.81$ )	22.4	0.000
		Copepoda (Subclass)	11.74 (0.00)	-24.74 (0.00)	2	0.000
		Mysida (Order)				
		<i>Neomysis interger</i>	12.32 ( $\pm 0.65$ )	-24.66 ( $\pm 0.38$ )	760.8	0.640
Ostracoda (Class)	8.31 ( $\pm 0.60$ )	-17.43 ( $\pm 4.18$ )	3582.4	0.319		

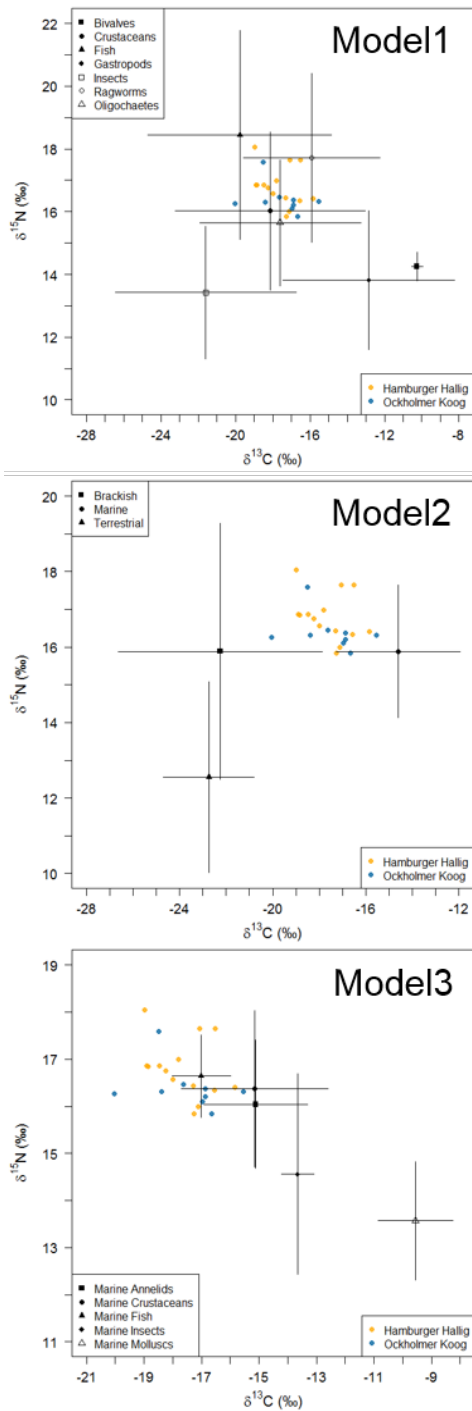


Habitat	Site	Prey item	Mean $\delta^{15}\text{N}$	Mean $\delta^{13}\text{C}$	Abundance (individuals/m <sup>2</sup> )	Biomass (g/m <sup>2</sup> )
		<b>Insecta</b>				
		Diptera (Order)	10.75 ( $\pm 0.41$ )	-26.88 ( $\pm 0.42$ )	40.4	0.009
		Chironomidae larvae	10.52 (0.00)	-28.67 (0.00)	0.8	0.001
		Diptera (terrestrial)	8.70 ( $\pm 1.24$ )	-23.53 ( $\pm 0.90$ )	4	0.011
		Hemiptera (Order) (terrestrial)				
		<b>Mollusca</b>	10.06 ( $\pm 1.88$ )	-17.95 ( $\pm 3.10$ )	7.6	0.008
		Gastropoda (Class)				
		<b>Annelida</b>	11.38 ( $\pm 2.40$ )	-24.06 ( $\pm 3.87$ )	328.8	0.006
		Oligochaeta (Subclass)				

**Appendix 2:** Summary of three mixing models used to estimate the contributions of prey items to the diet of avocets.

	Source (sample size)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Contribution (%)	95% Confidence interval
<b>Model 1</b>	Bivalves (5)	-11.55 ( $\pm 0.23$ )	11.35 ( $\pm 0.29$ )	0.15 ( $\pm 0.11$ )	0.02-0.44
	Crustaceans (74)	-19.45 ( $\pm 5.03$ )	13.12 ( $\pm 2.36$ )	0.15 ( $\pm 0.13$ )	0.01-0.50
	Fish (4)	-21.07 ( $\pm 4.85$ )	15.54 ( $\pm 3.17$ )	0.12 ( $\pm 0.10$ )	0.01-0.38
	Gastropods (8)	-14.14 ( $\pm 4.54$ )	10.92 ( $\pm 2.05$ )	0.17 ( $\pm 0.13$ )	0.02-0.51
	Insects (25)	-22.89 ( $\pm 4.79$ )	10.52 ( $\pm 1.96$ )	0.14 ( $\pm 0.11$ )	0.01-0.42
	Ragworms (15)	-17.21 ( $\pm 3.60$ )	14.81 ( $\pm 2.53$ )	0.14 ( $\pm 0.12$ )	0.01-0.48
	Oligochaetes (16)	-18.90 ( $\pm 4.25$ )	12.75 ( $\pm 1.85$ )	0.15 ( $\pm 0.13$ )	0.01-0.51
<b>Model 2</b>	Brackish (60)	-23.55 ( $\pm 4.32$ )	12.99 ( $\pm 3.23$ )	0.27 ( $\pm 0.06$ )	0.16-0.38
	Marine (101)	-15.91 ( $\pm 2.58$ )	12.99 ( $\pm 1.60$ )	0.64 ( $\pm 0.05$ )	0.55-0.74
	Terrestrial (10)	-24.04 ( $\pm 1.88$ )	9.66 ( $\pm 2.37$ )	0.09 ( $\pm 0.04$ )	0.02-0.18
<b>Model 3</b>	Marine annelids (41)	-16.42 ( $\pm 1.73$ )	13.14 ( $\pm 1.20$ )	0.03 ( $\pm 0.03$ )	0.00-0.11
	Marine crustaceans (42)	-16.45 ( $\pm 2.48$ )	13.47 ( $\pm 1.50$ )	0.04 ( $\pm 0.03$ )	0.00-0.13
	Marine fish (3)	-18.31 ( $\pm 0.95$ )	13.74 ( $\pm 0.71$ )	0.90 ( $\pm 0.05$ )	0.77-0.97
	Marine insects (6)	-14.96 ( $\pm 0.49$ )	11.66 ( $\pm 1.97$ )	0.02 ( $\pm 0.02$ )	0.00-0.07
	Marine molluscs (9)	-10.86 ( $\pm 1.24$ )	10.67 ( $\pm 1.09$ )	0.01 ( $\pm 0.01$ )	0.00-0.04

**Appendix 3:** Biplot of models (mean and SD) of carbon and nitrogen isotopes. Model 1: prey components found in droppings; Model 2: prey species grouped according to habitat origin; Model 3: marine prey components.







## CHAPTER III

### Foraging ecology and diet of Eurasian spoonbills (*Platalea leucorodia*) in the German Wadden Sea

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## CHAPTER III: FORAGING ECOLOGY AND DIET OF EURASIAN SPOONBILLS (*PLATALEA LEUCORODIA*) IN THE GERMAN WADDEN SEA

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### Abstract

Eurasian spoonbills (*Platalea leucorodia*) were first recorded breeding in the German Wadden Sea in 1995. Since then, the breeding numbers have been increasing. However, the foraging habitats and diet of spoonbills in this area remain largely unknown. We therefore analysed the foraging ecology of spoonbills from three colonies in this area using GPS telemetry and examined their diet based on regurgitates and stable isotope analysis. GPS logger data (2014–2016) implied that tidal creeks near the mainland coast are used as the main foraging hotspots in the breeding season. Regurgitates (n = 77) and blood samples (n = 78) collected from spoonbill chicks in 2014 and 2016 showed slight variations in diet compositions between years and among colonies. Regurgitates (reflecting the diet during the day prior to sampling) included prey items ranging from ragworms and shrimps to fish, indicating an opportunistic foraging strategy. Smelts (31.9 %) (*Osmerus eperlanus*), sticklebacks (22.6 %) (*Gasterosteus aculeatus*), and gobies (13.3 %) (*Pomatoschistus minutus*) were the dominant prey organisms by mass. Analyses of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in blood serum of spoonbill chicks (reflecting the diet 1 week before sampling) showed a diverse diet composition, with flatfish, smelts, gobies, and sticklebacks as the main prey species at the end of May. In contrast, values in red blood cells (reflecting the diet up to 3 weeks prior to sampling) demonstrated that sticklebacks and flatfish were the main dietary components of spoonbills in the German Wadden Sea in early May. The combination of different diet analyses determined the diet choice of spoonbills in the German Wadden Sea on different time scales. Telemetry data enabled the study of fine-scale habitat use.

**Keywords:** *Platalea leucorodia*, regurgitates, stable isotope analyses, diet, GPS-telemetry

## 1 Introduction

The Eurasian spoonbill (*Platalea leucorodia*) was first recorded breeding in the German Wadden Sea in 1995. Breeding populations in Lower Saxony and later in Schleswig-Holstein have since increased continuously (Krüger et al., 2010), with a total of 261 breeding pairs in the four colonies of Schleswig-Holstein, at the islands of Oland, Trischen, Föhr, and Südfall, in 2016 (Günther, K.; pers. comm.).

Predation events and food availability during the breeding season are known to have an important influence on population trends and breeding success (Oudman et al., 2017; Jouta et al., 2018). Eurasian spoonbills feed mainly on fish and crustaceans, which they catch by wading through shallow water whilst making sideways movements with their bill (van Wetten and Wintermans, 1986; Veen et al., 2012). Previous studies of foraging behaviour and diet composition were mainly conducted in the Netherlands (van Wetten and Wintermans, 1986; El-Hacen et al., 2014; Jouta et al., 2018), in Mauritania (Veen et al., 2012; El-Hacen et al., 2013) and Spain (Aguilera et al., 1996) where both freshwater and the intertidal zone were shown to be used as foraging habitats. Jouta et al. (2018) identified small flatfish and gobies as the dominant prey species for spoonbills in the Dutch Wadden Sea, and stable isotope analyses of feathers of chicks in this area demonstrated a shift in diet from freshwater to more marine prey during the breeding season (El-Hacen et al., 2014). A study of the African subspecies *Platalea leucorodia balsaci* suggested that the diets of chicks and adults appeared to be similar and may reflect the general foraging behaviour (Veen et al., 2012). However, there is currently no information on the utilisation of foraging and resting areas and the diet composition of spoonbills along the northern rim of their distribution in the newly colonized German Wadden Sea.

We investigated the foraging ecology of spoonbills in the German Wadden Sea by equipping birds with GPS data loggers and collecting regurgitates and blood samples from spoonbill chicks from three breeding colonies from 2014 to 2016. Fresh regurgitates reflect the short-term diet, while stable isotope analysis reflects the longer-term diet up to several weeks preceding the sampling event (Hobson and Clark, 1993; Phillips et al., 2014).

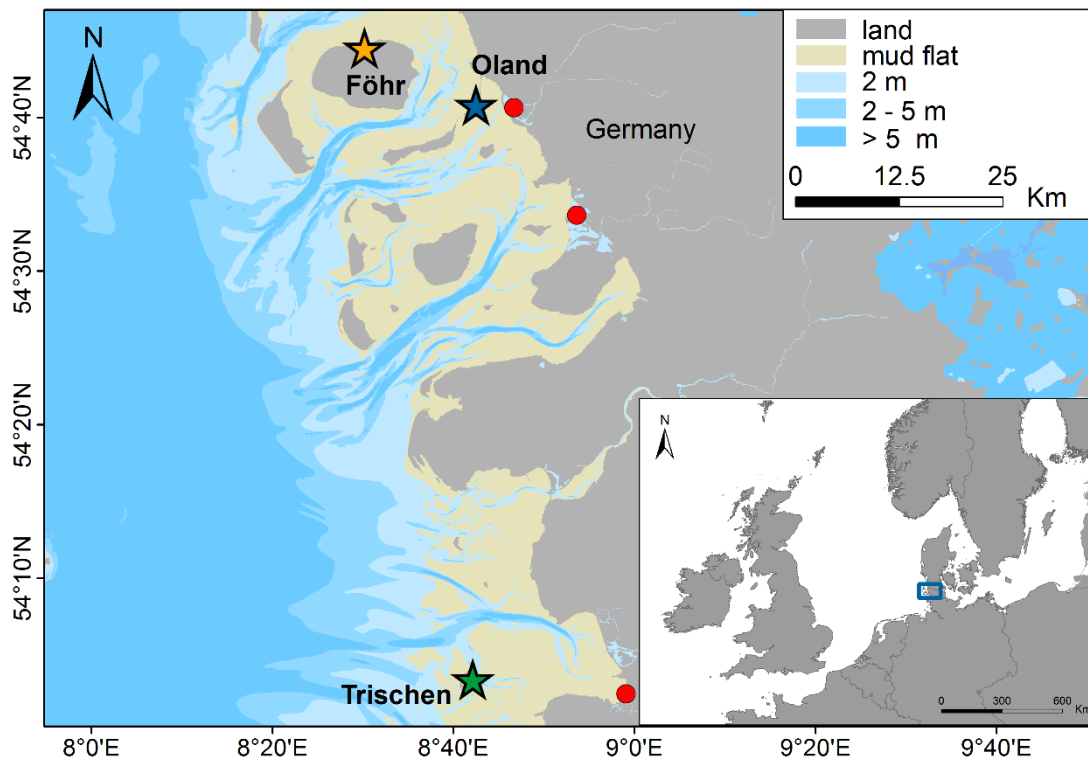
## 2 Materials and methods

### 2.1 Study area

This study was conducted on the islands of Föhr (54°43'N, 8°30'E; 83 km<sup>2</sup> total area), Oland (54°40'39"N, 8°42'14"E; 2 km<sup>2</sup>), and Trischen (54°3'34"N, 8°41'0"E; 2 km<sup>2</sup>) in the German Wadden Sea from 2014 to 2016 (Figure 1). The first spoonbills started to breed on Oland in 2000, on Trischen in 2002, and on Föhr in 2007. All three islands are surrounded by tidal flats and tidal creek systems. The breeding colony on Föhr is located in a large salt marsh in the north of the island and comprises



45 breeding pairs 2014 and 42 breeding pairs 2016 (Günther, K.; pers. comm.). Trischen is a small uninhabited island surrounded by high sandbanks and large tidal creeks (2014: 101, 2016: 127 pairs; Günther, K.; pers. comm.). The spoonbill colony on Oland is smaller than those on Föhr and Trischen (2014: 27, 2016: 30 pairs; Günther, K.; pers. comm.), and is mostly surrounded by mixed-sediment mud flats and tidal creek systems. Oland is connected to the mainland by a small artificial dam.



**Figure 1:** Study area – spoonbill breeding colonies on the islands of Föhr, Oland, and Trischen, with the main roosts marked in red. Inserted map: location of the study area within Northern Europe.

## 2.2 Telemetry

Adult spoonbills (2013:  $n = 1$ , 2015:  $n = 1$ ) and almost-fledged chicks (2014:  $n = 3$ ) were caught on their nests using a trap rope or by hand, respectively. All birds were ringed, weighed, and equipped with an e-obs Bird Solar 42 g logger (e-obs GmbH, München, Germany) (Table 1). The logger was attached to the back of the bird using a body harness, as described by Thaxter et al. (2014). The total mass of the logger plus harness was 54 g, accounting for 3 % of the average body mass of all equipped birds (mean  $\pm$  standard deviation, adult:  $1,759 \pm 189$  g, chick:  $1,706 \pm 21$  g), which was within the 3 %–5 % of additional body mass (Kenward, 2001; Barron et al., 2010) considered acceptable for birds. All transmitted birds were observed regularly, and none showed any behavioural responses related to the attachment of the loggers.

Each logger sent five positions per day via GSM to locate the birds and to download the rest of the data via an ultra-high frequency connection. Date, time, geographical position, and velocity data were recorded at 5-min intervals, increased to 40-min intervals if low sunlight levels reduced battery power.

Telemetry data from adult spoonbills in the German Wadden Sea were available for 2015 and 2016 (Bird ID 2701: 2015 and 2016, Bird ID 4117: 2016) and spatio-temporal patterns during the breeding (May) and post-breeding (June/July) periods were analysed. Data for juvenile spoonbills was collected in 2014, and data fixes were analysed for tagged juvenile spoonbills after fledging (June/July).

GPS fixes with large gaps ( $\geq 30$  min;  $n = 23$ ) between consecutive positions were excluded from the analyses. Small gaps ( $< 30$  min) were interpolated to an interval of 5 min based on state-space modelling (R package *bsam*; Jonsen et al., 2005; Jonsen et al., 2017) to allow comparison of the collected data. To determine where spoonbills were foraging, we only analysed foraging fixes; i.e. all positions recorded in the breeding colony and at roosts were excluded from the analysis. Based on the frequency distribution of the movement speed of the equipped individuals, all fixes with a speed  $\geq 2$  m/s were defined as flying behaviour and were therefore also excluded from the analysis (Shamoun-Baranes et al., 2011; Enners et al., 2018). Visualisations were performed using ArcGis 10.1 (ESRI, 2011).

**Table 1:** Study location, age, sex, and study periods of tagged spoonbills.

Bird ID	Colony	Age	Sex	Breeding	Post-breeding
2701	Oland	adult	unknown	08/05/2015– 31/05/2015	15/06/2015– 31/07/2015
				01/05/2016– 31/05/2016	15/06/2016– 31/07/2016
4117	Oland	adult	female	01/05/2016– 31/05/2016	15/06/2016– 31/07/2016
3808	Oland	juvenile	male		15/06/2014– 31/07/2014
2702	Oland	juvenile	male		15/06/2014– 31/07/2014
3806	Föhr	juvenile	male		23/07/2014– 31/07/2014

### 2.3 Diet analyses - regurgitates

We collected regurgitates and blood samples during the process of ringing spoonbill chicks, to compare the prey compositions of individuals among the three colonies (Föhr: 1 July 2014 & 31 May 2016; Oland: 26/28 May 2014 & 30 May 2016; Trischen: 28 May 2016). The collected regurgitates were from

different birds, but cannot be linked to specific individuals (Föhr: n = 28; Oland: n = 29; Trischen: n = 20). All chicks sampled were close to fledging.

The samples were stored frozen and analysed individually. After defrosting, samples were rinsed with running water through a 300 µm sieve and preserved in 70 % ethanol. The diagnostic contents (otoliths, jaws, spines) were identified to the lowest possible taxon and measured using a binocular microscope (Olympus SZH 10 Research Stereo) with an attached digital camera (Olympus Cameida, software: Olympus DP-Soft Version 3.2). In contrast to faeces, the dietary remains in regurgitates are often only partly digested and thus allow the prey species and size to be identified (Barrett et al., 2007; Veen et al., 2012).

Also bristles and jaws of ragworms (*Hediste diversicolor*) were found in the samples. Jaws were paired and the total length and mass were calculated accordingly to Witteveen and Leopold (unpub. data). Pairs, as well as single left or single right jaws, were each counted as one ragworm. Additionally, if only bristles could be found in a sample, it was assumed that at least one ragworm had been consumed, which was assigned the median total length and biomass for Nereididae in the same colony.

Whole shrimps, as well as carapaces and telsons, were measured and grouped. All regressions between the carapace or telson and the total length of *Crangon crangon* were obtained from Jansen (2002) and mass was calculated accordingly to Hufnagl et al. (2010). For other shrimps (e.g. *Macrobrachium sintangense* and *Caridea* sp.) lacking specific regression formulae, the remains were paired and counted, and each individual was assigned the median total length and biomass of *C. crangon* for the respective sample (bird).

All sagittal otoliths and pelvic and dorsal stickleback spines were photographed and identified according to Härkönen (1986) and Leopold et al. (2001), in combination with our own reference collection. Each otolith was identified as left, right, or unknown and subsequently paired, and pairs or single otoliths were each counted as representing one fish (Dirksen et al., 1995). The average length and mass of each fish were calculated based on the respective otolith or spine length and width. Regressions for estimating fish length and mass were obtained from Leopold et al. (1998, 2001), Courtens et al. (2017), and Leopold (unpub. data). If prey remains could not be identified to species level, the regression formula for the most common species of the next higher taxonomic level was used to estimate fish size and mass. The total size and mass of Percidae sp. was calculated based on the median values for all perches in the same sample. There were no regression formulae for pipefish (Syngnathidae sp.), and the remains were therefore only used to determine fish numbers. However, to compare the prey compositions among the breeding colonies, the total pipefish length and mass, as well as those of unidentified fish species (2.87 %), were calculated on the basis of the median values

for all fish species in the same sample. Detailed information on the applied formulae is provided in Appendix 1.

Although hard parts were generally well-preserved in regurgitates, there were also signs of wear, and calculations of total length and mass based on worn hard fragments could lead to a systematic underestimation (Duffy and Jackson, 1986; Guse et al., 2009). Worn hard parts (otoliths, spines, telsons, carapaces) were therefore corrected to their presumed original size based on four different wear classes ranging from no wear (class 0) to extensive wear (class 3), according to Guse et al. (2009). Hard parts with wear class 3 were not used to reconstruct the original total length and mass of the prey item, and these measurements were derived from the median value for the respective species in the sample (or colony) in these cases. For species where no length and mass could be reconstructed, presence and absence were documented and analysed.

To test differences in prey composition between years and among colonies a permutational multivariate analyses (PERMANOVA; Anderson, 2014) with *adonis* function was used (R package *vegan* 2.5-5).

#### **2.4 Diet analyses – blood samples**

Compared with regurgitates, which reflect the diet during the day prior to sampling, stable isotope analyses of blood samples from spoonbill chicks provide information about the diet composition up to several weeks preceding the sampling event (Barrett et al., 2007; Phillips et al., 2014). The blood samples were centrifuged to separate serum and red blood cells; serum reflected the short-term diet over the past week, whereas red blood cells represented the longer-term diet over the preceding 3 weeks (Hobson and Clark, 1993; Phillips et al., 2014). A total of 77 serum (Föhr: n = 28; Oland: n = 28; Trischen: n = 21) and 78 red blood cell samples (Föhr: n = 29; Oland: n = 28; Trischen: n = 21) were analysed.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in blood samples were used to analyse the predominant foraging habitat as well as the trophic level of food given to the spoonbill chicks (Barrett et al., 2007; Inger and Bearhop, 2008). Carbon reflects the foraging habitat, with lower ratios of  $\delta^{13}\text{C}$  indicating foraging in a freshwater habitat and increasing ratios a more marine feeding location, while nitrogen represents the consumer's trophic level (Hobson and Clark, 1993; Barrett et al., 2007; Inger and Bearhop, 2008).

Based on the spatio-temporal foraging patterns of spoonbills equipped with loggers and on visual observations of feeding spoonbills, potential prey source in the German Wadden Sea were sampled in 2016. Blood and prey samples were then freeze-dried and the prey items were homogenized before analysis by mass spectrometry. Approximately 0.3–0.5 mg of each sample was combusted in an elemental analyser (FlashEA, ThermoFisher Scientific, Bremen, Germany) and the resulting gases were routed via a ConFlo III (ThermoFisher Scientific) to a stable isotope ratio mass spectrometer (Delta V

Advantage mass spectrometer; ThermoFisher Scientific) to measure the ratios of light/heavy stable nitrogen and carbon isotopes. Stable isotope values were expressed in delta ( $\delta$ ) notation as ‰ deviations from international standards (air nitrogen for N and V-PDB for C), according to the following equation:  $\delta X = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1000$ ; where X is  $^{13}\text{C}$  or  $^{15}\text{N}$  and R is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . The analytical precision was < 0.3 ‰ (one standard deviation) for stable carbon and < 0.2 ‰ for nitrogen isotopes.

Due to differences in isotopic signatures between the two breeding years, ratios of carbon and nitrogen isotopes were compared among serum (short-term diet) and red blood cells (longer-term diet) for each year using a likelihood ratio test (ANOVA; Faraway, 2006).

The relative contributions of several potential prey species to the spoonbill diet were determined using the MixSIAR Bayesian mixing model (Stock and Semmens, 2016a; Stock et al., 2018). Separate models were conducted for serum and blood cells in 2014 and 2016, due to inter-annual differences within the colonies.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were used as biotracer data, while colony was treated as a fixed-effect within the consumer data. Prey species that occurred > 5 % of the spoonbill diet in regurgitate by mass were used as source and were included as means and standard deviations (replicates: n = 5). In the analysis proportions for each source were used as an “informative” prior assessed by regurgitate analysis. We used discrimination factors of 0.72 ‰ for  $^{13}\text{C}$  values and 2.25 ‰ for  $^{15}\text{N}$  values to account for trophic enrichment between the prey and bird blood, following Caut et al. (2009). The probability of the source in the mixture was estimated by running Markov chain Monte Carlo models (long: chain length = 300,000; burn-in = 200,000; thin = 100; number of chains = 3). Model convergence was verified based on two diagnostic tests (Gelman–Rubin and Geweke Diagnostic) and trace plots.

All statistical analyses were performed using the open-source software R 3.4.2 (R Development Core Team, 2017).

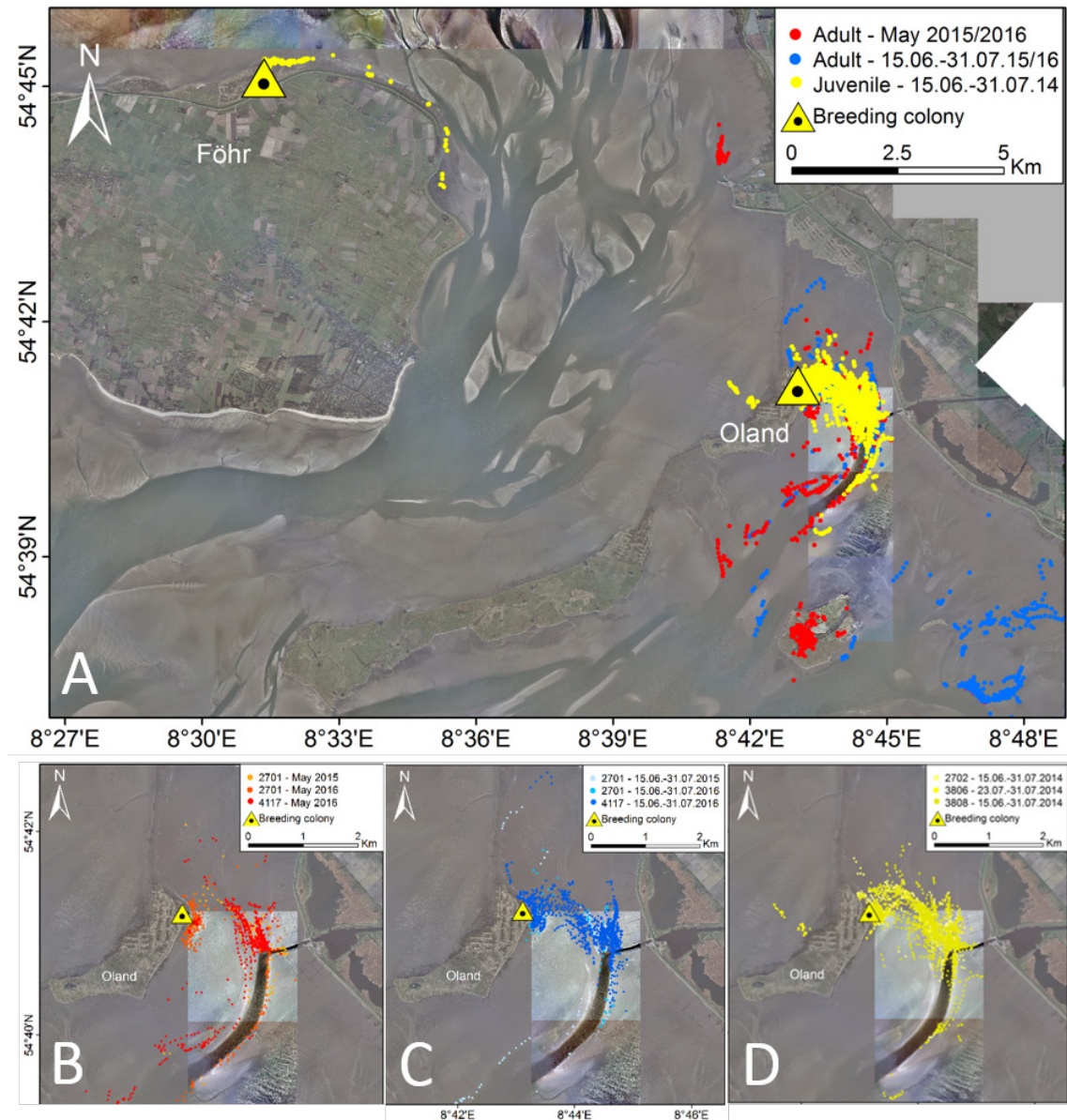
### **3 Results**

#### **3.1 Foraging patterns**

Although the sample size was small, our telemetry data consistently showed that the tidal creeks between Oland and the mainland were used extensively for foraging by both adult and juvenile spoonbills during the breeding season (May), as well as during the post-breeding season (15 June to 31 July) over the years (Figure 2).

GPS data for juvenile spoonbills were available from the post-breeding period of 2014. The juvenile spoonbill caught on Föhr started to forage in the tidal creeks near the island and later switched to the

intertidal area between Oland and the mainland. Juveniles as well as adults mostly foraged within a radius of < 5 km from the colony (Figure 2).



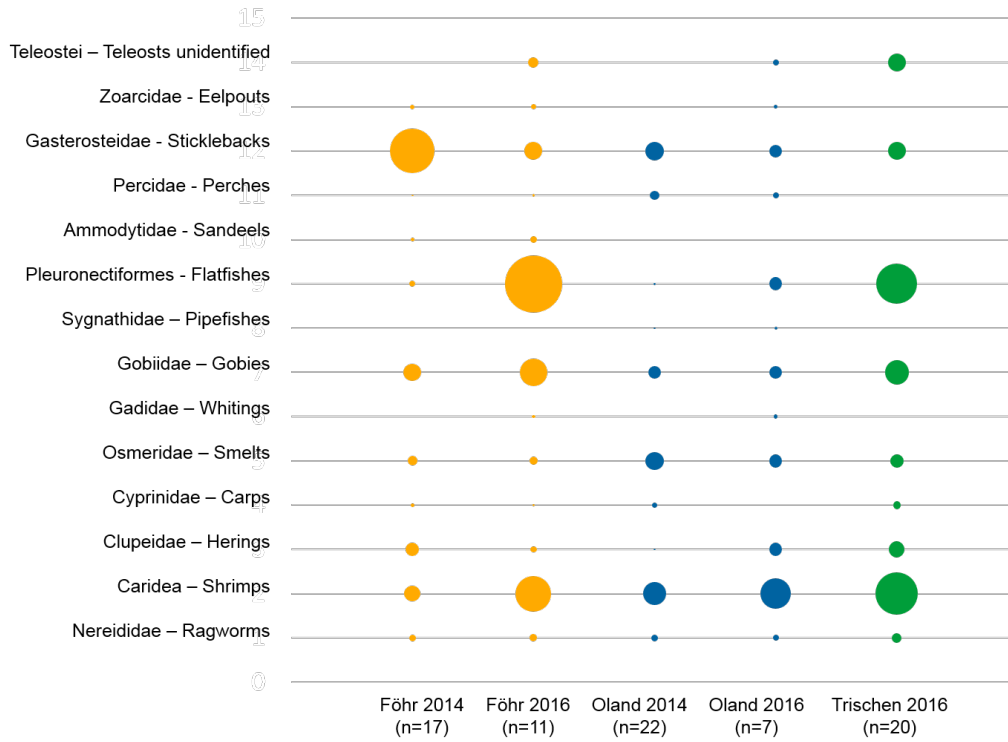
**Figure 2:** Distribution of foraging GPS logger fixes of spoonbills from Föhr and Oland in the main foraging area. A: Breeding (May 2015 and 2016, adults) and post-breeding seasons (15 June to 31 July, adults and juveniles). B: Adult spoonbills from May 2015 and 2016 (breeding season). C: Adult spoonbills from 15 June to 31 July (post-breeding season). D: Juvenile spoonbills from 15 June to 31 July (post-breeding season).

### 3.2 Diet composition - regurgitates

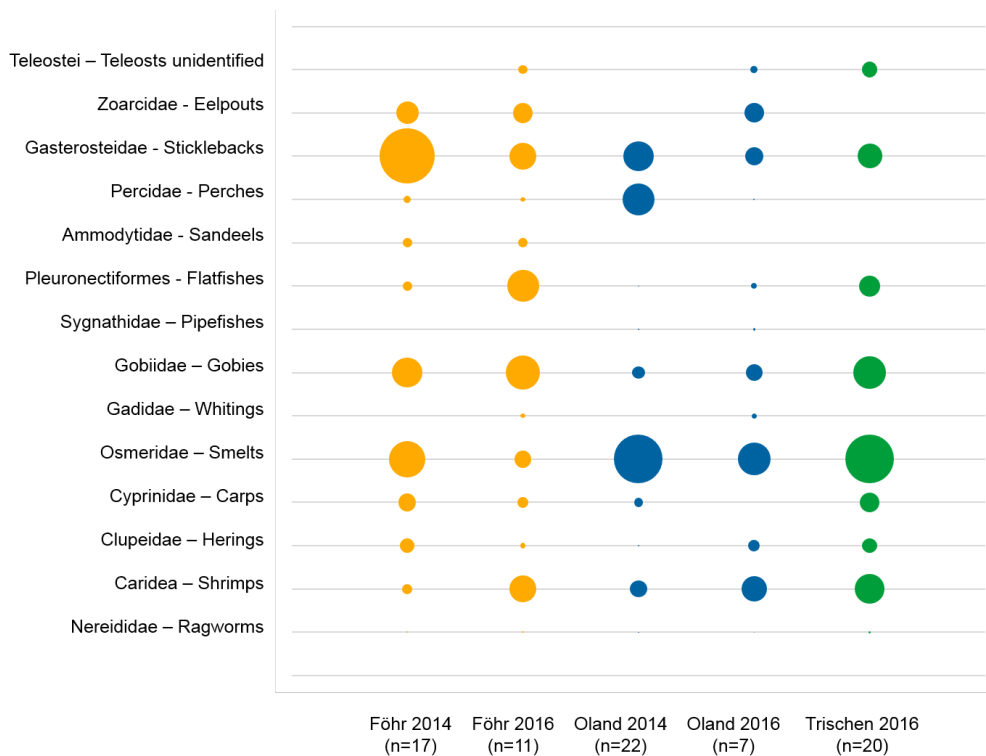
Regurgitates from spoonbill chicks showed a variable diet, including ragworms, shrimps, and fish. Insects, bivalves, and gastropods were present in some samples, but were insignificant in terms of the general diet composition. These groups were therefore excluded from further analyses.

A total of 4,247 prey items were detected and identified to the lowest possible taxon. Specific groups dominated the prey composition: Shrimps (27 %), flatfish (26.5 %), and sticklebacks (19.5 %) were the most abundant groups in terms of numbers (Figure 3, Appendix 2). The abundances of dietary components from spoonbill chick regurgitates varied significantly between years (PERMANOVA:  $p < 0.001$ ,  $R^2 = 0.13$ ,  $df = 1$ ) and among colonies (PERMANOVA:  $p < 0.003$ ,  $R^2 = 0.14$ ,  $df = 2$ ). Smelts (31.9 %), sticklebacks (22.6 %), and gobies (13.3 %) were the dominant prey groups by mass (Figure 4, Appendix 3). The diet composition varied significantly between years (PERMANOVA:  $p < 0.001$ ,  $R^2 = 0.11$ ,  $df = 1$ ) and among colonies (PERMANOVA:  $p < 0.001$ ,  $R^2 = 0.12$ ,  $df = 2$ ). However, yearly changes in diet composition in the Oland colony were not as pronounced as in the colony on Föhr. Sticklebacks were consumed more frequently in 2014 than in 2016, whereas more flatfishes were found in samples from Föhr in 2016.

Across all colonies and years, 227 smelts could be identified, and ranged from 1 to 18.8 cm (mean  $9.6 \pm 2.5$  cm) (Table 2). Among a total of 828 sticklebacks, three-spined sticklebacks were the most common ( $n = 814$ ), while the mean length of all sticklebacks was  $5.1 \pm 1.4$  cm (Table 2). Sand gobies were the dominant species of gobies (mean length of all gobies  $5.1 \pm 1.1$  cm) (Table 2). The mean length of all flatfish was  $2.8 \pm 0.7$  cm, while shrimps showed a mean length of  $3.8 \pm 0.9$  cm (Table 2).



**Figure 3:** Abundances of dietary components from spoonbill chick regurgitates according to colony and year. Area of circles are proportional to the mean number of prey items per regurgitate (range: 0–52.2).



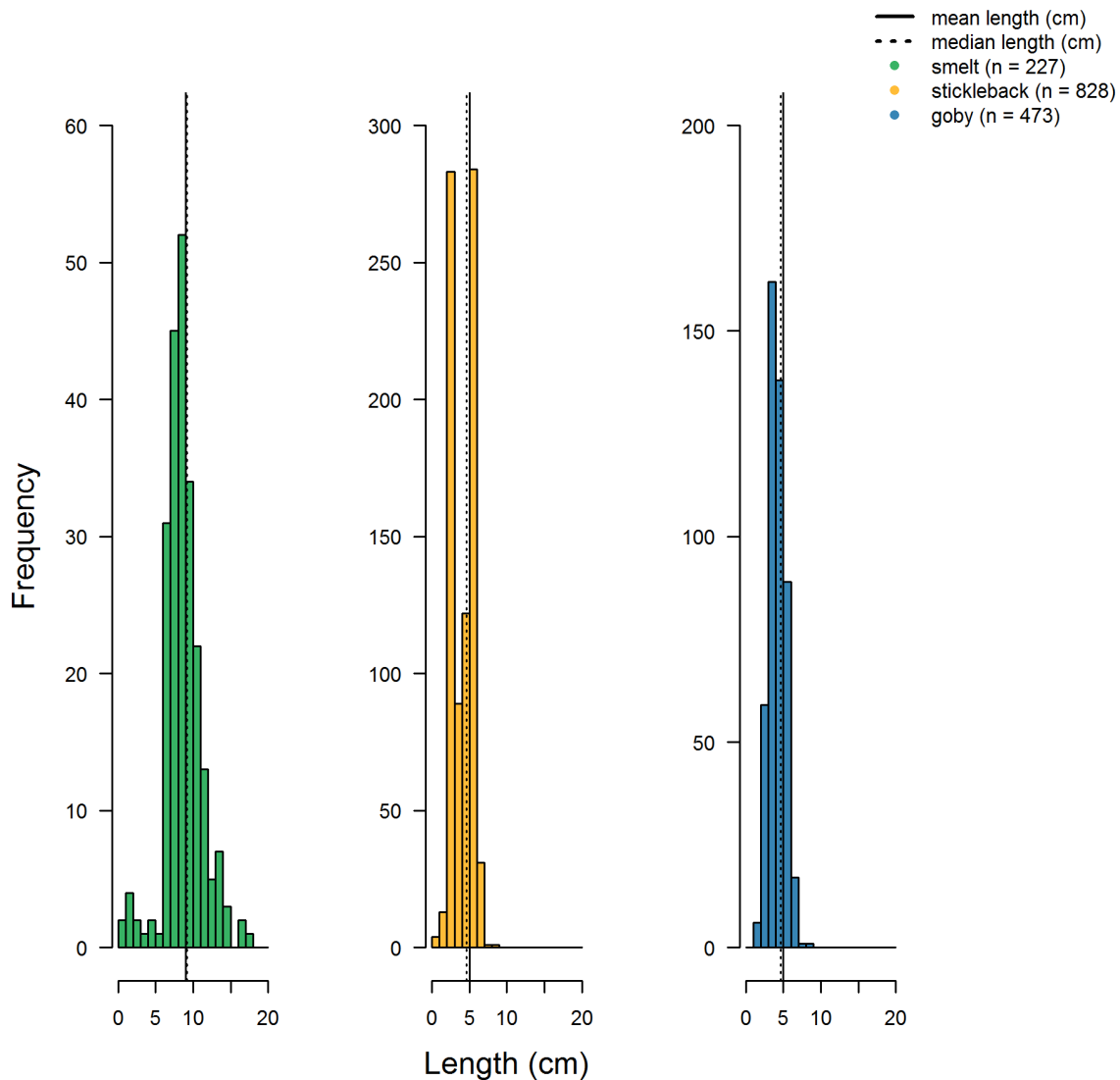
**Figure 4:** Masses of dietary components from spoonbill chick regurgitates according to colony and year. Area of circles are proportional to the mean mass (wet weight) of prey items per regurgitate consumed (range: 0–35.9 gram).



**Table 2:** Sizes of all prey items (in cm), based on regurgitates from spoonbill chicks.

Group	Common name	Föhr 2014 average (SD±; n)	Föhr 2016 average (SD±; n)	Oland 2014 average (SD±; n)	Oland 2016 average (SD±; n)	Trischen 2016 average (SD±; n)
Nereididae	Ragworms	2.6 (± 0.1; 13)	2.4 (± 0.7; 10)	1.4 (± 0.3; 16)	1.4 (± 0.0; 4)	2.5 (± 0.5; 29)
Caridea	Shrimps	3.4 (± 0.8; 69)	4.0 (± 0.6; 222)	3.9 (± 0.7; 188)	4.1 (± 0.9; 104)	3.6 (± 1.0; 563)
Clupeidae	Herings	5.1 (± 0.5; 51)	4.7 (± 0.3; 7)	3.9 (± 0.0; 1)	4.8 (± 0.5; 18)	4.7 (± 0.7; 78)
Cyprinidae	Carps	12.1 (± 0.0; 4)	12.1 (± 0.0; 1)	6.9 (± 0.9; 8)		7.9 (± 1.9; 19)
Osmeridae	Smelts	11.2 (± 2.0; 26)	7.9 (± 2.5; 11)	9.1 (± 2.1; 114)	8.3 (± 2.5; 19)	10.7 (± 2.6; 57)
Gadidae	Whitings		6.0 (± 0.0; 2)		5.5 (± 0.4; 2)	
Gobiidae	Gobies	6.2 (± 0.7; 84)	4.9 (± 1.0; 129)	4.1 (± 0.8; 58)	5.0 (± 0.6; 19)	5.1 (± 0.9; 183)
Pleuronectiformes	Flatfish	5.2 (± 2.1; 9)	2.9 (± 0.6; 574)	2.6 (± 0.1; 2)	2.6 (± 0.5; 19)	2.7 (± 0.7; 523)
Ammodytidae	Sandeels	11.8 (± 1.4; 4)	8.8 (± 0.7; 7)			
Percidae	Perches	9.9 (± 0.0; 1)	6.1 (± 0.0; 1)	8.8 (± 1.7; 30)	1.8 (± 0.0; 4)	
Gasterosteidae	Sticklebacks	4.8 (± 1.4; 531)	5.7 (± 1.0; 55)	6.0 (± 0.9; 123)	5.7 (± 0.3; 18)	5.2 (± 1.4; 101)
Zoarcidae	Eelpouids	15.3 (± 1.7; 5)	11.7 (± 3.4; 5)		14.2 (± 0.0; 2)	

We analysed the length frequencies for the dominant prey categories. Most smelts (93.4 %) were I-group fish (i.e. born in the previous year), and smelts < 7 cm total length were rarely taken (Figure 5). The dominant size class of sticklebacks ranged from 3 to 6 cm (Figure 5), with a bimodal size-frequency distribution. Most dominant size classes of gobies found in the regurgitates ranged from 2 to 6 cm (Figure 5). The consumed size classes of sticklebacks and gobies encompassed most age classes.



**Figure 5:** Size (total length in cm) frequency distributions of smelts (*Osmerus eperlanus*), sticklebacks (*Gasterosteidae*), and gobies (*Gobiidae*) of all wear classes in regurgitates based on regression formulae.

### 3.3 Diet composition - blood samples

There were no differences in  $\delta^{13}\text{C}$  values between red blood cells and serum; however,  $\delta^{15}\text{N}$  showed a clear relationship between short- and longer-term diet (ANOVA: 2014:  $f = 25.28$ ,  $df = 1$ ,  $p < 0.001$ ; 2016:  $f = 123.3$ ,  $df = 1$ ,  $p < 0.001$ ). Serum samples had significantly higher  $\delta^{15}\text{N}$  values than red blood cells (Appendix 4).

Overall, flatfish and sticklebacks were the dominant prey species in the spoonbill diet according to stable isotope analyses, but there were differences among colonies and between years (Table 3). In general, flatfish were the main prey source in 2014 in the longer-term diet (red blood cell analysis) (e.g. mean 2014: Föhr = 39 %; Oland = 37 %) (Table 3), while 2016 the spoonbill diet was dominated by sticklebacks (e.g. mean 2016: Föhr = 59 %; Oland = 39 %; Trischen = 52 %) (Table 3). In contrast, the short-term diet (serum) was more diverse, with flatfish, smelts, gobies, and sticklebacks as the main prey source (e.g. mean Föhr 2016: gobies = 26 %; flatfish = 25 %; sticklebacks = 20 %; smelts = 13 %) (Table 3).

**Table 3:** Contribution of prey items to the diet of spoonbill chicks estimated using MixSIAR (50 % quantiles, range = 95 % credible intervals). The maximum value per colony and year is shown in bold.

		Föhr				Oland				Trischen	
Source		2014		2016		2014		2016		2016	
Scientific name	Common name	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
<b>Serum (short-term diet)</b>		n = 9		n = 19		n = 16		n = 13		n = 21	
<i>Crangon crangon</i>	Shrimps	10.5	9.5	15.4	12.3	4.5	5.6	9.8	9.7	10.1	10
<i>Gasterosteus aculeatus</i>	Sticklebacks	20.0	14.2	20.3	14.9	8.4	14.0	18.3	18.3	18.5	18.6
<i>Osmerus eperlanus</i>	Smelts	26.1	15.2	13.2	10.5	<b>45.9</b>	31.5	15.0	16.4	15.5	16.6
<i>Pomatoschistus minutus</i>	Gobies	14.9	10.7	<b>25.9</b>	12.9	3.6	3.5	12.4	9.0	12.4	8.9
<i>Platichthys flesus</i>	Flatfish	<b>28.5</b>	13.6	25.2	12.2	37.5	27.7	<b>44.5</b>	21.0	<b>43.5</b>	21.1
<b>Red blood cells (longer-term diet)</b>		n=10		n=19		n=16		n=12		n=21	
<i>Crangon crangon</i>	Shrimps	8.2	7.1	5.6	5.1	11.5	11.9	5.8	6.5	4.0	4.4
<i>Gasterosteus aculeatus</i>	Sticklebacks	29.0	17.3	<b>59.3</b>	13.3	23.0	17.9	<b>39.0</b>	12.3	<b>51.6</b>	12.0
<i>Osmerus eperlanus</i>	Smelts	11.5	9.3	6.3	5.8	17.9	16.3	9.2	10.8	6.3	7.5
<i>Pomatoschistus minutus</i>	Gobies	12.6	10.3	13.1	11.2	10.8	9.9	10.7	10.4	8.0	8.4
<i>Platichthys flesus</i>	Flatfish	<b>38.7</b>	14.8	15.7	7.4	<b>36.8</b>	17.4	35.3	13.7	30.1	10.9

## **4 Discussion**

### **4.1 Foraging behaviour**

Spoonbills in the German Wadden Sea showed an opportunistic foraging strategy, with marine fish as the dominant prey during the breeding season. Previous studies analysed that the diet of spoonbills consisted mainly of brown shrimps and small fish (van Wetten and Wintermans, 1986; Aguilera et al., 1996; Veen et al., 2012; El-Hacen et al., 2014; Jouta et al., 2018). In our study, shrimps were an important prey in terms of numbers, but less important in terms of mass. Fish might be preferred prey items due to their higher biomass, in accordance with the findings of Jouta et al. (2018) who showed that small flatfish and gobies were the main prey items of breeding spoonbills in the Dutch Wadden Sea.

In the Netherlands, spoonbills are breeding on the Wadden Sea islands as well as on the mainland and are using both marine and freshwater habitats for foraging (Oudman et al., 2017; Jouta et al., 2018). Diet analyses of spoonbill chicks from the Dutch Wadden Sea islands mainly consisted of marine prey, indicating foraging areas in local intertidal areas (Jouta et al., 2018). The abundance of small fish close to the breeding place might limit the colony size (Oudman et al., 2017; Jouta et al., 2018). In Germany, spoonbills are so far exclusively breeding in small colonies in the Wadden Sea area and show growing breeding numbers. In our study all samples from spoonbill chicks contained prey species originating from marine habitats. Although the sample size was small, spatio-temporal patterns based on telemetry data as well as visual observations indicated a small foraging range of <5 km from the breeding areas. Prey depletion close to the breeding colony may force birds to make longer flights with higher trip costs and an increased risk of nest predation (Morris and Black, 1980; Pierotti and Annett, 1991). However, there was no evidence of prey depletion in our study, given that the logger data showed the highest foraging activity close to the colony. Our telemetry data as well as visual observations indicated the importance of tidal creeks in the German Wadden Sea as foraging habitat for spoonbills, while spoonbills mainly used nature reserves on the mainland for resting. These areas provide an important habitat for the spoonbills in the German Wadden Sea. Spoonbills might also forage mostly in tidal creeks adjacent to these nature reserves, due to the abundant creek systems and high biomasses of prey organisms.

### **4.2 Seasonal changes**

The spoonbill diet varied between years and among colonies, with notably different diet compositions between the neighbouring colonies of Föhr and Oland. Geographical fine-scale differences in diet choice were also shown for breeding spoonbills in the Dutch Wadden Sea (Jouta et al., 2018). Overall however, all colonies in the German Wadden Sea used similar prey species.

Different methods were combined to analyse the diet composition of spoonbills in the German Wadden Sea. While stable isotope analyses reflect the diet over a longer time span and are less susceptible to under- or overestimating different types of prey, this method is limited in terms of determining single prey species (Barrett et al., 2007; Inger and Bearhop, 2008; Phillips et al., 2014). In contrast, analyses of regurgitates enable the identification of dietary remains up to species level and provide information on the size and mass of individual prey items, but reflect only the diet during the day prior to sampling and may underrepresent rapidly digestible items (Duffy and Jackson, 1986; Barrett et al., 2007). We used information from regurgitates to identify the main prey species and included the regurgitates' proportions in the MixSIAR model as informative prior.

During the chick-rearing season nitrogen values increased and implied that prey species of higher trophic levels were more available during the end of May. The longer-term diet of spoonbills during early May (red blood cells) was mainly based on sticklebacks and flatfish, while the short-term diet at the end of May (serum) was more diverse, with flatfish, gobies, sticklebacks, and smelts as the main prey items. In addition, the regurgitates reflected the diet during the day prior to sampling end of May and were also dominated by sticklebacks and smelts. Flatfish were a dominant prey item in terms of numbers but not mass, due to their short lengths. However, end of May sticklebacks, gobies and smelts might be available in high numbers in the coastal area.

Sticklebacks are euryhaline species that can be found in both marine and freshwater habitats (van Wetten and Wintermans, 1986; Heessen et al., 2015; Camphuysen and Henderson, 2017). In the North Sea, sticklebacks spawn in the coastal areas from April to May (Vorberg and Breckling, 1999) and are then available to spoonbills. The diet analyses by regurgitates showed a bimodal size-frequency distribution indicating the presence of at least two age classes (Rollins, 2017). Red blood cells, serum and regurgitates implied that in the German Wadden Sea sticklebacks were available for spoonbills during the whole chick-rearing season. The importance of sticklebacks as a main prey source for spoonbills was previously shown (van Wetten and Wintermans, 1986; Kemper, 1995).

Gobies, in particular sand gobies, were a dominant prey species during end of May (serum, regurgitates). In early May gobies might still be in the deeper waters (Hesthagen, 2011). After wintering in deeper areas, gobies spawn in the shallow coastal waters from March to July (Hesthagen, 2011; Vorberg and Breckling, 1999) and are available in high numbers in the coastal zone.

In contrast, smelts spawn in the lower courses of rivers between March and April and then migrate downstream to marine waters after hatching (Vorberg and Breckling, 1999; Dänhardt and Becker, 2008; Heessen et al., 2015; Camphuysen and Henderson, 2017). Juveniles and adults are therefore mostly still inland during May, which is in accordance with our finding that only subadults were consumed by spoonbills in the coastal area end of May (serum, regurgitates). The mean length of

consumed smelts was 9.6 cm and were therefore an energy-rich prey source for the German spoonbills. According to Dänhardt and Becker (2008) the available fraction of smelts in the coastal area has an average length of 9 cm during this time. In contrast to El-Hacen et al. (2014) and Jouta et al. (2018), smelts were an important prey species for spoonbills breeding in the German Wadden Sea. Spoonbills are known for a tactile and visual foraging strategy (van Wetten and Wintermans, 1986); however, in our study their prey choice was not specialized and a wide spectrum of prey items was consumed, with relatively high prey diversity within a single sample. Previous studies concluded that the habitat specialization depends on the breeding time, such that spoonbills breeding early in the season might be specialized for foraging in freshwater habitats, whereas the marine habitat might be preferred later (van Wetten and Wintermans, 1986; El-Hacen et al., 2014). Although no data on early diet was available for the German Wadden Sea, differences among colonies and between years supported an opportunistic foraging strategy by the spoonbills during the breeding season. Diet analyses (regurgitates, blood) revealed that the freshwater environment was less important as foraging habitat for breeding spoonbills in the German Wadden Sea, as marine species dominated the diet composition. Ratios of carbon isotopes showed no differences between red blood cells and serum and implied that the marine environment is the important foraging habitat during the chick-rearing period.

### **Conclusions**

We used different methods (telemetry, regurgitates, stable isotopes) to reveal foraging habitats and prey composition of spoonbills in the German Wadden Sea. Our results suggest that brown shrimps might be less important in the spoonbill diet during the chick-rearing period than previously assumed, with marine fish being the main prey source. The diet of spoonbills was dominated by flatfish and sticklebacks (red blood cells) during early May, while the diet at the end of May was more diverse (serum). Regurgitates consisted mainly of sticklebacks and smelts, suggesting seasonal shifts in prey choice, possibly also reflecting changes in prey abundance during these periods. These differences between years and among colonies also indicate that spoonbills adopt an opportunistic foraging strategy. This study also provides the first fine-scale evidence for habitat utilisation by breeding spoonbills in the German Wadden Sea, based on logger data. Telemetry data indicated the importance of intertidal creeks in coastal areas as foraging habitats. The prey items caught by spoonbills also apparently depend on the prey availability in the vicinity of the respective breeding colony, and the small-scale mosaic of tidal flats and creeks, as a function of tidal stage, thus affect local prey choice and foraging behaviour by spoonbills in the German Wadden Sea.

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### **Data accessibility**

Tracking data are archived at Movebank (<https://www.movebank.org>). Bird-ringing data are archived at the Beringungszentrale Vogelwarte Helgoland Institute for Avian Research, Wilhelmshaven.

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**Appendix 1:** Applied regressions between object (jaw, carapace, telson, otolith, and spine) length/width and total length and between total length and mass.

Group	Species name	Scientific name	Object	Formula	Basic formula: species	Source
<b>Nereididae</b>	ragworm	<i>Hediste diversicolor</i>	J: left jaw length (mm)	Length (cm) = 2.5143 * J <sup>1.5665</sup>	<i>Hediste diversicolor</i>	Witteveen & Leopold unpub.
			J: right jaw length (mm)	Length (cm) = 1.9862 * J <sup>1.8878</sup>	<i>Hediste diversicolor</i>	Witteveen & Leopold unpub.
			J: left jaw length (mm)	Mass (g) = 0.0319 * J <sup>3.93</sup>	<i>Hediste diversicolor</i>	Witteveen & Leopold unpub.
			J: right jaw length (mm)	Mass (g) = 0.028 * J <sup>4.0915</sup>	<i>Hediste diversicolor</i>	Witteveen & Leopold unpub.
<b>Caridea</b>	common brown shrimp	<i>Crangon crangon</i>	CX: carapace length (mm)	Length (mm) = 3.87 + CX * 4.194	<i>Crangon crangon</i>	Jansen 2002
			T: telson length (mm)	Length (mm) = 0.33 + T * 6.219	<i>Crangon crangon</i>	Jansen 2002
			TL: total length (mm)	Mass (g) = 4.625 * 10 <sup>-6</sup> * TL <sup>3.084</sup>	<i>Crangon crangon</i>	Hufnagl et al. 2010
<b>Caridea</b>	rockpool prawn	<i>Macrobrachium sintangense</i>	TL: total length (mm)	TL = median sample of <i>Crangon crangon</i>	<i>Crangon crangon</i>	Jansen 2002
			M: mass (g)	M = median sample of <i>Crangon crangon</i>	<i>Crangon crangon</i>	Hufnagl et al. 2010
<b>Caridea</b>	shrimp unidentified	Caridea sp.	TL: total length (mm)	TL = median sample of <i>Crangon crangon</i>	<i>Crangon crangon</i>	Jansen 2002
			M: mass (g)	M = median sample of <i>Crangon crangon</i>	<i>Crangon crangon</i>	Hufnagl et al. 2010

Group	Species name	Scientific name	Object	Formula	Basic formula: species	Source
Clupeidae	herring	<i>Clupea harengus</i>	OW: otolith width ( $\mu\text{m}$ )	$\text{Length (mm)} = 5 * 10^{-5} * \text{OW}^2 - 0.0009 * \text{OW} + 31.185$	<i>Clupea harengus</i>	Courtens et al. 2007
			TL: total length (cm)	$\text{Mass (g)} = (0.18 * \text{TL})^{3.11}$	<i>Clupea harengus</i>	Leopold et al. 2001
Clupeidae	sprat	<i>Sprattus sprattus</i>	OW: otolith width ( $\mu\text{m}$ )	$\text{Length (mm)} = 9 * 10^{-5} * \text{OW}^2 - 0.0379 * \text{OW} + 43.603$	<i>Sprattus sprattus</i>	Courtens et al. 2017
			TL: total length (cm)	$\text{Mass (g)} = (0.18 * \text{TL})^{3.50}$	<i>Sprattus sprattus</i>	Leopold et al. 2001
Clupeidae	herring unidentified	<i>C. harengus/Sprattus sprattus/Clupeidae sp.</i>	OW: otolith width ( $\mu\text{m}$ )	$\text{Length (mm)} = 5 * 10^{-5} * \text{OW}^2 - 0.0009 * \text{OW} + 31.185$	<i>Clupea harengus</i>	Courtens et al. 2017
			TL: total length (cm)	$\text{Mass (g)} = (0.18 * \text{TL})^{3.11}$	<i>Clupea harengus</i>	Leopold et al. 2001
Cyprinidae	roach	<i>Rutilus rutilus</i>	OW: otolith width (mm)	$\text{Length (cm)} = -2.48 + 7.66 * (\text{OW})$	<i>Rutilus rutilus</i>	Leopold et al. 2001
			OL: otolith length (mm)	$\text{Length (cm)} = 6.9 * (\text{OL})$	<i>Rutilus rutilus</i>	Leopold et al. 2001
			CL: chewpad length (mm)	$\text{Length (cm)} = 3.86 + 2.13 * (\text{CL})$	<i>Rutilus rutilus</i>	Leopold et al. 2001
			TL: total length (cm)	$\text{Mass (g)} = (0.19 * \text{TL})^{3.32}$	<i>Rutilus rutilus</i>	Leopold et al. 2001
Cyprinidae	carp	Cyprinidae sp.	OW: otolith width (mm)	$\text{Length (cm)} = -2.48 + 7.66 * (\text{OW})$	<i>Rutilus rutilus</i>	Leopold et al. 2001
			OL: otolith length (mm)	$\text{Length (cm)} = 6.9 * (\text{OL})$	<i>Rutilus rutilus</i>	Leopold et al. 2001

Group	Species name	Scientific name	Object	Formula	Basic formula: species	Source
			CL: chewpad length (mm)	Length (cm) = $3.86+2.13*(CL)$	<i>Rutilus rutilus</i>	Leopold et al. 2001
			TL: total length (cm)	Mass (g) = $(0.19*TL)^{3.32}$	<i>Rutilus rutilus</i>	Leopold et al. 2001
<b>Osmeridae</b>	smelt	<i>Osmerus eperlanus</i>	OW: otolith width (mm)	Length (cm) = $4.29+7.51*(OW)$	<i>Osmerus eperlanus</i>	Leopold et al. 2001
			OL: otolith length (mm)	Length (cm) = $1.63+3.97*(OL)$	<i>Osmerus eperlanus</i>	Leopold et al. 2001
			TL: total length (cm)	Mass (g) = $(0.17*TL)^{3.4}$	<i>Osmerus eperlanus</i>	Leopold et al. 2001
<b>Gadidae</b>	whiting	<i>Merlangius merlangus</i>	OW: otolith width (mm)	Length (cm) = $2.97+6.74*(OW)$	<i>Merlangius merlangus</i>	Leopold et al. 2001
			OL: otolith length (mm)	Length (cm) = $0.81+1.73*(OL)$	<i>Merlangius merlangus</i>	Leopold et al. 2001
			TL: total length (cm)	Mass (g) = $(0.19*TL)^{3.09}$	<i>Merlangius merlangus</i>	Leopold et al. 2001
<b>Gobiidae</b>	sand goby	<i>Pomatoschistus minutus</i>	OW: otolith width (mm)	Length (cm) = $1.74+5.27*(OW)$	<i>Pomatoschistus minutus</i>	Leopold et al. 2001
			OL: otolith length (mm)	Length (cm) = $0.43+3.92*(OL)$	<i>Pomatoschistus minutus</i>	Leopold et al. 2001
			TL: total length (cm)	Mass (g) = $(0.21*TL)^{2.83}$	<i>Pomatoschistus minutus</i>	Leopold et al. 2001
<b>Gobiidae</b>	common goby	<i>Pomatoschistus microps</i>	OW: otolith width (mm)	Length (cm) = $3.55*(OW)$	<i>Pomatoschistus microps</i>	Leopold et al. 2001
			OL: otolith length (mm)	Length (cm) = $3.35*(OL)$	<i>Pomatoschistus microps</i>	Leopold et al. 2001
			TL: total length (cm)	Mass (g) = $(0.22*TL)^{3.27}$	<i>Pomatoschistus microps</i>	Leopold et al. 2001

Group	Species name	Scientific name	Object	Formula	Basic formula: species	Source
<b>Gobiidae</b>	goby unidentified	<i>P. minutus</i> / <i>P. microps</i> / <i>P. pictus</i> /sp.	OW: otolith width (mm)	Length (cm) = - $1.74+5.27*(OW)$	<i>Pomatoschistus</i> <i>minutus</i>	Leopold et al. 2001
			OL: otolith length (mm)	Length (cm) = - $0.43+3.92*(OL)$	<i>Pomatoschistus</i> <i>minutus</i>	Leopold et al. 2001
			TL: total length (cm)	Mass (g) = $(0.21*TL)^{2.83}$	<i>Pomatoschistus</i> <i>minutus</i>	Leopold et al. 2001
<b>Syngnathidae</b>	Pipefish unidentified	Syngnathidae sp.	TL: total length (mm)	TL = median sample of all fish species		
			M: mass (g)	M = median sample of all fish species		
<b>Pleuronectiformes</b>	dab	<i>Limanda limanda</i>	OW: otolith width (mm)	Length (cm) = $4.4721$ $* (OW)^{1.4077}$	<i>Limanda limanda</i>	Leopold et al. 1998
			OL: otolith length (mm)	Length (cm) = $3.0857$ $* (OL)^{1.2664}$	<i>Limanda limanda</i>	Leopold et al. 1998
			TL: total length (cm)	Mass (g) = $0.0067$ * $(TL)^{3.1389}$	<i>Limanda limanda</i>	Leopold et al. 1998
<b>Pleuronectiformes</b>	plaice	<i>Pleuronectes platessa</i>	OW: otolith width (mm)	Length (cm) = $4.644$ * $(OW)^{1.2704}$	<i>Pleuronectes</i> <i>platessa</i>	Leopold et al. 1998
			OL: otolith length (mm)	Length (cm) = $3.5352$ $* (OL)^{1.1255}$	<i>Pleuronectes</i> <i>platessa</i>	Leopold et al. 1998
			TL: total length (cm)	Mass (g) = $0.0099$ * $(TL)^{3.0209}$	<i>Pleuronectes</i> <i>platessa</i>	Leopold et al. 1998
<b>Pleuronectiformes</b>	flounder	<i>Platichthys flesus</i>	OW: otolith width (mm)	Length (cm) = $4.9929*(OW)^{1.3681}$	<i>Platichthys flesus</i>	Leopold et al. 1998
			OL: otolith length (mm)	Length (cm) = $3.3615*(OL)^{1.2217}$	<i>Platichthys flesus</i>	Leopold et al. 1998
			TL: total length (cm)	Mass (g) = $0.0103*(TL)^{2.9976}$	<i>Platichthys flesus</i>	Leopold et al. 1998

Group	Species name	Scientific name	Object	Formula	Basic formula: species	Source
<b>Pleuronectiformes</b>	flatfish unidentified	<i>L. limanda/ P. flesus/ P. platessa/ Pleuronectiformes sp.</i>	OW: otolith width (mm)	Length (cm) = 4.4721 * (OW) <sup>1.4077</sup>	<i>Limanda limanda</i>	Leopold et al. 1998
			OL: otolith length (mm)	Length (cm) = 3.0857 * (OL) <sup>1.2664</sup>	<i>Limanda limanda</i>	Leopold et al. 1998
			TL: total length (cm)	Mass (g) = 0.0067 * (TL) <sup>3.1389</sup>	<i>Limanda limanda</i>	Leopold et al. 1998
<b>Ammodytidae</b>	small sandeel	<i>Ammodytes tobianus</i>	OW: otolith width (mm)	Length (cm) = 10.92*(OW)	<i>Ammodytes tobianus</i>	Leopold et al. 2001
			OL: otolith length (mm)	Length (cm) = 1.16+5*(OL)	<i>Ammodytes tobianus</i>	Leopold et al. 2001
			TL: total length (cm)	Mass (g) = (0.13*TL) <sup>3.46</sup>	<i>Ammodytes tobianus</i>	Leopold et al. 2001
<b>Ammodytidae</b>	sandeel unidentified	Ammodytidae sp.	OW: otolith width (mm)	Length (cm) = 10.92*(OW)	<i>Ammodytes tobianus</i>	Leopold et al. 2001
			OL: otolith length (mm)	Length (cm) = 1.16+5*(OL)	<i>Ammodytes tobianus</i>	Leopold et al. 2001
			TL: total length (cm)	Mass (g) = (0.13*TL) <sup>3.46</sup>	<i>Ammodytes tobianus</i>	Leopold et al. 2001
<b>Percidae</b>	ruffe	<i>Gymnocephalus cernua</i>	OW: otolith width (mm)	Length (cm) = - 0.94+3.61*(OW)	<i>Gymnocephalus cernua</i>	Leopold et al. 2001
			OL: otolith length (mm)	Length (cm) = 1.98*(OL)	<i>Gymnocephalus cernua</i>	Leopold et al. 2001
			TL: total length (cm)	Mass (g) = (0.22*TL) <sup>3.18</sup>	<i>Gymnocephalus cernua</i>	Leopold et al. 2001
<b>Percidae</b>	perch	<i>Perca fluviatilis</i>	OW: otolith width (mm)	Length (cm) = - 3.21+7.3*(OW)	<i>Perca fluviatilis</i>	Leopold et al. 2001
			OL: otolith length (mm)	Length (cm) = - 2.54+3.44*(OL)	<i>Perca fluviatilis</i>	Leopold et al. 2001

Group	Species name	Scientific name	Object	Formula	Basic formula: species	Source
			TL: total length (cm)	$\text{Mass (g)} = (0.2 * \text{TL})^{3.44}$	<i>Perca fluviatilis</i>	Leopold et al. 2001
<b>Percidae</b>	perch unidentified	Percidae sp.	TL: total length (mm)	TL = median sample of <i>Perca fluviatilis</i> and <i>Gymnocephalus cernua</i>		
			M: mass (g)	M = median sample of <i>Perca fluviatilis</i> and <i>Gymnocephalus cernua</i>		
<b>Gasterosteidae</b>	three-spined stickleback	<i>Gasterosteus aculeatus</i>	OW: otolith width (mm)	Length (cm) = $4.95 + 21.47 * (\text{OW})$	<i>Gasterosteus aculeatus</i>	Leopold et al. 2001
			OL: otolith length (mm)	Length (cm) = $2.58 + 14.84 * (\text{OL})$	<i>Gasterosteus aculeatus</i>	Leopold et al. 2001
			SDL: dorsal spine length (mm)	Length (cm) = $1.7245 * (\text{SDL})^{0.7138}$	<i>Gasterosteus aculeatus</i>	Leopold unpub.
			SDW: dorsal spine width (mm)	Length (cm) = $3.5609 * (\text{SDW})^{0.9809}$	<i>Gasterosteus aculeatus</i>	Leopold unpub.
			SVL: pelvic spine length (mm)	Length (cm) = $0.9314 * (\text{SVL})^{0.8606}$	<i>Gasterosteus aculeatus</i>	Leopold unpub.
			SVW: pelvic spine width (mm)	Length (cm) = $2.666 * (\text{SVW})^{0.8589}$	<i>Gasterosteus aculeatus</i>	Leopold unpub.
			TL: total length (cm)	Mass (g) = $(0.2 * \text{TL})^{3.21}$	<i>Gasterosteus aculeatus</i>	Leopold et al. 2001

Group	Species name	Scientific name	Object	Formula	Basic formula: species	Source
<b>Gasterosteidae</b>	stickleback unidentified	<i>Spinachia spinachia</i> / Gasterosteidae sp.	OW: otolith width (mm)	Length (cm) = - 4.95+21.47*(OW)	<i>Gasterosteus aculeatus</i>	Leopold et al. 2001
			OL: otolith length (mm)	Length (cm) = - 2.58+14.84*(OL)	<i>Gasterosteus aculeatus</i>	Leopold et al. 2001
			SDL: dorsal spine length (mm)	Length (cm) = 1.7245*(SDL) <sup>0.7138</sup>	<i>Gasterosteus aculeatus</i>	Leopold unpub.
			SDW: dorsal spine width (mm)	Length (cm) = 3.5609*(SDW) <sup>0.9809</sup>	<i>Gasterosteus aculeatus</i>	Leopold unpub.
			SVL: pelvic spine length (mm)	Length (cm) = 0.9314*(SVL) <sup>0.8606</sup>	<i>Gasterosteus aculeatus</i>	Leopold unpub.
			SVW: pelvic spine width (mm)	Length (cm) = 2.666*(SVW) <sup>0.8589</sup>	<i>Gasterosteus aculeatus</i>	Leopold unpub.
			TL: total length (cm)	Mass (g) = (0.2*TL) <sup>3.21</sup>	<i>Gasterosteus aculeatus</i>	Leopold et al. 2001
<b>Gasterosteidae</b>	nine-spined stickleback	<i>Pungitus pungitus</i>	SVL: pelvic spine length (mm)	Length (cm) = 0.75+1.09*(SVL)	<i>Pungitus pungitus</i>	Leopold et al. 2001
			TL: total length (cm)	Mass (g) = (0.21*AVG TL) <sup>2.86</sup>	<i>Pungitus pungitus</i>	Leopold et al. 2001
<b>Zoarcidae</b>	eelpout	<i>Zoarcetes viviparus</i>	OW: otolith width (mm)	Length (cm) = - 5.54+19.29*(OW)	<i>Zoarcetes viviparus</i>	Leopold et al. 2001
			OL: otolith length (mm)	Length (cm) = - 1.98+9.24*(OL)	<i>Zoarcetes viviparus</i>	Leopold et al. 2001
			TL: total length (cm)	Mass (g) = (0.16*TL) <sup>3.34</sup>	<i>Zoarcetes viviparus</i>	Leopold et al. 2001

Group	Species name	Scientific name	Object	Formula	Basic formula: species	Source
Teleostei	teleost unidentified	Teleostei sp.	TL: total length (mm) M: mass (g)	TL = median sample of all fish M = median sample of all fish		

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**Appendix 2:** Mean abundances of prey items per regurgitate with  $SD \pm$  and number of samples containing the specified prey item. Sample size:  $n=77$  regurgitates (Föhr 2014:  $n=17$ ; Föhr 2016:  $n=11$ ; Oland 2014:  $n=22$ ; Oland 2016:  $n=7$ ; Trischen 2016:  $n=20$ ).

Group	Species name	Scientific name	Föhr 2014	Föhr 2016	Oland 2014	Oland 2016	Trischen 2016	Total
Nereididae	ragworm	<i>Hediste diversicolor</i>	0.8 $\pm 0.5$ n=12	0.9 $\pm 0.7$ n=8	0.7 $\pm 0.9$ n=12	0.6 $\pm 0.5$ n=4	1.5 $\pm 1.5$ n=17	0.9 $\pm 1.0$ n=53
Caridea	common brown shrimp	<i>Crangon crangon</i>	2.9 $\pm 8.4$ n=5	10.8 $\pm 10.7$ n=6	3.4 $\pm 3.6$ n=14	14.6 $\pm 10.3$ n=6	27.1 $\pm 16.4$ n=19	11.5 $\pm 14.6$ n=50
Caridea	rockpool prawn	<i>Macrobrachium sintangense</i>	0.8 $\pm 1.3$ n=7	9.4 $\pm 14.5$ n=5	5.0 $\pm 14.5$ n=9	0.0 $\pm 0.0$ n=0	0.5 $\pm 1.3$ n=5	3.1 $\pm 10.1$ n=26
Caridea	shrimp unidentified	Caridea sp.	0.4 $\pm 0.8$ n=3	0.0 $\pm 0.0$ n=0	0.2 $\pm 0.7$ n=2	0.3 $\pm 0.7$ n=1	0.6 $\pm 2.6$ n=1	0.3 $\pm 1.5$ n=7
Clupeidae	herring	<i>Clupea harengus</i>	0.0 $\pm 0.0$ n=0	0.1 $\pm 0.3$ n=1	0.0 $\pm 0.0$ n=0	1.0 $\pm 1.7$ n=3	0.6 $\pm 1.3$ n=4	0.3 $\pm 0.9$ n=8
Clupeidae	sprat	<i>Sprattus sprattus</i>	0.0 $\pm 0.0$ n=0	0.0 $\pm 0.0$ n=0	0.0 $\pm 0.0$ n=0	0.3 $\pm 0.7$ n=1	0.1 $\pm 0.2$ n=1	0.0 $\pm 0.3$ n=2
Clupeidae	herring unidentified	<i>C. harengus/Sprattus sprattus/Clupeidae sp.</i>	3.0 $\pm 4.4$ n=7	0.5 $\pm 0.8$ n=4	0.0 $\pm 0.2$ n=1	1.3 $\pm 0.9$ n=5	3.3 $\pm 4.1$ n=13	1.7 $\pm 3.3$ n=30
Cyprinidae	roach	<i>Rutilus rutilus</i>	0.1 $\pm 0.3$ n=2	0.0 $\pm 0.0$ n=0	0.2 $\pm 0.5$ n=4	0.0 $\pm 0.0$ n=0	0.9 $\pm 1.4$ n=7	0.3 $\pm 0.8$ n=13
Cyprinidae	carp	Cyprinidae sp.	0.1	0.1	0.1	0.0	0.1	0.1

Group	Species name	Scientific name	Föhr 2014	Föhr 2016	Oland 2014	Oland 2016	Trischen 2016	Total
			± 0.5 n=1	± 0.3 n=1	± 0.3 n=3	± 0.0 n=0	± 0.4 n=1	± 0.4 n=6
Osmeridae	smelt	<i>Osmerus eperlanus</i>	1.5 ± 2.6 n=7	1.0 ± 2.3 n=3	5.2 ± 3.3 n=20	2.7 ± 2.1 n=6	2.9 ± 3.2 n=14	2.9 ± 3.3 n=50
Gadidae	whiting	<i>Merlangius merlangus</i>	0.0 ± 0.0 n=0	0.2 ± 0.4 n=2	0.0 ± 0.0 n=0	0.3 ± 0.5 n=2	0.0 ± 0.0 n=0	0.1 ± 0.2 n=4
Gobiidae	sand goby	<i>Pomatoschistus minutus</i>	2.0 ± 3.7 n=6	1.4 ± 1.1 n=8	0.6 ± 1.4 n=5	0.7 ± 1.4 n=2	1.4 ± 1.7 n=12	1.2 ± 2.2 n=33
Gobiidae	common goby	<i>Pomatoschistus microps</i>	0.0 ± 0.0 n=0	0.1 ± 0.3 n=1	0.0 ± 0.2 n=1	0.1 ± 0.3 n=1	0.0 ± 0.0 n=0	0.0 ± 0.2 n=3
Gobiidae	goby unidentified	<i>P. minutus/P. microps/P. pictus/sp.</i>	2.9 ± 5.5 n=10	10.3 ± 10.2 n=10	2.0 ± 4.2 n=9	1.9 ± 2.5 n=3	7.8 ± 9.0 n=19	4.9 ± 7.7 n=51
Syngnathidae	Pipefish unidentified	Syngnathidae sp.	0.0 ± 0.0 n=0	0.0 ± 0.0 n=0	0.0 ± 0.2 n=1	0.1 ± 0.3 n=1	0.0 ± 0.0 n=0	0.0 ± 0.2 n=2
Pleuronectiformes	dab	<i>Limanda limanda</i>	0.1 ± 0.2 n=1	22.7 ± 26.5 n=7	0.0 ± 0.0 n=0	1.7 ± 3.8 n=2	3.1 ± 6.2 n=7	4.2 ± 13.1 n=17
Pleuronectiformes	plaice	<i>Pleuronectes platessa</i>	0.1 ± 0.2 n=1	0.0 ± 0.0 n=0	0.0 ± 0.0 n=0	0.0 ± 0.0 n=0	0.0 ± 0.0 n=0	0.0 ± 0.1 n=1
Pleuronectiformes	flounder	<i>Platichthys flesus</i>	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.1

Group	Species name	Scientific name	Föhr 2014	Föhr 2016	Oland 2014	Oland 2016	Trischen 2016	Total
			n=1	n=0	n=0	n=0	n=0	n=1
Pleuronectiformes	flatfish unidentified	<i>L. limanda</i> / <i>P. flesus</i> / <i>P. platessa</i> /Pleuronectiformes sp.	0.4 ± 1.2	29.5 ± 32.4	0.1 ± 0.3	1.0 ± 2.4	23.1 ± 20.5	10.4 ± 20.3
			n=2	n=8	n=2	n=1	n=19	n=32
Ammodytidae	small sandeel	<i>Ammodytes tobianus</i>	0.1 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.2
			n=2	n=0	n=0	n=0	n=0	n=2
Ammodytidae	sandeel unidentified	Ammodytidae sp.	0.1 ± 0.3	0.6 ± 0.9	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.4
			n=2	n=4	n=0	n=0	n=0	n=6
Percidae	ruffe	<i>Gymnocephalus cernua</i>	0.1 ± 0.2	0.1 ± 0.3	0.6 ± 1.3	0.6 ± 1.4	0.0 ± 0.0	0.2 ± 0.9
			n=1	n=1	n=6	n=1	n=0	n=9
Percidae	perch	<i>Perca fluviatilis</i>	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 1.4	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.8
			n=0	n=0	n=6	n=0	n=0	n=6
Percidae	perch unidentified	Percidae sp.	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.1
			n=0	n=0	n=1	n=0	n=0	n=1
Gasterosteidae	three-spined stickleback	<i>Gasterosteus aculeatus</i>	31.2 ± 31.7	4.9 ± 4.8	5.6 ± 5.0	2.6 ± 4.7	4.4 ± 4.7	10.6 ± 19.0
			n=15	n=9	n=18	n=4	n=18	n=64
Gasterosteidae	stickleback unidentified	<i>Spinachia spinachia</i> /Gasterosteidae sp.	0.0 ± 0.0	0.1 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 1.4	0.2 ± 0.8
			n=0	n=1	n=0	n=0	n=4	n=5
Gasterosteidae	nine-spined stickleback	<i>Pungitius pungitus</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.1
			n=0	n=0	n=0	n=0	n=1	n=1

Group	Species name	Scientific name	Föhr 2014	Föhr 2016	Oland 2014	Oland 2016	Trischen 2016	Total
Zoarcidae	eelpout	<i>Zoarcetes viviparus</i>	0.3 ± 0.7 n=3	0.5 ± 0.5 n=5	0.0 ± 0.0 n=0	0.3 ± 0.7 n=1	0.0 ± 0.0 n=0	0.2 ± 0.5 n=9
Teleostei	teleost unidentified	Teleostei sp.	0.0 ± 0.0 n=0	1.7 ± 2.5 n=5	0.0 ± 0.0 n=0	0.6 ± 0.7 n=3	5.0 ± 7.9 n=9	1.6 ± 4.6 n=17

**Appendix 3:** Mean masses of prey items per regurgitate in gram with  $SD \pm$  and number of samples containing the specified prey item. Sample size:  $n=77$  regurgitates Föhr 2014:  $n=17$ ; Föhr 2016:  $n=11$ ; Oland 2014:  $n=22$ ; Oland 2016:  $n=7$ ; Trischen 2016:  $n=20$ .

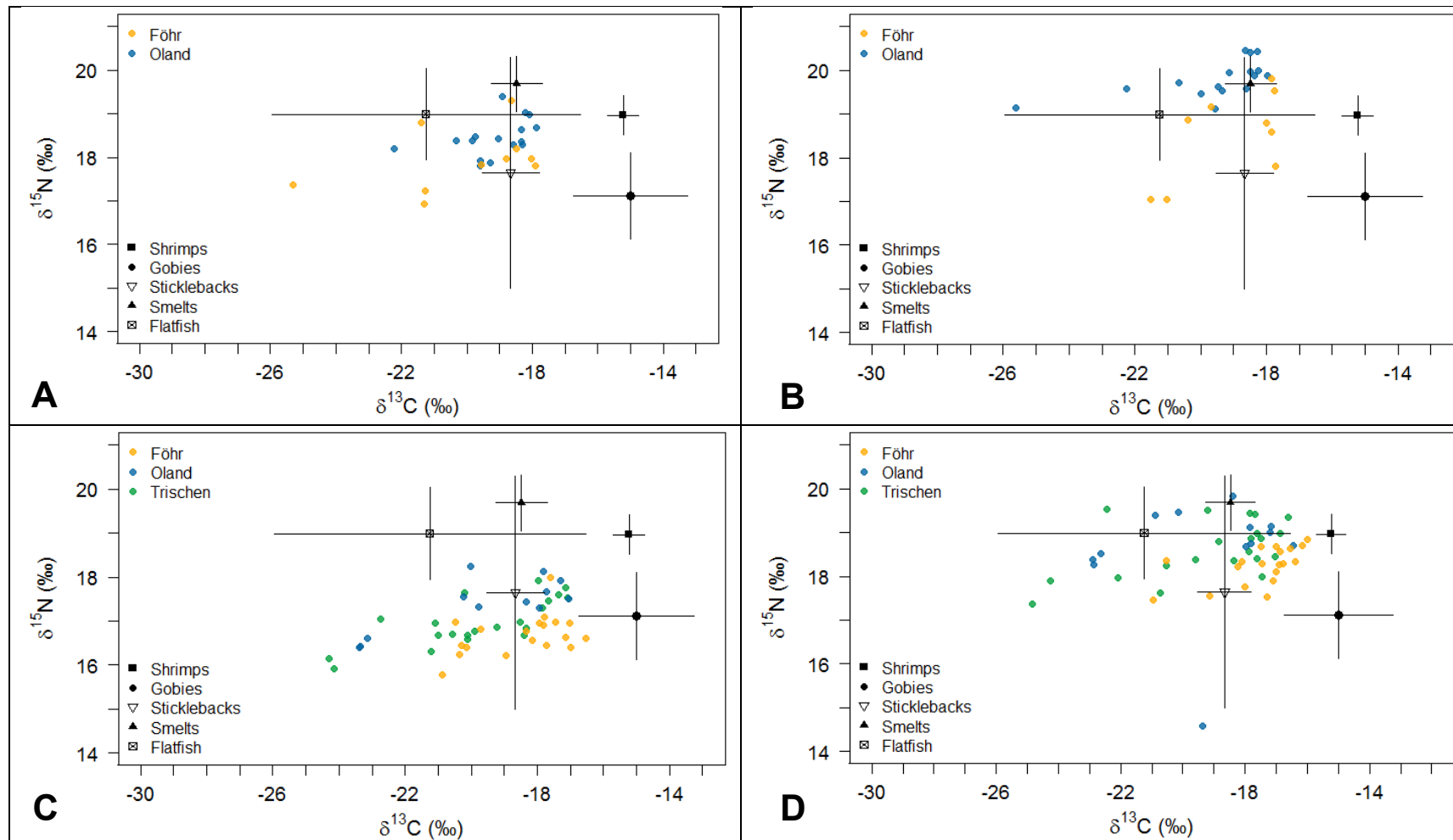
Group	Species name	Scientific name	Föhr 2014	Föhr 2016	Oland 2014	Oland 2016	Trischen 2016	Total
<b>Nereididae</b>	ragworm	<i>Hediste diversicolor</i>	0.03 $\pm 0.02$ n=12	0.04 $\pm 0.03$ n=8	0.01 $\pm 0.01$ n=12	0.01 $\pm 0.01$ n=4	0.06 $\pm 0.06$ n=17	0.03 $\pm 0.04$ n=53
<b>Caridea</b>	common brown shrimp	<i>Crangon crangon</i>	0.80 $\pm 1.67$ n=5	5.26 $\pm 5.37$ n=6	1.57 $\pm 1.90$ n=14	7.45 $\pm 5.54$ n=6	10.03 $\pm 5.44$ n=19	4.66 $\pm 5.52$ n=50
<b>Caridea</b>	rockpool prawn	<i>Macrobrachium sintangense</i>	0.30 $\pm 0.50$ n=7	3.62 $\pm 5.62$ n=5	1.86 $\pm 4.76$ n=9	0.00 $\pm 0.00$ n=0	0.30 $\pm 0.87$ n=5	1.19 $\pm 3.57$ n=26
<b>Caridea</b>	shrimp unidentified	Caridea sp.	0.14 $\pm 0.30$ n=3	0.00 $\pm 0.00$ n=0	0.07 $\pm 0.30$ n=2	0.14 $\pm 0.33$ n=1	0.20 $\pm 0.87$ n=1	0.12 $\pm 0.50$ n=7
<b>Clupeidae</b>	herring	<i>Clupea harengus</i>	0.00 $\pm 0.0$ n=0	0.07 $\pm 0.23$ n=1	0.00 $\pm 0.00$ n=0	0.71 $\pm 1.07$ n=3	0.55 $\pm 1.17$ n=4	0.22 $\pm 0.74$ n=8
<b>Clupeidae</b>	sprat	<i>Sprattus sprattus</i>	0.00 $\pm 0.00$ n=0	0.00 $\pm 0.00$ n=0	0.00 $\pm 0.00$ n=0	0.28 $\pm 0.68$ n=1	0.27 $\pm 1.16$ n=1	0.09 $\pm 0.64$ n=2
<b>Clupeidae</b>	herring unidentified	<i>C. harengus/Sprattus sprattus/Clupeidae</i> sp.	2.41 $\pm 3.71$ n=7	0.30 $\pm 0.43$ n=4	0.01 $\pm 0.07$ n=1	0.69 $\pm 0.53$ n=5	1.81 $\pm 1.98$ n=13	1.11 $\pm 2.25$ n=30
<b>Cyprinidae</b>	roach	<i>Rutilus rutilus</i>	1.84 $\pm 5.04$ n=2	0.00 $\pm 0.00$ n=0	0.67 $\pm 1.62$ n=4	0.00 $\pm 0.00$ n=0	4.32 $\pm 9.25$ n=7	1.72 $\pm 5.60$ n=13
<b>Cyprinidae</b>	carp	Cyprinidae sp.	1.84	1.42	0.28	0.00	0.35	0.78

Group	Species name	Scientific name	Föhr 2014	Föhr 2016	Oland 2014	Oland 2016	Trischen 2016	Total
			± 7.37 n=1	± 4.50 n=1	± 0.71 n=3	± 0.00 n=0	± 1.51 n=1	± 4.01 n=6
<b>Osmeridae</b>	smelt	<i>Osmerus eperlanus</i>	15.57 ±25.72 n=7	3.51 ± 8.82 n=3	27.88 ± 23.98 n=20	12.66 ± 10.36 n=6	28.15 ± 35.37 n=14	20.37 ± 27.19 n=50
<b>Gadidae</b>	whiting	<i>Merlangius merlangus</i>	0.00 ± 0.00 n=0	0.27 ± 0.56 n=2	0.00 ± 0.00 n=0	0.33 ± 0.53 n=2	0.00 ± 0.00 n=0	0.07 ± 0.29 n=4
<b>Gobiidae</b>	sand goby	<i>Pomatoschistus minutus</i>	5.40 ±10.16 n=6	2.55 ± 2.26 n=8	0.71 ± 1.59 n=5	1.18 ± 2.39 n=2	3.14 ± 4.12 n=12	2.68 ± 5.67 n=33
<b>Gobiidae</b>	common goby	<i>Pomatoschistus microps</i>	0.00 ± 0.00 n=0	0.10 ± 0.31 n=1	0.05 ± 0.23 n=1	0.11 ± 0.27 n=1	0.00 ± 0.00 n=0	0.04 ± 0.19 n=3
<b>Gobiidae</b>	goby unidentified	<i>P. minutus/P. microps/P. pictus/sp.</i>	5.49 ±10.61 n=10	11.61 ±13.18 n=10	1.20 ± 2.48 n=9	1.99 ± 2.94 n=3	9.17 ± 11.09 n=19	5.78 ± 9.97 n=51
<b>Syngnathidae</b>	Pipefish unidentified	Syngnathidae sp.	0.00 ± 0.00 n=0	0.00 ± 0.00 n=0	0.05 ± 0.21 n=1	0.07 ± 0.18 n=1	0.00 ± 0.00 n=0	0.02 ± 0.13 n=2
<b>Pleuronectiformes</b>	dab	<i>Limanda limanda</i>	0.08 ± 0.33 n=1	6.36 ± 6.95 n=7	0.00 ± 0.00 n=0	0.33 ± 0.71 n=2	1.07 ± 2.20 n=7	1.23 ± 3.58 n=17
<b>Pleuronectiformes</b>	plaice	<i>Pleuronectes platessa</i>	0.39 ± 1.57 n=1	0.00 ± 0.00 n=0	0.00 ± 0.00 n=0	0.00 ± 0.00 n=0	0.00 ± 0.00 n=0	0.09 ± 0.75 n=1
<b>Pleuronectiformes</b>	flounder	<i>Platichthys flesus</i>	0.27 ± 1.06	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.51

Group	Species name	Scientific name	Föhr 2014	Föhr 2016	Oland 2014	Oland 2016	Trischen 2016	Total
			n=1	n=0	n=0	n=0	n=0	n=1
<b>Pleuronectiformes</b>	flatfish	<i>L. limanda/P. flesus/P.</i>	0.38	5.67	0.01	0.09	4.05	1.96
	unidentified	<i>platessa/Pleuronectiformes sp.</i>	± 1.47	± 5.44	± 0.04	± 0.21	± 4.30	± 3.82
			n=2	n=8	n=2	n=1	n=19	n=32
<b>Ammodytidae</b>	small sandeel	<i>Ammodytes tobianus</i>	0.65	0.00	0.00	0.00	0.00	0.14
			± 1.78	± 0.00	± 0.00	± 0.00	± 0.00	± 0.88
			n=2	n=0	n=0	n=0	n=0	n=2
<b>Ammodytidae</b>	sandeel unidentified	Ammodytidae sp.	0.44	1.03	0.00	0.00	0.00	0.24
			± 1.37	± 1.54	± 0.00	± 0.00	± 0.00	± 0.94
			n=2	n=4	n=0	n=0	n=0	n=6
<b>Percidae</b>	ruffe	<i>Gymnocephalus cernua</i>	0.69	0.24	4.42	0.03	0.00	1.45
			± 2.76	± 0.75	± 9.97	± 0.08	± 0.00	± 5.81
			n=1	n=1	n=6	n=1	n=0	n=9
<b>Percidae</b>	perch	<i>Perca fluviatilis</i>	0.00	0.00	6.91	0.00	0.00	1.97
			± 0.00	± 0.00	± 12.85	± 0.00	± 0.00	± 7.54
			n=0	n=0	n=6	n=0	n=0	n=6
<b>Percidae</b>	perch unidentified	Percidae sp.	0.00	0.00	0.34	0.00	0.00	0.10
			± 0.00	± 0.00	± 1.55	± 0.00	± 0.00	± 0.84
			n=0	n=0	n=1	n=0	n=0	n=1
<b>Gasterosteidae</b>	three-spined stickleback	<i>Gasterosteus aculeatus</i>	35.87	8.45	10.71	3.95	6.96	14.35
			±26.43	±10.28	± 10.82	± 7.22	± 5.30	± 18.70
			n=15	n=9	n=18	n=4	n=18	n=64
<b>Gasterosteidae</b>	stickleback unidentified	<i>Spinachia spinachia/Gasterosteidae sp.</i>	0.00	0.02	0.00	0.00	0.22	0.06
			± 0.00	± 0.05	± 0.00	± 0.00	± 0.62	± 0.33
			n=0	n=1	n=0	n=0	n=4	n=5
<b>Gasterosteidae</b>	nine-spined stickleback	<i>Pungitus pungitus</i>	0.00	0.00	0.00	0.00	0.02	0.00
			± 0.00	± 0.00	± 0.00	± 0.00	± 0.08	± 0.04
			n=0	n=0	n=0	n=0	n=1	n=1

Group	Species name	Scientific name	Föhr 2014	Föhr 2016	Oland 2014	Oland 2016	Trischen 2016	Total
Zoarcidae	eelpout	<i>Zoarcetes viviparus</i>	6.13	4.79	0.00	4.47	0.00	2.44
			±15.61	± 6.79	± 0.00	± 10.94	± 0.00	± 8.87
			n=3	n=5	n=0	n=1	n=0	n=9
Teleostei	teleost unidentified	Teleostei sp.	0.00	0.92	0.00	0.57	2.93	0.94
			± 0.00	± 1.47	± 0.00	± 0.89	± 5.09	± 2.93
			n=0	n=5	n=0	n=3	n=9	n=17





**Appendix 4:** Isoplots of blood samples from spoonbill chicks and prey source. A: Red blood cells 2014,  $n = 26$ ; B: Serum 2014,  $n = 25$ ; C: Red blood cells 2016,  $n = 52$ ; D: Serum 2016,  $n = 53$ .





## CHAPTER IV

### Suitability of herring gulls (*Larus argentatus*) as indicators for detecting intertidal bivalve beds in the Wadden Sea

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**CHAPTER IV: SUITABILITY OF HERRING GULLS (*LARUS ARGENTATUS*) AS INDICATORS FOR DETECTING INTERTIDAL BIVALVE BEDS IN THE WADDEN SEA**

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**Abstract**

Germany is an EU member state and is thus obliged to monitor and protect its marine and coastal areas in the context of international treaties (e.g. EU Marine Strategy Framework Directive, EU Natura2000 directives, Trilateral Monitoring and Assessment Programme, OSPAR) to achieve the good environmental status (GES). Suitable indicators thus need to be developed to assess the status of relevant ecosystems. Intertidal bivalve beds belong to the most productive habitats in the shallow coastal waters of the Wadden Sea but are highly dynamic and difficult to monitor. Extensive benthos and sediment sampling are required to study their development and distribution. We therefore evaluated the suitability of herring gulls (*Larus argentatus*) as a bioindicator species for monitoring these habitats. As flexible and opportunistic top-predators, herring gulls prefer to forage on intertidal flats and feed on bivalves (*Cerastoderma edule*, *Mytilus edulis*, *Ensis leei*) and crustaceans, with intertidal habitats near the breeding colony preferred during the incubation period. We used state of the art tracking devices to analyse habitat selection by herring gulls, and assessed how this was driven by biotic and abiotic factors. We then designed a habitat model to predict the occurrence of intertidal bivalve beds for directed monitoring, based on GPS logger data from herring gulls and hydrodynamic data. Both methods showed high correlations of herring gull foraging patterns with bivalve biomass and inundation time, depending on the distance from the breeding colony. The movement patterns of herring gulls clearly mirrored intertidal bivalve distributions. These results showed that combining GPS-logger data for top-predators, such as birds, with environmental data has great potential for monitoring and assessing the GES. We propose that herring gulls may be used as an indicator to locate bivalve beds in the Wadden Sea and to detect changes in the food web.

**Keywords:** Habitat model, *Larus argentatus*, *Ensis leei*, *Cerastoderma edule*, *Mytilus edulis*, Telemetry

## 1 Introduction

The marine environment is impacted by numerous anthropogenic activities, such as fisheries, aquaculture, shipping traffic, the construction of offshore wind farms, and coastal infrastructures (Halpern et al., 2015; Emeis et al., 2015; Mendel et al., 2018). Knowledge of the environmental status of marine habitats and their ecosystem components is therefore essential for marine spatial planning (Reiss et al., 2011; Goyert et al., 2016; Yates et al., 2018). However, information on the distribution and ecological functioning of habitats in marine ecosystems is still lacking (Thaxter et al., 2012; Reiss et al., 2015). National and international treaties oblige Germany to fill these gaps and to consider conservation aims in relation to marine spaces and resource planning (Emeis et al., 2015; Kukkala et al., 2016).

The Wadden Sea refers to the south-eastern coastal part of the heavily exploited North Sea, adjoining a densely inhabited area of the mainland (Halpern et al., 2008). It represents an economically and ecologically important region comprising a mosaic of different habitats, constituting a complex, highly dynamic, and productive ecosystem (Asmus and Asmus, 1985; Reise et al., 2010; van Roomen et al., 2012; Blew et al., 2016). Intertidal bivalve beds have high biodiversity and complex food web structures, and thus provide important habitats and feeding grounds for various species (Jensen, 1992; Piersma et al., 1993; van der Heide et al., 2014; Reise and Buschbaum, 2017). Only a few bivalve species compose extended intertidal bivalve beds in the Wadden Sea. Blue mussels (*Mytilus edulis*) and Pacific oysters (*Magallana gigas*) constitute mixed epibenthic reefs, which are highly productive and provide habitat and shelter from predation to a rich benthic fauna (Büttger et al., 2008; Reise et al., 2017). Cockle beds (*Cerastoderma edule*) are very diverse and represent important foraging habitats for fish and birds, due to their high prey density (Horn et al., 2017). The invaded American razor clam (*Ensis leei*) has been increasingly used as a prey source by various species, but there is a lack of information on its distribution and influence in the Wadden Sea (Horn et al., 2017; Schwemmer et al., 2019a).

Regular monitoring of bivalve beds is crucial for assessing the ecological status of the Wadden Sea ecosystem. Epibenthic bivalve beds consisting of blue mussels and Pacific oysters are regularly monitored by aerial images and sampling stations in the German federal state of Schleswig-Holstein (Millat et al., 2012; Nehls et al., 2011; IfAÖ, 2018). However, the application of aerial images is limited to detecting species living on the surface in the intertidal area. Endobenthic bivalve species (e.g., common cockles, American razor clam) cannot be monitored with this methodology, although their distribution and status are similarly relevant.

In general, habitat status is usually monitored by abiotic factors such as temperature or salinity, as well as by indicator species, mostly top predators (de Wolf, 1983). For example, various bird species are currently used as indicators to assess the ecological status of the marine system by recording changes

in parameters such as population dynamics or behaviour (Temple and Wiens, 1989; Furness and Greenwood, 1993; van Franeker et al., 2011; Courtens et al., 2017). In addition, the development of miniaturized tracking devices now enables tracking of individual birds (Thaxter et al., 2015; Garthe et al., 2017; Schwemmer et al., 2017), allowing direct conclusions to be drawn from the distribution and status of the foraging habitats of the tagged birds.

In the current study, we investigated the use of herring gulls (*Larus argentatus*) as indicators of the distribution of bivalve beds in the intertidal area in the Wadden Sea. During the breeding season herring gulls prefer to forage in the intertidal zone and feed mainly on crustaceans and bivalves (Dernedde, 1993; Kubetzki and Garthe, 2003; Camphuysen and Gronert, 2012; Camphuysen, 2013; van Donk et al., 2017). Previous studies on diet choice and foraging movements in herring gulls identified common cockles (*C. edule*), blue mussels (*M. edulis*), and the invaded American razor clam (*E. leei*) as the main prey sources in the German Wadden Sea, with herring gulls preferring to use intertidal bivalve beds close to their breeding colony during the incubation period (Enners et al., 2018). Furthermore, based on the approach of Libralato et al. (2006), herring gulls have been identified as keystone organisms in the Wadden Sea food web, due to their various direct and indirect interactions in the food web and their important role as top predators (Horn et al., 2019).

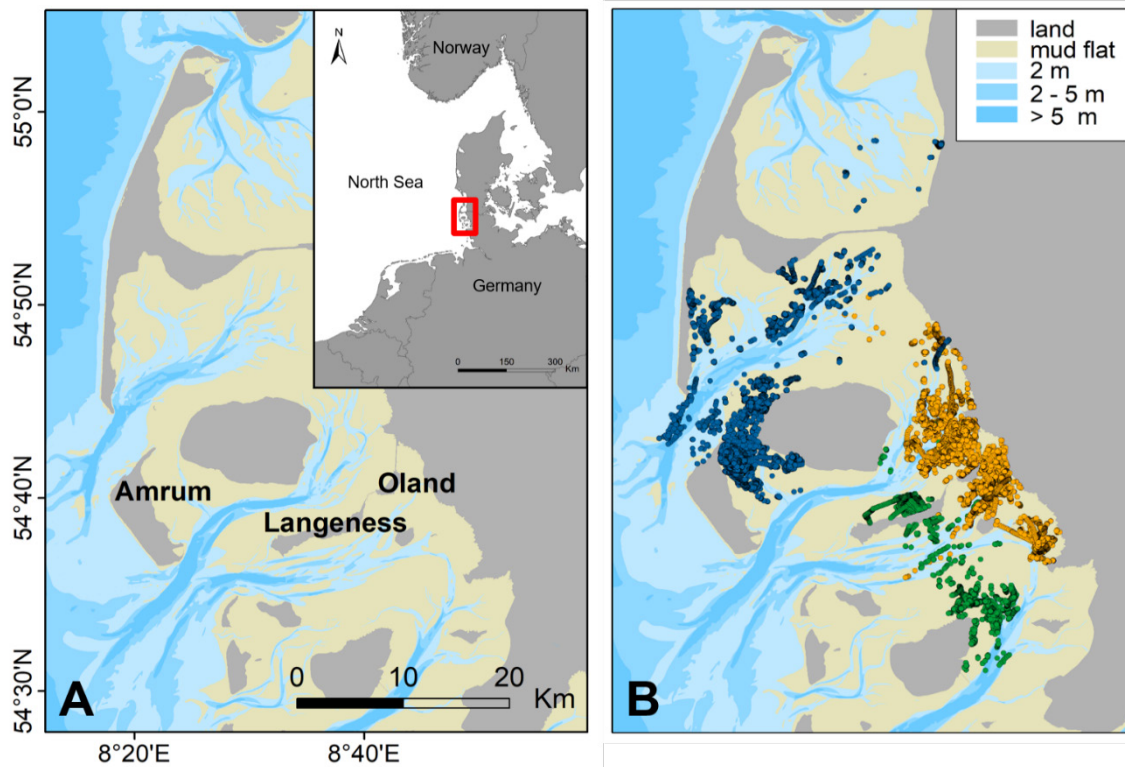
In this study, we tested the hypothesis that breeding herring gulls might act as bioindicators for detecting intertidal bivalve beds, based on the assumption that the gulls will select intertidal flats with high bivalve densities as foraging habitats. We validated this by applying an integrated step selection model (iSSM), specifically designed to analyse animal tracks, to the herring gull GPS-tracking data (Avgar et al., 2015; Mercker et al., 2021). This statistical approach enabled us to analyse the foraging behaviour at an individual level and to identify the most important biotic and abiotic factors influencing the birds' foraging strategy (for more information on the used variables see 2.3). However, positive selection for bivalves does not necessarily mean that all areas with high bivalve densities near the colony are exploited and thus indicated by herring gulls. Given that this would be a precondition of using tracking data as an appropriate proxy of bivalve distribution, we developed and applied a universal spatial model to predict the occurrence of intertidal bivalve beds based on herring gull foraging patterns and hydrodynamic data.

## **2 Materials and methods**

### **2.1 Study area**

The study was conducted in the Wadden Sea area of Schleswig-Holstein, Germany, from 2009–2016 (Figure 1). This area is characterised by an arrangement of several barrier islands in front of the

mainland coast, surrounded by intertidal flats, creeks, and tidal channels. A variety of birds use the intertidal bivalve beds, sandflats, and little creeks as important foraging hotspots, and use the islands as breeding and resting sites. We caught herring gulls on the islands of Oland, Langeness, and Amrum (Figure 1). Oland is located closest to the mainland (2.5 km), followed by Langeness (9 km), and Amrum (23 km) (Figure 1).



**Figure 1:** A: Study area in the Wadden Sea of Schleswig-Holstein, Germany. Breeding herring gulls were caught on the islands Oland, Langeness, and Amrum. Inserted map: location of the study area within northern Europe. B: Foraging GPS-fixes for tagged herring gulls on intertidal flats (orange = Oland, green = Langeness, blue = Amrum).

## 2.2 Study design

We investigated different biotic and abiotic factors (including local bivalve biomass) influencing habitat selection by herring gulls by applying a spatio-temporal integrated step selection model (iSSM) to the tracking data. This model is specialised to analyse habitat selection based on tracking data (Avgar et al., 2015) and is currently the method with the highest statistical power for such analyses (Mercker et al., 2021). Motivated by the iSSM results, we also developed an appropriate pure spatial generalised additive model (GAM) to predict the occurrence of intertidal bivalve beds based on logger data from herring gulls and hydrodynamic data. The variables used for iSSM and GAM analyses are detailed described in Section 2.3.



We thus investigated the correlation between herring gull habitat use and local bivalve distribution by two distinct methods, based on substantially different data structures, to increase the reliability of the results. All statistical analyses were performed using the open-source software R 3.4.2 (R Development Core Team, 2017). Visualisation was performed using ArcGIS 10.1 (ESRI, 2011).

## **2.3 Database**

We used herring gull tracking data, local bivalve biomass, and a set of variables that describes the geography (distances, bathymetry) as well as variables that describe or influence the sea floor (bed shear stress, sediment, inundation time) for iSSM and GAM analyses. Further descriptions are detailed below.

### **2.3.1 Tracking data of herring gulls**

Foraging patterns were analysed based on GPS logger data from herring gulls. Breeding individuals were caught on their nests using walk-in traps in the years 2012–2015 (Oland,  $n = 27$ ; Langeness,  $n = 9$ ; Amrum,  $n = 27$ ). Two different types of logging devices were applied (CatLog-S; Catnip Technologies, Hong Kong SAR, China,  $n = 47$ ; E-obs Bird Solar 28 g loggers; e-obs GmbH, Munich, Germany,  $n = 16$ ), as described previously (Enners et al., 2018). The loggers recorded date, time, geographical position, and velocity, usually every 2 min when optimally charged, and at a maximum of every 30 min at lower battery levels. Large gaps ( $\geq 30$  min;  $n = 3$ ) between consecutive positions were excluded and small gaps ( $< 30$  min) were interpolated linearly (R package `data.table` 1.10.4) to an interval of 2 min.

GPS fixes were classified as flying, roosting, breeding, or feeding behaviour, based on the frequency distribution of the movement speed of the equipped individuals (Shamoun-Baranes et al., 2011; Enners et al., 2018) and their geographic position (Schwemmer et al., 2016; Enners et al., 2018). Only foraging fixes on intertidal flats were included in subsequent analyses (GPS fixes:  $n = 80,164$ ; Figure 1B). For a detailed description of logger data preparation, see Enners et al. (2018).

### **2.3.2 Bivalve biomass**

A total of 536 stations (Table 1) were sampled throughout the intertidal zone in the entire study area during 2009–2016. Bivalve species were identified to species level and measured, and the ash-free dry weight (AFDW in g) was determined as a measure of biomass (Beukema, 1974; Choi et al., 2017). Different sampling corers were used, and we therefore normalised the data to the smallest unit (small corer: sampled area = 86.59 cm<sup>2</sup>; mesh size  $\leq 2$  mm). Three replicates per station were usually taken. We summed the biomass of cockles, blue mussels, and razor clams per station and divided it by the number of replicates to calculate the mean biomass per station.

Because of the opportunistic foraging strategy of herring gulls, we focused on the intertidal bivalve beds in general, rather than on specific bivalve species.

**Table 1:** Number of benthos stations during the study period.

Year	Stations
2009	223
2012	84
2013	76
2014	109
2015	23
2016	21
$\Sigma$	536

### 2.3.3 Sediment–mud content

Sediments were sampled at each of the 543 stations and the grain-size fractions were analysed. The samples were dried in the lab for 12 h at 100°C and treated with H<sub>2</sub>O<sub>2</sub> to remove the organic content. The sediment remains were rinsed over a cascade of sieves, dried, and the single grain-size fractions were weighed. For modelling, the proportion of mud content (< 63 µm) was used (Wentworth, 1922).

### 2.3.4 Bed shear stress intensity

Bed shear stress ( $\tau_{95}$ ; i.e. the 95<sup>th</sup> percentile of local bed shear stress exhibited on 1 m<sup>2</sup> seafloor and expressed in N/m<sup>2</sup>) indicated the magnitude of sediment transport. For the study area, published data from high-resolution models were used (Kösters and Winter, 2014; 1 x 1 km resolution in the Wadden Sea and 3 x 3 km in the offshore zone).

### 2.3.5 Distance to the coast

The minimum distances of each GPS fix to the mainland and islands (in metres) were calculated in ArcGIS (version 10.3; Environmental System Research Institute, 2016).

### 2.3.6 Bathymetry

Bathymetry data (in metres) were provided by the Federal Maritime and Hydrographic Agency at a resolution of 50 x 50 m for the entire North Sea and German Wadden Sea (Asprion et al., 2013).

### **2.3.7 Flooding time**

The study area is mainly characterised by the tide. Depending on the location of intertidal areas the time of inundation differs. Based on the General Estuarine Transport Model, the inundation time (in hours) was simulated for the period from May to June 2011 (total 409 hours) and displayed at a resolution of 50 x 50 m (Burchard and Bolding, 2002; Gräwe et al., 2015).

### **2.3.8 Water level**

Water level (in centimetres) measured every minute at stationary positions was obtained by state authorities (Wasserstraßen- und Schifffahrtsverwaltung des Bundes, Bundesanstalt für Gewässerkunde, Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein provided the measurement data). These data were used to analyse spatio-temporal water-level patterns.

## **2.4 iSSM-based habitat analysis**

We applied the iSSMs presented by Avgar et al. (2015), because this approach is specialised for the analysis of habitat selection based on tracking data and shows the highest statistical power compared to alternative methods (Mercker et al., 2021).

### **2.4.1 Covariates**

Data on biotic and abiotic covariates were generated from different spatial resolutions (grid and point data). We propagated these values precisely to iSSM-tracking and available point locations by fitting a GAM separately to each covariate data frame using the *gam()*-function of the R-package *mgcv*. We used a 2D-regression spline smooth of longitude-latitude values with a maximal number of knots, which corresponds to a cubic interpolation. Covariate values were subsequently predicted based on the GAM-prediction function straight to the point for each observation or available point.

### **2.4.2 iSSM model**

To account for pseudo-replicated tagging data (i.e. various GPS fixes for the same individual bird), we extended the methods of Avgar et al. (2015) by the approach of Muff et al. (2020) in order to allow for mixed modelling in the context of iSSMs. In particular, we make use of the fact that the likelihood of a Poisson model with stratum-specific intercepts is equivalent to the likelihood of a conditional logistic regression model, integrating a random factor for both, step-id as well as bird-id, the latter accounting for the nested data structure (Muff et al., 2020). Since random slope models did not properly converge, we also used the bird-id as a random intercept. As fixed effects, we used the following formula:

$$\textit{tracking data} \sim \textit{angle\_sin} + \textit{sediment} + \textit{bivalve biomass} + \textit{water level} + \textit{tau95} + \textit{flooding} + \textit{distance nest} + \textit{depth} + \textit{distance coast},$$

where *tracking data* is a binary variable contrasting foraging fixes for breeding herring gulls on intertidal flats with available points, *angle\_sin* reflects directional persistence, *sediment* is the proportion of mud content, *bivalve biomass* is the bivalve biomass of sampling stations, *water level* is the water level, *tau95* is the bed shear stress, *flooding* is the potential inundation time, *distance nest* is the distance of each GPS fix to the nest, *depth* is the water depth, and *distance coast* is the distance of each GPS fix to the mainland and the islands. Temporal and spatial distance to the foregoing tracking point have not been used as additional predictors, because model convergence was distinctly impaired.

Furthermore, we applied a second formula to analyse potential interactions between bivalve biomass and water level, augmenting the fixed effect *bivalve biomass:water level*, which is the linear interaction term of bivalve biomass with water level investigating if attraction strength to high *bivalve biomass* values additionally depends on water level. Regression results were additionally validated comparing estimated regression coefficients to results of the standard iSSM analysis (Avgar et al., 2015) neglecting the nested data structure.

## **2.5 Bivalve prediction model**

Bivalve distribution was predicted based on herring gull logger data densities and environmental variables using a spatial GAM using the function *gam()* in the R-package *mgcv*. The procedure is summarised below.

### **2.5.1 Data preparation and spatial pooling**

The bivalve habitat modelling approach was based on a GAM-regression analysis applied to gridded spatial data. To account for spatially varying sample densities (and thus statistical reliability) with respect to bivalve occurrence, the number of samples per grid cell was evaluated to use them in the context of a weighted GAM. In contrast to the spatio-temporal iSSM, the GAM was purely spatial. The spatio-temporal variable “water level” could therefore not be used and the spatial variable “flooding” (the average flooding time) was included instead. The same was true for the tracking points, which entered the model in a purely spatial manner (number of tracking points per grid cell). Based on the movement behaviour, colony distance was included as predictor and classified as level 1, colony distance < 5 km, or level 2, colony distance > 5 km. All predictors were merged by pooling the covariates within the same regular grid (see below) and calculating the number of tracking points,

mean flooding time, and mean colony distance separately for each grid cell. Finally, only grid cells including bivalve data were used for GAM modelling.

### **2.5.2 Model and grid-size selection**

Bivalve biomass, as the dependent variable, was used as a proxy for bivalve distribution, and was modelled using the above predictors using spatial GAMs with a Gaussian probability distribution. Different probability distributions were compared using AIC analysis (Akaike, 1974), where a Gaussian distribution was always strongly favoured. To obtain and validate the optimal model, predictor selection was performed by comparing various biologically reasonable models applied to different grid sizes (0.2 to 1.5 km) based on the AIC. The five best models were subsequently used to systematically test different grid sizes with respect to their predictive performance using 50 % cross-validation, where predictive performance was quantified by the sum of squares of real vs. predicted bivalve biomass. Cross-validation was performed 25 times. Spatial autocorrelation was included in the calculations using appropriate residual correlation structures.

This selection led to an optimal grid size of 0.5 x 0.5 km in combination with the following final model:

$$\text{Bivalve biomass} = \text{te}(\log(\text{tracking data}+1), \text{flooding}, \text{by}=\text{distance colony level}),$$

where *bivalve biomass* is the bivalve biomass within each grid cell, *te(log(tracking data+1), flooding, by=distance colony level)* are the logarithmised tracking points and flooding time, nonlinearly dependent on the colony distance (distance colony level) per grid cell, respectively. The robustness of the results was indicated by the observation that the first five favoured models all contained the same set of predictors, and only differed by slight changes in linear vs. nonlinear formulations. Although some models showed a slightly better SS value, the m1 model was chosen to demonstrate and discuss its predictive performance based on the better interpretability of the nonlinear terms.

### **2.5.3 Model validation and autocorrelation**

The models were validated based on appropriate residual plots. Possible spatial autocorrelation of model residuals was examined based on semi-variogram- and spatial bubble-plots.

### **2.5.4 Prediction**

The values of the coordinates in the prediction grid were predicted using the *predict()*-function in the R-package *mgcv*. Visualisation was performed based on *ggplot2*.

## **3 Results**

### 3.1 Herring gull habitat selection (iSSM)

The results of the first model, including all investigated covariates, reflected that the habitat selection by foraging herring gulls during the breeding period is driven by a complex interplay among different variables. Herring gulls significantly preferred habitats with high bivalve biomass ( $p < 0.001$ , Table 2) close to their nesting place ( $p < 0.001$ ) for foraging. These areas are characterized by low flooding times ( $p < 0.001$ ), low bed shear stress ( $p < 0.001$ ) and low mud contents ( $p < 0.01$ ), located not directly close to the coast ( $p < 0.001$ ). Water depth as well as water level were no significant predictors. Due to the spatio-temporal data structure of the tracking and water level data, we constructed a second iSSM with the linear interaction term of bivalve biomass with water level. However, in the second model the main effect could not be interpreted in the presence of the interaction term (Field et al., 2012). The interaction term of bivalve biomass with water level contributed significantly to the explanation of herring gull habitat selection (Table 3). These results indicated that herring gulls positively selected areas with high bivalve biomass combined with low water levels.

**Table 2:** Modelling results of iSSM, model 1.

variable	beta	SE	t-value	p-value
cos_ta	-0.437	0.004	-107.216	< 0.001
sediment	-0.018	0.006	-2.976	< 0.01
bivalve biomass	0.059	0.005	11.917	< 0.001
water level	0.002	0.004	0.434	0.6644
tau95	-0.075	0.007	-10.403	< 0.001
flooding	-0.039	0.010	-3.776	< 0.001
distance nest	-0.059	0.007	-8.785	< 0.001
depth	-0.005	0.0098	-0.495	0.6209
distance coast	0.061	0.008	7.997	< 0.001

**Table 3:** Modelling results of iSSM, model 2.

variable	beta	SE	t-value	p-value
cos_ta	-0.436	0.004	-107.127	< 0.001
sediment	-0.016	0.006	-2.636	< 0.00
bivalve biomass	0.041	0.005	7.872	< 0.001
water level	-0.007	0.004	-1.623	0.1045
tau95	-0.083	0.007	-11.447	< 0.001
flooding	-0.030	0.010	-2.857	< 0.01
distance nest	-0.048	0.007	-7.091	< 0.001
depth	-0.006	0.010	-0.597	0.5502
distance coast	0.061	0.008	7.985	< 0.001
Bivalve biomass:water level	-0.058	0.005	-11.414	< 0.001

### 3.2 Predicted bivalve distribution (GAM)

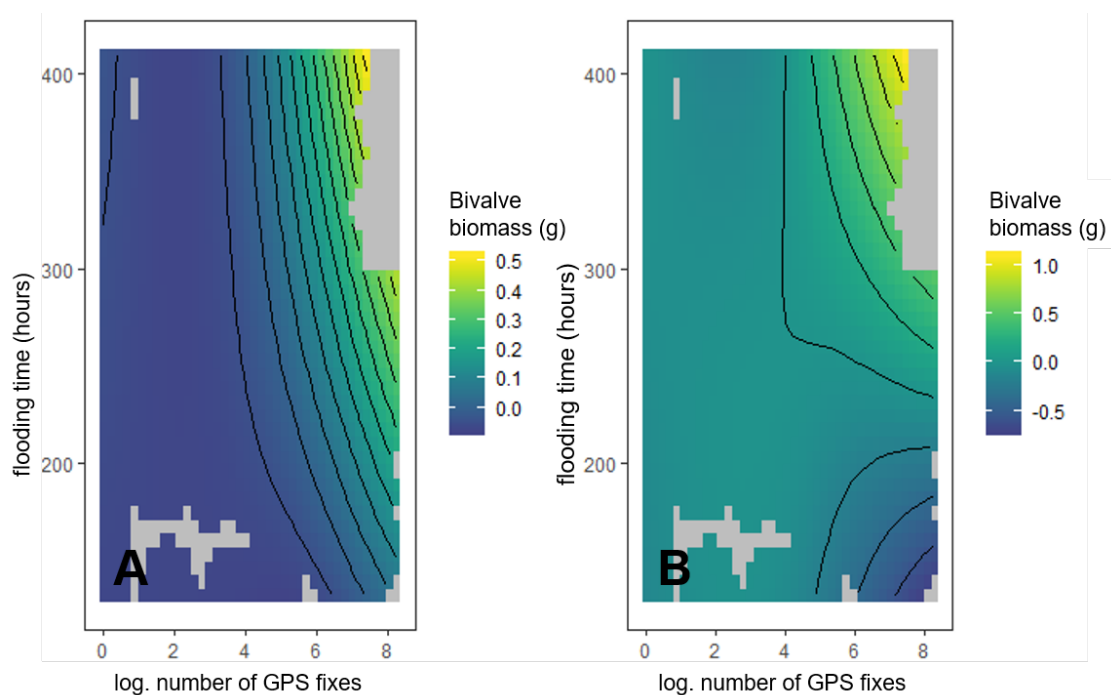
Regression analysis of the optimal prediction model revealed that local bivalve biomass was highly significantly explained by the nonlinear interaction between flooding time and herring gull tracking data densities (similar to the iSSM results), additionally depending on the colony distance (Table 4; Figure 2).

Graphical analyses were based on smooth rather than spatial plots (longitude/latitude) dependent on the colony distance. For colony distances < 5 km (c.f., Figure 2A), bivalve biomass increased continuously with tracking-point density, whereas flooding time only had a minor influence (slight preference for flooding times > 200 h). For colony distances > 5 km (c.f., Figure 2B), GPS fixes accumulated in areas with specific flooding times, suggesting that the influence of flooding was much more pronounced for colony distances > 5 km (c.f., Figure 2B).

**Table 4:** Results of the GAM.

	Estimate	Standard error	t-value	p-value
<b>(Intercept)</b>	0.1203	0.0202	5.949	< 0.001
<b>(Smooth terms)</b>		<b>edf</b>	<b>F</b>	<b>p</b>
<b>te(tracking data, flooding, by=distance colony level (&lt; 5 km))</b>		4.816	4.700	< 0.001
<b>te(tracking data, flooding, by=distance colony level (&gt; 5 km))</b>		4.766	4.282	< 0.001

Edf, estimated degrees of freedom

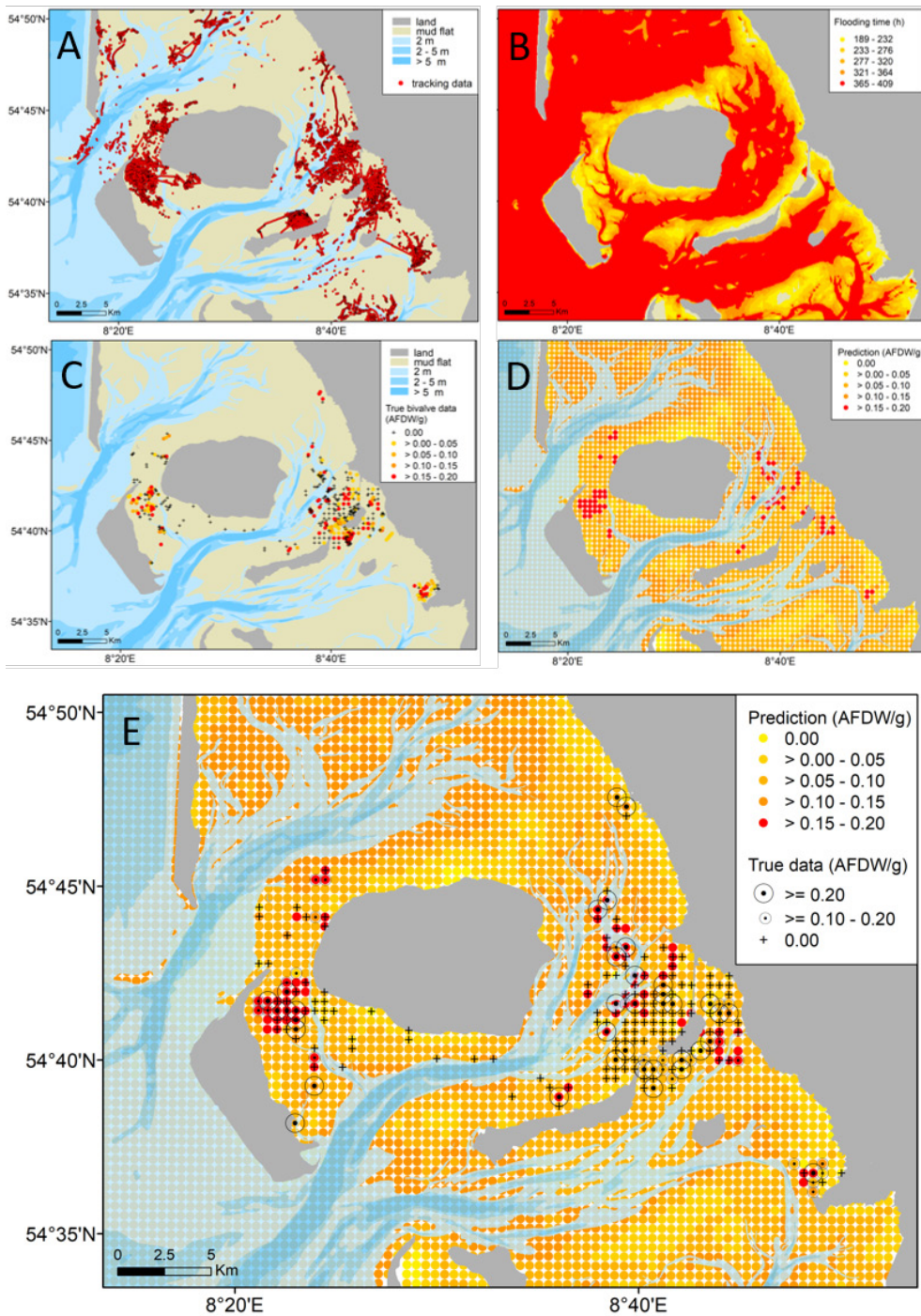


**Figure 2:** Smooth plots for two colony-distance levels. A: Smooth plot for colony distances < 5 km. B: Smooth plot for colony distances > 5 km. Bivalve biomass (g) plotted in graduated colours (blue = low bivalve biomass, yellow = high bivalve biomass). Missing data are represented in grey.

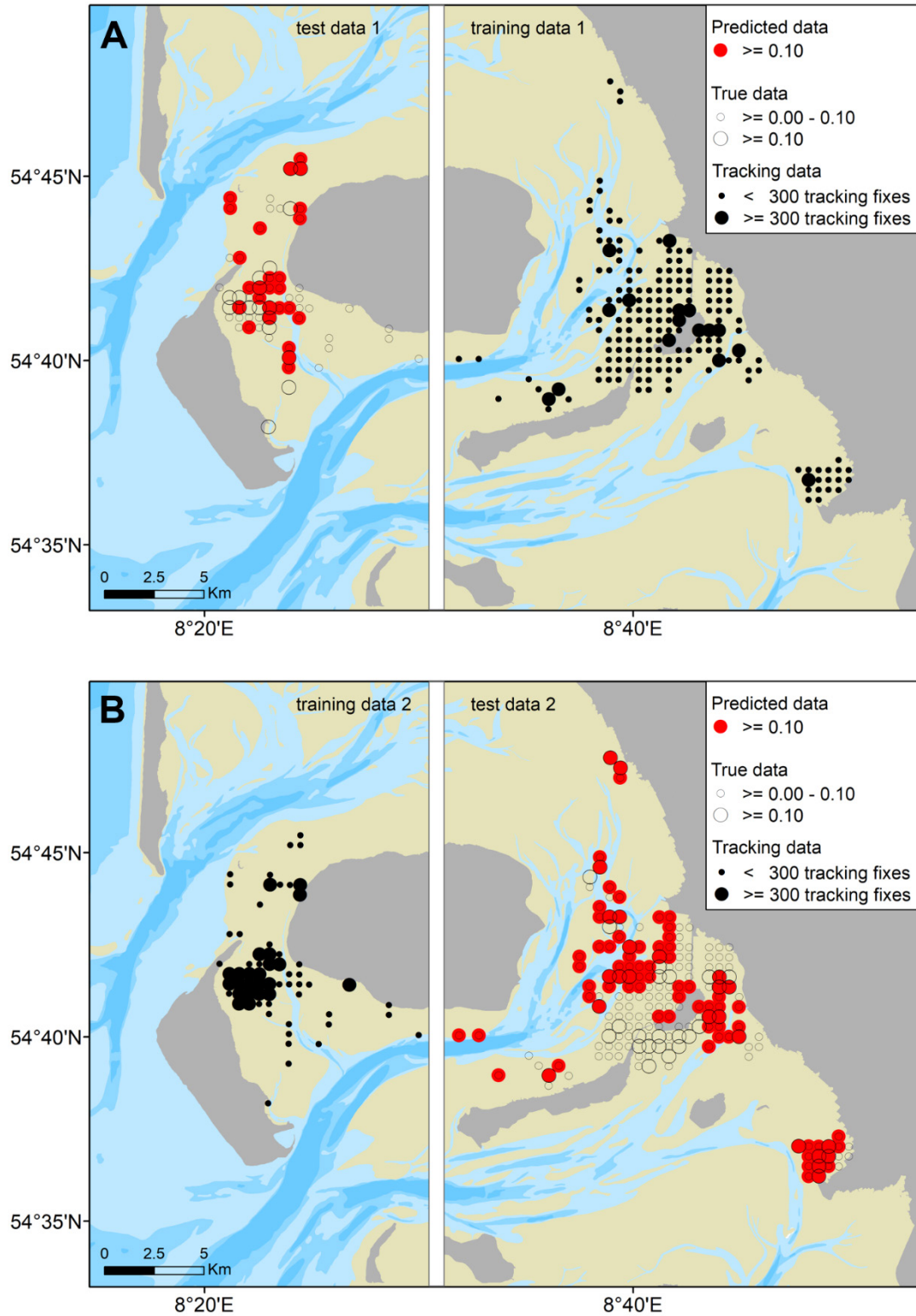
The predictive performance of the model was additionally evaluated by graphical analyses (Figure 3). Depending on the colony distance, the highest bivalve biomass was predicted between the islands of Amrum and Föhr and between Föhr and the mainland (Figure 3). In contrast to the area between Amrum and Föhr, bivalve biomass between Föhr and the mainland was predicted to occur as small hotspots between the tidal channels. Predicted hotspots of high bivalve biomass were confirmed by true bivalve data (Figure 3E).

Predictive performance was quantified by the sum of squares of real vs. predicted bivalve biomass using 50 % cross-validation. Even with only 50 % of the dataset, the prediction model mapped similar bivalve hotspots to the true bivalve biomass (Figure 4).





**Figure 3:** A: Foraging GPS fixes for herring gulls on intertidal flats. B: Simulated flooding time (in hours) at a resolution of 50 x 50 m. C: Mean bivalve biomass per sampling station (grams), plotted in graduated colours (yellow = low bivalve biomass, red = high bivalve biomass, black crosses = cells with no bivalves). D: Predicted bivalve biomass (grams), plotted in graduated colours (yellow = low bivalve biomass, red = high bivalve biomass). The prediction model was fitted to the entire data frame. Due to the Gaussian probability distribution, negative values were also generated in the prediction. These values were set to zero (1.4 %). Different appropriate probability distributions were compared via AIC analysis, where a Gaussian distribution was always strongly favoured. To better visualise predicted bivalve hotspots, 0.2 was chosen as the upper limit. E: Predicted vs. true pooled bivalve biomass: predicted bivalve biomass was plotted in graduated colours (yellow = low bivalve biomass, red = high bivalve biomass). Large black circles indicate high true bivalve biomass ( $\geq 0.2$ ), small black circles indicate low biomass ( $\geq 0.1-0.2$ ), and black crosses indicate cells with no bivalves.



**Figure 4:** Two examples of cross-validation, where the data for the eastern part was used to fit the model (“training data”) to predict the western part (“test data”) (A) and vice versa (B). For this visualisation, only cells with true bivalve data were used. Test data: red circles show high predicted bivalve biomass ( $\geq 0.1$ ), large black circles depict high true bivalve biomass ( $\geq 0.1$ ), and small black circles low true biomass ( $< 0.1$ ). Training data: large filled black circles represent pooled tracking data for  $\geq 300$  foraging fixes, small filled black circles pooled tracking data for  $< 300$  foraging fixes.

## 4 Discussion

### 4.1 Species distribution

In the present study we focused on the habitat selection of breeding herring gulls. While nonbreeding herring gulls are known to follow fishing vessels or use terrestrial sources for foraging, breeding herring gulls prefer to use the intertidal area as foraging habitat (Spaans, 1971; Garthe et al., 1999a; Kubetzki and Garthe, 2003). This foraging strategy imply that herring gulls use predictable and reliable food sources in the intertidal during the breeding season, instead of the patchy distributed and unpredictable marine prey (van Donk et al., 2017; Enners et al., 2018).

The iSSM included tracking data as well as water levels as a spatio-temporal variable, allowing the foraging patterns to be analysed at an individual level. The first iSSM included all investigated covariates, demonstrating that areas with high bivalve biomass were highly significantly preferred by herring gulls. The sea floor and therefore the potential bivalve habitats are influenced by different abiotic factors, such as sediments, bed shear stress, or inundation time. The iSSM results reflected that areas with low bed shear stress and mud contents were significantly used by herring gulls, indicating the habitats of the dominant bivalve species. We conducted a second iSSM with the interaction term of bivalve biomass with water level, due to the significant low inundation times in the first iSSM. The statistical approach confirmed former results indicating that intertidal bivalve beds were increasingly used by herring gulls if they were optimally accessible (depending on the water level).

In general, food availability is a major factor affecting habitat selection by birds (Goss-Custard et al., 1991; Piersma et al., 1993; Yates et al., 1993). Herring gulls were previously shown to prefer to forage on bivalve beds near the breeding colony, but shifted to distant terrestrial habitats as a result of increasing water levels or prey depletion (Enners et al., 2018). Herring gulls are known to feed on common cockles, blue mussels, and razor clams (Spaans, 1971; Dervede, 1993; Garthe et al., 1999a; Enners et al., 2018), which differ in terms of the ecological requirements of their habitat (Schwemmer et al., 2019a; Horn et al., 2017).

As central-place foragers, the foraging strategy of herring gulls is additionally affected by distance to the colony during the breeding season (Steenweg et al., 2011; Isaksson et al., 2016; van Donk et al., 2017). Long flight distances increase the risk of nest predation and therefore compromise breeding success (Morris and Black, 1980; Pierotti and Annett, 1991). The influence of specific prey species on habitat selection by herring gulls can be investigated using the iSSM approach on a finer scale, including only foraging patterns for single breeding colonies.

Overall, species distribution models are essential for spatial planning of the dynamic marine ecosystem (Reiss et al., 2015; Renner et al., 2015; Yates et al., 2018). Especially in terms of conservation

management, distribution models enable the identification of important areas and the analysis of past, present, and future changes in the marine environment (Singer et al., 2016; Cleasby et al., 2020). For future scenarios, habitat-selection models are central to predicting and assessing the relationship between species distribution and climate change (Reiss et al., 2015; Eskildsen et al., 2013).

#### **4.2 Habitat modelling**

The prediction model (GAM) revealed a highly significant correlation between herring gull foraging patterns, flooding times, and local intertidal bivalve biomass. While the spatio-temporal iSSM approach represented the optimal accessibility of intertidal bivalve beds as foraging habitats for herring gulls, the spatial GAM reflected the optimal habitat for intertidal bivalves. Herring gull foraging patterns, in combination with flooding times, indicated areas of local intertidal bivalve distribution in the coastal region.

The GAM predicted higher bivalve biomass with increasing number of logger fixes of herring gulls at locations close to the breeding colony (colony distances < 5 km). Geographically, high bivalve biomass was predicted close to the breeding colony on Amrum, where benthos sampling revealed a large cockle bed that was only inundated for short periods. At longer distances (> 5 km) from the breeding colony, the model predicted high bivalve biomass in small patches. These hotspots represented razor clam beds between the island of Föhr and the mainland, which were only exposed for a short time during low tide. Flooding time is an important factor for intertidal bivalve beds, and probably reflects the required ecological niche of intertidal bivalves. Flooding time was more important for colony distances > 5 km compared with shorter distances < 5 km, possibly indicating that only bivalve-rich areas with optimal flooding times were visited if they were further from the breeding colony, to compensate for higher flight costs.

The combination of the prediction model with mapped benthos data showed that the GAM approach was suitable for predicting bivalve distribution. In the current study, we used the herring gull as a bioindicator of intertidal bivalve beds in general. The use of herring gull tracking data as an additional predictor provides further information compared with habitat models based on abiotic predictors alone. Foraging patterns of herring gulls allow the detection of intertidal bivalve beds and provide a tool for directed monitoring of these dynamic habitats.

To identify potential areas for specific bivalve species, the model approach used in this study can also be adapted to analyse and predict single species. Cockles, blue mussels, and razor clams prefer different hydrodynamic and sedimentological characteristics (Schwemmer et al., 2019a; Horn et al., 2017). For example, Schwemmer et al. (2019a) showed that razor clams preferred areas with moderately high bed shear stress, coarse and muddy sediments, and constant inundation time. These

specific preferred abiotic parameters would need to be included in the model to predict the distributions of specific bivalve species.

### **4.3 Herring gulls as bioindicators of intertidal bivalve beds**

Herring gull foraging patterns clearly reflected the presence of intertidal bivalve beds close to their breeding sites, and thus provided additional information about this dynamic habitat. Previous studies on intertidal bivalve beds revealed dramatic declines and critical changes in these important habitats in the coastal ecosystem (Millat et al., 2012; van der Heide et al., 2014). Anthropogenic influences, such as shipping traffic or fisheries have an important impact (Kabat et al., 2012). Although the declaration of Marine Protected Areas and the regulation of bivalve fisheries has led to recoveries in some areas (Millat et al., 2012), numbers of bivalves in Schleswig-Holstein are still decreasing (Millat et al., 2012; van der Heide et al., 2014). However, the distribution and status of bivalve beds is difficult to assess (Reiss et al., 2015).

Blue mussels in the German Wadden Sea have been monitored by aerial images and sampling stations in selected areas since 1998 (Nehls et al., 2011; Millat et al., 2012; IfAÖ, 2018). In some years, only aerial images of previous years were available for monitoring. However, the distribution of blue mussels in the intertidal area is generally well mapped. In contrast, broad-scale monitoring methods are largely unavailable for endobenthic bivalve species, such as cockles and razor clams and the densities and distributions of these species thus remain unknown, resulting in difficulties in assessing their overall effects on the Wadden Sea ecosystem. The American razor clam was introduced to the Wadden Sea in the late 1970s (Swennen et al., 1985), since when it has extended its distribution and is now increasingly used as a prey source by various bird species (Tulp et al., 2010; Enners et al., 2018; Schwemmer et al., 2019a; Schwemmer et al., 2019b). However, razor clam beds in the intertidal area are difficult to monitor, and their natural population size and dynamics in the German Wadden Sea are thus largely unknown. The use of herring gulls as bioindicators can help to identify hotspots for introduced razor clams, as well as other endobenthic species in the intertidal area, such as cockles. Additionally, in contrast to aerial images, foraging patterns of herring gulls also allow areas with recent settlement of young bivalves to be detected.

The distribution of benthic communities in the intertidal area can currently only be monitored by extensive sampling campaigns (Bijleveld et al., 2018). Intertidal mud flats in the Dutch Wadden Sea are monitored annually by gridded sampling and random sampling points (Bijleveld et al., 2012; Compton et al., 2013; Bijleveld et al., 2018; project SIBES), and although this represents a valid monitoring design, it is also very time and cost intensive. The prediction model presented in this study might thus help to supplement the existing monitoring program in the German Wadden Sea in relation to

conservation planning, by detecting and monitoring specific habitats, such as intertidal bivalve beds. Changes in the dynamic habitat of intertidal bivalve beds are directly reflected by the foraging behaviour of herring gulls. The resulting movement data might supplement the aerial images to improve the sampling design for directed monitoring.

During the breeding season, herring gulls are tide-dependent and forage on bivalve beds near their colony (Steenweg et al., 2011; van Donk et al., 2017; Enners et al., 2018). The foraging patterns of herring gulls thus indicate available bivalve beds near their breeding colony and provide important information for monitoring the distribution of these intertidal habitats. Ethical and financial issues mean that the number of tagged birds has to be a trade-off between data accuracy and low disturbance. Individual foraging-site fidelity (van Donk et al., 2019), as well as segregation of the foraging grounds of birds from different breeding colonies (Enners et al., 2018), has to be considered. Competition between colonies is minimized by spatial segregation and foraging habitat selection (Wakefield et al., 2015; Corman et al., 2016; Enners et al., 2018; see also Figure 1B). Therefore, we tagged herring gulls from different colonies. The existing classical bivalve monitoring program might thus be extended by tagging herring gulls from representative breeding colonies to detect intertidal bivalve beds in their vicinity. In the current study region, herring gulls from the breeding colonies on Amrum, Föhr, and Oland might be used as bioindicators for the northern part of the German north-Frisian Wadden Sea, and birds from the island of Trischen for the southern part. The application of tagged herring gulls might improve the monitoring sampling design and indicate changes in the environment. However, field surveys are crucial for ground-truthing to determine species-specific distributions and to assess the status of specific bivalve beds. Further studies are also needed to extrapolate the model approach to other regions and to test the optimal sample size of tagged herring gulls.

As an opportunistic and omnivorous top-predator, herring gulls adapt to changes in their environment and might thus be a valuable bioindicator. In regions without herring gulls, the presented model approach might be tested for other species feeding on bivalves. Diet analyses (e.g., pellets, faeces) provide important information which species are feeding on intertidal bivalves during the breeding season. Conservation planning requires fine-scale information to assess the impact of climatic or anthropogenic pressures on the ecosystem (Albuquerque and Beier, 2016; Singer et al., 2016).

## 5 Conclusions

The existing monitoring program for intertidal bivalve beds in the German Wadden Sea is based mainly on aerial images, and focuses on blue mussels and oysters. Despite their important role in the Wadden Sea ecosystem, endobenthic bivalve beds are not included in any regular, national monitoring program. In addition, areas with recently settled young bivalves are hard to detect with the current methods. Herring gulls have great potential as a bioindicator species to locate intertidal bivalve beds and to detect changes in the intertidal system. Habitat selection by herring gulls is mainly influenced by high bivalve biomass and low water levels. The combination of herring gull tracking and hydrodynamic data thus has the potential to extend the existing monitoring program to predict the occurrence of intertidal bivalve beds and to assess the environmental status of the system.

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### Data Accessibility

Tracking data are archived at Movebank (<https://www.movebank.org>). Bird-ringing data are archived at the Beringungszentrale Vogelwarte Helgoland (Institute for Avian Research, Wilhelmshaven).

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**Appendix 1:** Predictor selection was performed by comparing various biologically reasonable models applied to different grid sizes based on the AIC value.

<b>Model</b>	<b>AIC</b>	<b>Formula</b>
<b>m5</b>	65.16606	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4)) + tracking data + s(flooding)</i>
<b>m3</b>	66.86614	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4) + s(tracking data) + s(flooding)</i>
<b>m9</b>	66.86616	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4)) + tracking data + flooding)</i>
<b>m7</b>	66.86617	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4)) + s(tracking data) + flooding)</i>
<b>m1</b>	<b>72.26907</b>	<b><i>bivalve biomass = te (tracking data, flooding, by=distance colony level, k = c(4,4))</i></b>
<b>m4</b>	73.12821	<i>bivalve biomass = ti (tracking data, flooding, k = c(4,4)) + s(tracking data) + s(flooding)</i>
<b>m8</b>	73.12822	<i>bivalve biomass = ti (tracking data, flooding, k = c(4,4)) + s(tracking data) + flooding)</i>
<b>m6</b>	74.12795	<i>bivalve biomass = ti (tracking data, flooding, k = c(4,4)) + tracking data + s(flooding)</i>
<b>m10</b>	74.12795	<i>bivalve biomass = ti (tracking data, flooding, k = c(4,4)) + tracking data + flooding)</i>
<b>m2</b>	76.63119	<i>bivalve biomass = te (tracking data, flooding, k = c(4,4))</i>

AIC, Akaike information criterion

**Appendix 2:** The five best models were used to systematically test different grid sizes with respect to their predictive performance using 50% cross-validation, where predictive performance was quantified by the sum of squares of real vs. predicted bivalve biomass. Although some models showed a slightly better SS value, the model m1 was chosen because of the better interpretability of the nonlinear terms.

Model	SS	k	Formula
m5	0.118	0.5	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4)) + tracking data + s(flooding)</i>
m3	0.121	0.5	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4) + s(tracking data) + s(flooding)</i>
m7	0.124	0.5	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4)) + s(tracking data) + flooding</i>
<b>m1</b>	<b>0.126</b>	<b>0.5</b>	<b><i>bivalve biomass = te (tracking data, flooding, by=distance colony level, k = c(4,4))</i></b>
m3	0.130	0.7	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4) + s(tracking data) + s(flooding)</i>
m5	0.137	0.7	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4)) + tracking data + s(flooding)</i>
m9	0.138	0.7	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4)) + tracking data + flooding</i>
m7	0.139	0.7	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4)) + s(tracking data) + flooding</i>
m9	0.141	0.6	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4)) + tracking data + flooding</i>
m5	0.147	0.6	<i>bivalve biomass = ti (tracking data, flooding, by=distance colony level, k = c(4,4)) + tracking data + s(flooding)</i>

SS, shear stress





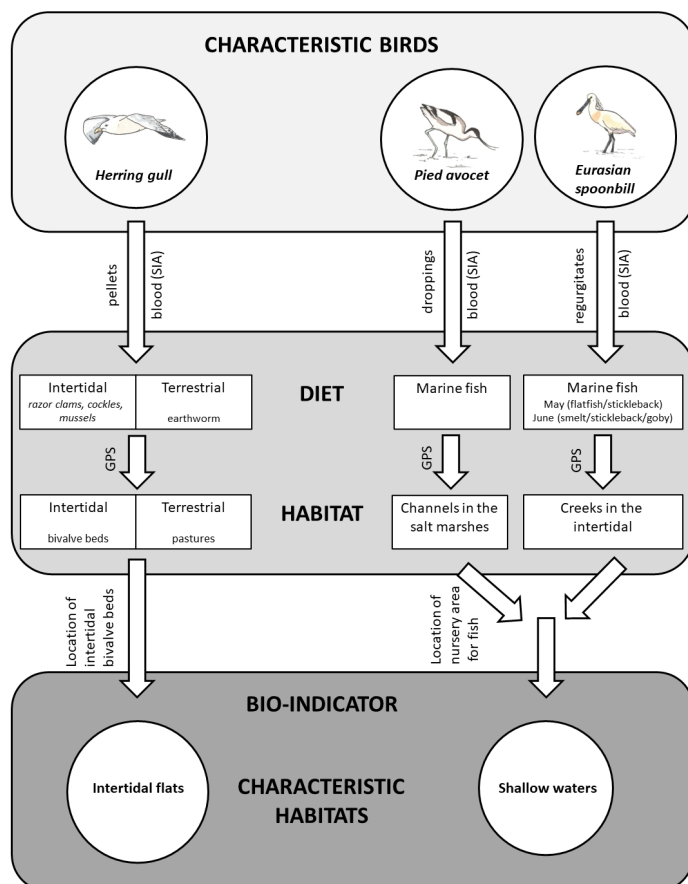


## **GENERAL DISCUSSION**



## GENERAL DISCUSSION

The present thesis provides detailed knowledge on the habitat selection and diet composition of characteristic coastal birds during the breeding season and gains information about the used foraging habitats of intertidal flats and shallow waters (Figure 1). Different methods were combined, based on data at the individual level (GPS data) and on the colony level (diet analyses) and enabled comprehensive analyses on the foraging ecology (**Chapter I-III**). In a multi-colony approach a segregated foraging behaviour in breeding herring gulls was demonstrated and intertidal bivalve beds, in particular of the introduced American razor clam (*Ensis leei*), were identified as important foraging habitats (**Chapter I; Enners et al., 2018**). Avocets (**Chapter II; Enners et al., 2019**) and spoonbills (**Chapter III; Enners et al., 2020**) were equipped with GPS devices in the Wadden Sea for the first time. Together with dietary analyses the data revealed the importance of marine fish as prey source and indicated the shallow waters in the salt marshes and the tidal system as main foraging habitats. Herring gulls were used as bio-indicator to detect bivalve beds in the intertidal, based on foraging patterns and flooding time (**Chapter IV; Enners et al., 2021**). In the following the main results will be considered in a broader context and future perspectives will be discussed.



**Figure 1:** Simplified flow chart of the study design.

## **1 Habitat selection and diet composition of characteristic coastal birds**

Herring gulls, avocets, and spoonbills are known as characteristic coastal birds for intertidal flats and shallow waters. Nevertheless, information on individual foraging strategies in the Wadden Sea was still lacking. In particular, for shorebirds weather conditions, time of day, tidal stage, and the movement range are limiting visual observations. Monitoring data mainly focuses on species distributions (e.g., seabird-at-sea counting programs, waterfowl census), without the possibility to identify the individual behaviour or the affiliation of individual birds to the breeding colonies (e.g., Tasker et al., 1984; Garthe et al., 2007). In this study, spatial-temporal tracking data enabled to investigate the individual habitat selection of the selected bird species and to analyse the available prey source by “ground-truthing”. At potential foraging sites sampling stations in the intertidal as well as mapping in the terrestrial habitat provided important information on the available prey species. For determining the diet choice, direct and indirect diet analyses methods were applied and combined with the tracking results.

### **1.1 Herring gull (*Larus argentatus*)**

Breeding herring gulls showed inter-colony differences in foraging habitat selection, based on GPS and diet data (**Chapter I**). The fine-scale GPS data revealed a wide range of foraging behaviours, from solely intertidal to mixed intertidal-terrestrial strategies. Benthos sampling stations and terrestrial mapping demonstrated that herring gulls prey on intertidal bivalve beds, but switched to terrestrial habitats during high water levels or prey depletion. During high water levels and during the day the terrestrial habitat were increasingly used, where pastures were the dominant foraging habitat (unpubl. data).

Diet analyses confirmed colony-specific differences and a dual intertidal-terrestrial foraging strategy. The herring gull diet composition, determined by pellet analyses, was dominated by common cockles (*Cerastoderma edule*), blue mussels (*Mytilus edulis*), and American razor clams (*Ensis leei*) in the intertidal and by earthworms in the terrestrial habitat. Herring gulls breeding in coastal colonies were known to forage mainly in the intertidal, preying on bivalves and crustaceans (Garthe et al., 1999b; Kubetzki & Garthe, 2003; Schwemmer et al., 2008). The spatial-temporal GPS data enabled a statistical evidence to analyse the foraging patterns on an individual level (Integrated Step Selection Model) and confirmed that herring gulls prefer to forage in areas with high bivalve biomass and low water levels in the intertidal (**Chapter IV**).

Prey depletion close to the breeding site might have forced herring gulls to use terrestrial prey sources. An increased use of the terrestrial habitat for foraging was also demonstrated for other gulls breeding at the coast or in urban localities (Schwemmer et al., 2008; O’Hanlon et al., 2017; Spelt et al., 2019). A similar change in foraging to a more terrestrial strategy was in particular shown before for lesser black-backed gulls (Corman et al., 2016; Garthe et al., 2016; Isaksson et al., 2016; Sotillo et al., 2019). Herring



gulls and lesser black-backed gulls are both visual foragers, using terrestrial habitats mainly during daytime. At night, lesser black-backed gulls often forage behind illuminated fishing vessels (Garthe et al., 2016), while herring gulls used the intertidal as foraging habitat. Herring gulls use well-known foraging habitats during the breeding season with predictable prey source. Van Donk et al. (2019) demonstrated that the foraging site fidelity depends on the body size, with larger individuals showing a higher site fidelity than smaller ones. Overall, herring gulls are opportunistic top predators that adapted their foraging strategy to the available prey source. They learned to use the neobiotic American razor clam in the intertidal as a novel food source. During field campaigns herring gulls were mainly observed opening the razor clam shells and only preying on the flesh inside. Therefore, it can be assumed that razor clam remains will be underrepresented in the pellet analyses and the diet proportions might be biased (e.g., González-Solís et al., 1997; Calado et al., 2018).

## 1.2 Pied avocet (*Recurvirostra avosetta*)

While intertidal flats and terrestrial habitats are characterised by more stable and predictable feeding conditions, shallow waters are more dynamic and unpredictable. Although the sample sizes were small, fine-scale GPS data of avocets (**Chapter II**) and spoonbills (**Chapter III**) provided new information on their habitat selection in shallow waters.

Breeding avocets foraged in intertidal channels close to the breeding sites (**Chapter II**). They performed short foraging trips mainly during daytime (maximum distance: 0.3–5.9 km; mean trip duration: 1.4 h). Hötker (1999) showed that the foraging time-activity pattern depends on the available prey. Avocets feeding on chironomid larvae need an extended time during day and night for foraging, while birds feeding on fish need only few hours during daytime (Hötker, 1999). Therefore, tracking data indicated high fish densities in the intertidal channels in the salt marshes and showed the importance of this habitat as nursery area for fish (**Chapter II**). Stable isotope analyses of blood samples confirmed this assumption and demonstrated that marine fish had the highest proportion in avocet diet composition in the study area. In contrast, droppings revealed former study results of ragworms as main prey source (e.g., Moreira, 1995b; Hötker, 1999), but these type of samples are known for their very small or strongly digested prey items, which complicate the reconstruction of the diet (González-Solís et al., 1997; Barrett et al., 2007). Stable isotope analyses provide information about the diet composition up to several weeks preceding the sampling event and is less susceptible to under- or overestimate (Barrett et al., 2007; Inger and Bearhop, 2008).

### **1.3 Eurasian spoonbill (*Platalea leucorodia*)**

For spoonbills, which have colonised the German Wadden Sea since 1995, there was a gap in knowledge on the habitat selection and foraging strategy. A previous study in Mauritania showed that spoonbills foraged in the intertidal during the ebbing tide exclusively during the night (El-Hacen et al., 2013). In the presented study, spatial-temporal GPS data enabled to analyse the foraging behaviour and implied high abundances of small fish in the used shallow waters (**Chapter III**). In particular, the tidal creeks between the islands and the mainland were preferred as foraging habitats. Overall, the foraging activities were tide-dependent and were conducted mainly during daytime (unpubl. data). Although the GPS sample sizes were small, direct (regurgitates) and indirect (stable isotope analyses of blood samples) diet analyses confirmed a marine foraging strategy with fish as preferred prey source. In contrast to droppings, regurgitates contain less digested prey remains and enable to calculate the original size and mass (Leopold et al., 1998; Guse et al., 2009). Accordingly, prey items of spoonbill regurgitates were identified and the total length and biomass calculated (**Chapter III**). This direct diet analysis suggested that brown shrimps might be less important in the spoonbill diet than previously assumed, while smelts (31.9%), sticklebacks (22.6%), and gobies (13.3%) were the dominant prey source. Stable isotope analyses of spoonbill blood samples confirmed the regurgitates results and enabled to investigate the diet composition on different time scales, indicating seasonal variations in prey availability. Red blood cells (reflecting the diet up to 3 weeks prior to sampling) showed that flatfish and sticklebacks were the main prey species in early May, while serum samples of spoonbill chicks reflecting the diet 1 week before sampling demonstrated a diverse diet, with flatfish, smelts, gobies, and sticklebacks end of May. Differences between years, colonies, and seasons indicated an opportunistic foraging strategy, depending on the available prey source. Tracking and diet analyses implied high abundances of small fish near the coast. Similar findings were shown in the Dutch Wadden Sea, where the diet of spoonbill chicks was dominated by small flatfish and gobies (Jouta et al., 2018).

### **1.4 Perspectives of the application of tracking and stable isotope data**

While the current study provides detailed information on habitat selection and diet composition during the breeding season (mostly restricted to the incubation time), still little information is available about the non-breeding season. The development of lighter GPS devices powered by solar panels will provide new possibilities to analyse the habitat selection over the whole year in the future (Wakefield et al., 2015; Mendes et al., 2018; Cleasby et al., 2020). In addition, accelerometer data can help to categorise the activities (e.g., resting, foraging, flying) and to calculate energetic costs of varying flight and foraging behaviours as well as to identify foraging areas (Shamoun-Baranes et al., 2016; Corman & Garthe, 2014).

The combination of direct and indirect diet analyses reflected the diet composition on different time scales and enhance our knowledge of available prey source. Stable isotope analyses were used to investigate the predominant foraging habitat ( $\delta^{13}\text{C}$ ) and trophic level of diet ( $\delta^{15}\text{N}$ ). Mixing models enable to determine the relative contributions of potential prey species to the diet by including data on the consumer (blood samples) and prey source as well as discrimination factors to account for the trophic enrichment between prey and bird blood (Phillips et al., 2014). The applied Bayesian mixing models MixSIAR (Stock & Semmens, 2016b; Stock et al., 2018) and *simmr* (Parnell et al., 2013; Parnell, 2016) represent improvements to the SIAR package and contain additional features, like incorporation of any number of prey items and the possibility to include information on the proportions of prey items by direct analyse methods. Accordingly, results from droppings and regurgitates were considered by stable isotope analyses of blood samples. However, for herring gulls, avocets, and spoonbills no species-specific discrimination factors were available. Similar to other studies comparable values were chosen (e.g., Ogden et al., 2004; Caut et al., 2009; Steenweg et al., 2011). Jouta et al. (2018) demonstrated that values of prey source differed dependent on the sampling area and time. In the presented study prey source of avocets was sampled in the same area and nearly in the same time span, while potential prey source of spoonbills occurred from the same system. Species-specific discrimination factors and GPS-GSM devices to detect foraging areas in real time might support further analyses.

## **2 Characteristic habitats – characteristic top predators**

The foraging behaviour and diet of characteristic coastal birds were investigated during the breeding season to draw direct conclusions on the distribution and status of their foraging habitats. This can aid in fulfilling monitoring requirements for intertidal flats and shallow waters. Recent studies used sedimentological and hydrodynamic data to model species distributions (Singer et al., 2016; Schwemmer et al., 2019a). However, tracking data from top predators provides a gain in knowledge compared to habitat models based solely on abiotic predictors. In particular, in dynamic ecosystems top predators mirror changes dynamically and might act as useful indicator species (Enners et al., 2021).

### **2.1 Intertidal flats**

Intertidal bivalve beds were chosen as one main habitat forming the intertidal flats. In the German Wadden Sea blue mussels, Pacific oysters, common cockles, and American razor clams are the dominant species and are known for their high productivity and importance as food source for various species (Reise et al., 2017; Horn et al., 2017; Schwemmer et al., 2019a). Commonly the distribution of habitats or species are monitored by time and cost intensive sampling campaigns, such as in the Dutch

Wadden Sea where the intertidal area is annually monitored by a gridded sampling and random sampling points (Bijleveld et al., 2012; Compton et al., 2013; Bijleveld et al., 2018). In contrast, in Germany only the epibenthic species of blue mussels and Pacific oysters are regularly monitored by aerial images and sampling stations in selected areas (Nehls et al., 2011; Millat et al., 2012; IfAÖ, 2018). The knowledge on the distribution and status of endobenthic bivalve species in the German intertidal was still lacking. The American razor clam was accidentally introduced to the Wadden Sea in the late 1970s and extended its range (Swennen et al., 1985). For a young system, such as the Wadden Sea, the dispersal of organism is a usual process with threats and/or benefits (Marencic & Vlas, 2009; Buschbaum et al., 2012; Büttger et al., 2019). International and national treaties oblige Germany to monitor and assess the influence of invasive species (e.g., MSRL, OSPAR). So far, no negative effects of razor clams have been identified. Several species learned to use this bivalve as prey source (Tulp et al., 2010; Horn et al., 2017; Schwemmer et al., 2019a; Schwemmer et al., 2019b). Nevertheless, precise knowledge of the distribution of razor clams is essential for assessing its effect on the ecosystem. The potential of herring gulls as bio-indicators was tested to detect epibenthic and endobenthic bivalve species in the intertidal to supplement the existing monitoring activities (**Chapter IV**). Herring gull movement data, flooding times, distance to the breeding site, and local bivalve biomass were highly significantly correlated. The application of tagged herring gulls indicates the presence of bivalve beds close to their breeding sites and can help planning monitoring effort. In this context, long flight distances indicate a reduced prey availability in the vicinity of the breeding site. Due to their opportunistic foraging strategy herring gulls reflect the general bivalve distributions, without focusing on single bivalve species. To detect the distribution of single bivalve species and to assess the environmental status, the necessary time and cost intensive sampling campaigns can be applied well-directed, based on herring gull movement data. In this study, benthos sampling stations at foraging hotspots revealed a wide-stretched common cockle bed between the islands Amrum and Föhr, as well as razor clam beds between the island Föhr and the mainland. Analyses based only on aerial images would have missed these intertidal bivalve beds. Further investigations are necessary to validate the shown statistical model approach to other regions. Overall, species distribution models (SDMs) enable to detect important areas for conservation management and to improve monitoring designs. Furthermore, SDMs provide important information on past, present and future changes in the dynamic marine ecosystem, especially to predict threats such as climate change and impacts of human activities (Reiss et al., 2015; Yates et al., 2018; Cleasby et al., 2020).

## **2.2 Shallow waters**

Similar difficulties in monitoring are present for other habitats in the highly dynamic Wadden Sea. Shallow waters are known as important nursery area for fish and invertebrates, but information on species distribution are still scarce (Reise et al., 2010; Dänhardt & Becker, 2011; Couperus et al., 2016). In the present study tracking and diet data of avocets (**Chapter II**) and spoonbills (**Chapter III**) revealed the importance of tidal channels in the salt marshes and intertidal creeks between the islands and the mainland as a nursery area for several fish species. Diet analyses demonstrated which fish species were available as prey source and provided important knowledge about their annual and seasonal variations. A combination of tracking and diet data might help to detect and protect important fish nursery areas.

## **2.3 Potential for further development**

Overall, herring gulls, avocets, and spoonbills were linked to their characteristic habitats and are suitable as bio-indicators for intertidal flats and shallow waters. A similar approach with other top predators might enhance our understanding of the heterogeneous habitats in the Wadden Sea. Information on foraging behaviour might improve the time- and cost intensive field campaigns for a directed monitoring. In this context, individual fine-scale information by tracking data would enable to investigate anthropogenic or climatic impacts on specific habitats and provide important information to predict future scenarios. Changes in foraging behaviour might reflect the impact of e.g., constructions of wind farms, ship traffic, or fishing activities (Corman & Garthe, 2014, Garthe et al., 2016; Sommerfeld et al., 2016, Furness et al., 2018; Thaxter et al., 2019). The use of characteristic top predators as indicator species reflect the ecological status of the used area and enables to develop monitoring tools for conservation management and spatial planning.

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## AUTHOR CONTRIBUTION

This thesis is based on four manuscripts, which have already been published to peer-reviewed scientific journals. In the following, I will describe my own contribution and that of all other authors to these manuscripts.

### Chapter I: Intercolony variations in movement patterns and foraging behaviors among herring gulls (*Larus argentatus*) breeding in the eastern Wadden Sea

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**Author contribution:** LE, PS, and SG designed the study. LE and PS conducted fieldwork. LE and CCV performed laboratory work. LE, PS, and AMC analysed the data. LE wrote the manuscript, to which all other authors contributed revisions.

### Chapter II: Foraging patterns and diet composition of breeding Pied avocets (*Recurvirostra avosetta*) in the German Wadden Sea

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**Author contribution:** LE, ALJC and SG developed the idea for the manuscript. LE, ALJC and PS conducted fieldwork. LE, ALJC and SMHIR performed laboratory work. LE and ALJC analysed the data. LE wrote the manuscript, to which all other authors contributed revisions.

### **Chapter III: Foraging ecology and diet of Eurasian spoonbills (*Platalea leucorodia*) in the German Wadden Sea**

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**Author contribution:** LE and SG designed the study. LE and PS conducted fieldwork. LE, NG, ALJC and CCV performed laboratory work. LE analysed the data. LE wrote the manuscript. NG, PS, ALJC, CCV and SG reviewed and approved the manuscript.

### **Chapter VI: Suitability of herring gulls (*Larus argentatus*) as indicators for detecting intertidal bivalve beds in the Wadden Sea**

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## **ERKLÄRUNG**

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbstständig angefertigt habe und dass sie in Inhalt und Form meine eigene Arbeit ist. Abgesehen von der Beratung meines wissenschaftlichen Betreuers, wurden keine anderen als die angegebenen Hilfsmittel und Quellen genutzt. Die Arbeit wurde unter Einhaltung der Regeln guter wissenschaftlicher Praxis der Deutschen Forschungsgemeinschaft erstellt.

Dies ist mein erster Promotionsversuch. Diese Arbeit wurde weder ganz noch zum Teil an einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt.

Für die mündliche Prüfung wird die Form der Disputation gewählt. Der Zulassung von Zuhörerinnen und Zuhörern bei der Disputation wird nicht widersprochen.

Büsum, den 24.06.2022

Leonie Enners



