Analysis of high tide roost use and benthos availability for twelve shorebird species in the Dutch Wadden Sea

Eelke Folmer, Bruno Ens en Els van der Zee

2022

Photo frontpage: Hanneke Dallmeijer

Cited as: Folmer[1], E.O., Ens[2], B.J. and E.M. van der Zee[3] (2022). Analysis of high tide roost use and benthos availability for twelve shorebird species in the Dutch Wadden Sea. A&W-rapport 19-469, Sovon-rapport 2021/52. In opdracht van Wij & Wadvogels.

[1] **Ecospace Ecological Research and Consultancy**
Graspieper 1
8532 AT Lemmer
06 14355536
eelke@ecospace.io
www.ecospace.io

[2] **Sovon Vogelonderzoek Nederland**
Toernooiveld 1
6525 ED Nijmegen
024 7 410 410
info@sovon.nl
www.sovon.nl

[3] **Altenburg & Wymenga ecologisch onderzoek bv**
Suderwei 2
9269 TZ Feanwâlden
0511 47 47 64
info@altwym.nl
www.altwym.nl

Commissioned by

In the multi-year cooperation program 'Wij & Wadvogels', the following parties are working together on the restoration of healthy bird populations in the Wadden Sea area: Het Groninger Landschap, It Fryske Gea, Landschap Noord-Holland, Natuurmonumenten, Rijksuniversiteit Groningen, Staatsbosbeheer, The Fieldwork Company, Vogelbescherming Nederland and the Waddenvereniging.

'Wij & Wadvogels' is made possible by the Waddenfonds, Ministery of LNV and the three Wadden provinces Fryslân, Groningen and Noord-Holland.

Contents

Nederlandse samenvatting

De Waddenzee is voor trekkende kustvogels een van de belangrijkste wetlands ter wereld. Het unieke gebied met uitgestrekte, productieve intergetijdengebieden en kwelders vormt een belangrijk broed-, rui-, doortrek- en overwinteringsgebied voor allerlei vogelsoorten. Helaas gaat het slecht met een aantal van deze soorten in het waddengebied. De aantallen van kustvogels als Scholekster, Kluut, Zwarte Ruiter en Groenpootruiter nemen af. Er zijn diverse redenen voor deze afnames. Zo kunnen foerageeromstandigheden veranderen, waardoor dieren zich niet goed kunnen voortplanten, of voldoende opvetten om verder te trekken, of de winter te overleven. Ook menselijke invloeden in het Waddengebied kunnen hierbij een rol spelen. Hierbij moeten we niet alleen denken aan visserij, luchtvaart en mijnbouw, maar ook aan verstoring ten gevolge van recreatieve activiteiten zoals wandelen, fietsen en kitesurfen.

Tijdens hoogwater verzamelen kustvogels, die met laagwater op de wadplaten naar voedsel zoeken, zich in grote groepen op hoogwatervluchtplaatsen om te rusten. Deze bevinden zich vaak aan de randen van kwelders, op hoge getijdenplaten, kwelders en stranden of, als natuurlijke plaatsen ontbreken, op dijken. Deze hoogwatervluchtplaatsen zijn van groot belang voor de energiehuishouding van wadvogels. Goede hoogwatervluchtplaatsen liggen dan ook in de buurt van geschikte foerageergronden en in gebieden waar de verstoring- en predatie risico's beperkt zijn.

Voorliggend onderzoek is onderdeel van het project Wij & Wadvogels. In dit meerjarige samenwerkingsprogramma werken Het Groninger Landschap, It Fryske Gea, Landschap Noord-Holland, Natuurmonumenten, Rijksuniversiteit Groningen, Staatsbosbeheer, The Fieldwork Company, Vogelbescherming Nederland en de Waddenvereniging aan het herstel van gezonde vogelpopulaties in het waddengebied.

Dit onderzoek bestaat uit analyses van de benutting van hoogwatervluchtplaatsen in relatie tot foerageermogelijkheden op de wadplaten. Het doel van de analyses is het in kaart brengen van knelpunten en kansen voor verbetering van hoogwatervluchtplaatsen in het Waddengebied, om handelingsperspectief te creëren voor bestuurders en beheerders van het gebied.

In het eerste deel van het onderzoek zijn de huidige aantallen en trends van een breed spectrum van wadvogels die afhankelijk zijn van de Nederlandse Waddenzee geanalyseerd: Scholekster, Kanoet, Wulp, Bonte Strandloper, Zilverplevier,Rosse Grutto, Steenloper, Bontbekplevier, Tureluur, Kluut, Groenpootruiter en Zwarte Ruiter. In het tweede deel zijn, met behulp van Structural Equation Modeling (SEM), de aantallen vogels op de hoogwatervluchtplaatsen geanalyseerd als functie van de beschikbaarheid van nabijgelegen voedselbronnen (foerageerpotentie).

Op deze manier zijn de vogelaantallen op hoogwatervluchtplaatsen statistisch gekoppeld aan het voedsel in de omgeving en konden "mismatches" geïdentificeerd worden. Als de mismatch negatief is ("onderbenutting"), dan zijn er minder vogels dan verwacht op basis van de voedselvoorzienig, en op plaatsen met positieve mismatch zijn er juist meer. Daarnaast is er informatie verzameld over de omgeving. Zo biedt in sommige gevallen verstoring een mogelijke verklaring voor de negatieve mismatches en in andere gevallen de hoeveelheid beschikbare ruimte voor de vogels, bijvoorbeeld bij heel hoog water.

Uit het onderzoek blijkt dat een aantal specifieke hoogwatervluchtplaatsen in de Waddenzee buitengewoon belangrijk zijn. Het westelijke deel van Vlieland, de kwelders bij Balgzand en Stroe, Westhoek-

Zwarte Haan, Friesland Buitendijks-West en de Rottums zijn hier goede voorbeelden van. De hoogwatervluchtplaatsen in deze gebieden laten positieve en stabiele trends zien, hebben een hoge foerageerpotentie en worden door grote aantallen vogels gebruikt zoals verwacht of zelfs beter. Griend is ook van wezenlijk belang als hoogwatervluchtplaats vanwege de grote en rijke oppervlakken wad in de omgeving en weinig verstoring. Bovendien ligt Griend op relatief grote afstand van andere hoogwatervluchtplaatsen. Maar de trends zijn hier wisselend en voor sommige soorten is er sprake van onderbenutting. Dit wordt deels veroorzaakt door uitwisseling met het nabijgelegen Richel. Het oostelijke deel van Ameland, het westelijke deel van Schiermonnikoog en de Groningse kwelders zijn van belang in termen van aantallen en foerageerpotentie, maar voor een groot deel van de onderzochte vogelsoorten is hier sprake van een afname in aantallen en een onderbenutting van het voedsel.

De problemen met het gebruik van hoogwatervluchtplaatsen ontstaan met name als de beschikbare ruimte op deze plaatsen beperkt is. Dit kan gebeuren tijdens (heel) hoog hoogwater, wanneer de vegetatie hoog is en/of wanneer mensen het gebied betreden. Vogels worden dan in de krappe ruimte gedwongen tussen het water en de verstoringsbron. Dit heeft vaak tot gevolg dat ze uit het gebied vertrekken. Mogelijk spelen ook verruiging en predatie een rol, maar dat is in deze studie niet expliciet onderzocht.

Een groot aantal gebieden op de eilanden, zoals de Noordzeestranden, delen van de Vliehors, het oostelijke deel van Vlieland, het Groene strand op Terschelling en de oostelijke punt van Terschelling hebben te kampen met relatief veel menselijke verstoring. Langs de vastelands kust zijn dat vooral de regio's Koehool - Westhoek - Zwarte Haan, Holwerd-sluizen Lauwersmeer en de kwelders bij de Westpolder in Groningen. De belangrijkste verstorende bronnen zijn fietsers, mountainbikers, wandelaars – al dan niet met honden – en (kite)surfers. Dit lijkt op sommige locaties een structureel probleem te zijn.

Wij bevelen aan om op de belangrijke hoogwatervluchtplaatsen de omstandigheden te behouden en/of te verbeteren. Menselijke verstoring kan beperkt worden door bezoekers van gebieden (beter) te informeren door middel van borden en ze te geleiden via paden om hun aanwezigheid en beweging in het gebied voorspelbaarder te maken voor vogels. Ook kan ervoor gekozen worden om specifieke gebieden af te sluiten voor bezoekers in periodes of op tijden wanneer vogels kwetsbaar zijn of gebieden zelfs helemaal af te sluiten. In gebieden waar de toegang al gereguleerd of (deels) verboden is, is het belangrijk om dit in stand te houden en waar nodig te verbeteren.

Verbetering zal met name effect hebben in gebieden waar de ruimte op de hoogwatervluchtplaatsen al gelimiteerd is, zoals bij Westhoek aan de kust bij Friesland en de Vogelpolle op Ameland. Deze relatief kleine hoogwatervluchtplaatsen (d.w.z. kleine kwelder tegen de dijk) kunnen minder vogels onderbrengen en bovendien zijn vogels hier gevoeliger voor verstoring door de afwezigheid van een bufferzone. Er zijn misschien mogelijkheden voor het creëren van nieuwe hoogwatervluchtplaatsen waar vogels ongestoord gebruik van kunnen maken. Langs de kust is de ruimte voor zulke nieuwe hoogwatervluchtplaatsen beperkt, maar aan de binnenzijde van de dijken zijn er mogelijk wel kansen in de vorm van bijvoorbeeld de 'Dubbele dijken', 'Wisselpolders' en rustig boerenland. Op sommige locaties, zoals het Balgzand, het traject Harlingen-Westhoek en het oostelijke deel van de Groningse kust, kunnen dijken functioneren als hoogwatervluchtplaatsen – mits hier geen verstoring optreedt. Dit vereist echter wel dat de plannen om de buitendijkse toegankelijkheid van dijken te vergroten voor wandelaars en fietsers, gestopt of beperkt worden.

Sommige plaatsen in het waddengebied laten ondanks het goede gebruik van hoogwatervluchtplaatsen, een afname in aantallen overtijende vogels zien van meerdere vogelsoorten, zoals op de kwelders van Ameland en Schiermonnikoog. Nader onderzoek naar de oorzaken van deze afnames is nodig. Het is mogelijk dat de voedselvoorziening in de Waddenzee of externe factoren, zoals reproductie, zo beslissend zijn voor de aantallen vogels, dat de maatregelen voor het verbeteren van de rust op hoogwatervluchtplaatsen slechts een klein effect zullen hebben.

De uitkomsten van voorliggend onderzoek worden meegenomen in de lopende en toekomstige projecten binnen Wij & Wadvogels en dijkversterkingstrajecten. Binnen dit kader gaat Vogelbescherming Nederland de resultaten vertalen naar concrete acties in het veld.

English summary

The Wadden Sea is one of the most important wetlands for migratory shorebirds in the world. This unique area with extensive, productive intertidal mudflats and salt marshes is an important breeding, moulting, migrating, and wintering area for many bird species. Unfortunately, there are indications that conditions are deteriorating for a number of these species in the Wadden Sea Region. The numbers of shorebirds such as Oystercatcher, Avocet, Spotted Redshank and Greenshank are declining. There are several reasons for these declining trends. For example, foraging conditions can change with low reproduction as result or not gaining enough fat to continue migrating or surviving the winter. Human influences in the Wadden Sea can also play a role. This includes not only fishing, aviation, and mining, but also disturbance caused by recreational activities such as hiking, cycling and kite surfing.

During low tide, shorebirds search for food on the mudflats and during high tide they gather in large flocks at high tide roost to rest. These roosts are often located on the edges of salt marshes, on elevated tidal flats, salt marshes and beaches or, if natural places are lacking, on dikes. These high-tide roosts are of great importance for optimising the energy budget of birds. Good high tide roosts are therefore located near suitable foraging grounds and in areas where the risks of disturbance and predation are limited.

This study is part of the project Wij & Wadvogels, in which Het Groninger Landschap, It Fryske Gea, Landschap Noord-Holland, Natuurmonumenten, University of Groningen, Staatsbosbeheer, The Fieldwork Company, Vogelbescherming Nederland and the Waddenvereniging collaborate on restoring healthy bird populations in the Wadden Sea Region.

In this study, we analysed the utilization of high tide roosts by shorebirds in relation to the foraging potential of the adjoining mudflats. The main aim is identifying bottlenecks and opportunities for improving high tide roosts in the Wadden Sea. This should help policy makers and managers to decide on the proper course of action.

In the first part of the study, the current numbers and trends of a broad spectrum of shorebirds that use the Dutch Wadden Sea, were analysed: Oystercatcher, Knot, Curlew, Dunlin, Grey Plover, Bar-tailed Godwit, Turnstone, Ringed Plover, Redshank, Avocet, Greenshank and Spotted Redshank. In the second part, the numbers of birds at the high tide roosts were analysed as a function of the availability of nearby food sources (foraging potential) using Structural Equation Modelling (SEM).

Bird numbers at high tide roosts were statistically linked to the food in the surrounding area to identify mismatches. If the mismatch is negative ("under-utilisation"), then there are fewer birds than expected based on the food supply, and in cases with a positive mismatch there are more birds than expected. In addition, information was collected about the environmental conditions of the high tide roosts. For example, in some cases disturbance offers a possible explanation for the negative mismatches and in other cases it is the amount of space available for the birds, for example during very high tides.

The research shows that a number of specific high tide roosts in the Wadden Sea are extremely important. The western part of Vlieland, the salt marshes at Balgzand and Stroe, Westhoek-Zwarte Haan, Friesland Buitendijks-West and the Rottums are good examples for this.

The high tide roosts in these areas show positive or stable trends, have a high foraging potential and are used by large numbers of birds and are utilized as expected, sometimes even exceeding the expectations. Griend is also essential as a high tide roost due to the large and rich mudflats in the area and little disturbance. Moreover, Griend is located at a relatively large distance from other high-tide refuges on the mainland. But trends are variable, and some species show underutilization, which is partly caused by exchange with the nearby roost on Richel. The eastern part of Ameland, the western part of Schiermonnikoog and the Groningen salt marshes are important in terms of numbers and foraging potential, but for a large part of the studied bird species there is a decrease in numbers and an underutilization.

Problems with the use of high tide roosting areas arise if the available space in these areas is limited. This can happen during (very) high tides, when the vegetation is high and/or when people enter the area. Birds are then forced into the tight space between the water and the source of disturbance. This often results in birds leaving the area. High vegetation and predation may locally also play a role, but this has not been explicitly investigated in this study.

Many areas on the islands, such as the North Sea beaches, parts of the Vliehors, the eastern part of Vlieland, the green beach on Terschelling and the eastern tip of Terschelling, suffer from relatively high levels of human disturbance. Along the mainland coast, areas with relatively high levels of human disturbance are the regions of Koehool - Westhoek - Zwarte Haan, Holwerd-Lauwersmeer and the salt marshes at the Westpolder in Groningen. The main sources of disturbance are cyclists, mountain bikers, hikers – with or without dogs – and (kite) surfers. This appears to be a structural problem in some locations.

We recommend preserving and/or improving the conditions at the important high tide roosting locations. Human disturbance can be limited by (better) informing visitors by means of signs and guiding them along paths to make their presence and movements in the area more predictable for birds. It is also possible to close off specific areas for visitors during periods when birds are vulnerable or even close off areas completely. In areas where access is already regulated or (partially) prohibited, it is important to maintain this and improve it when necessary.

Improvements are expected to have positive effects in areas where space at the high tide roosts is already limited, such as at Westhoek on the Friesian coast and the Vogelpolle on Ameland. These relatively small high tide roost (i.e. small salt marshes against the dike) can accommodate fewer birds and, moreover, birds are more sensitive to disturbance due to the absence of a buffer zone. Along the coast, there may be opportunities for creating new save high tide roosts for birds. The space for such new high-tide roosts is limited, but there may be opportunities inland, behind the dike, in the form of, for example, the 'Dubbele dijken', 'Wisselpolders' and quiet farmland. At some locations, such as Balgzand, the Harlingen-Westhoek section and the eastern part of the Groningen coast, the outer-dike part of the dike can function as high tide roost, if there is no disturbance. This requires that the plans to increase the accessibility for pedestrians and cyclists of the outward side of dikes must be stopped or limited.

Despite the good use of high-tide roosts, some places in the Wadden Sea Region show a decrease in numbers of roosting birds for several bird species, like the salt marshes of Ameland and Schiermonnikoog. Further local research is needed to investigate the causes of these declines. In addition, it is possible that the food supply in the Wadden Sea or other external factors, such as reproduction, are so decisive for the numbers of birds that the measures to improve the usage of high tide roosts will have only a small effect. These external factors also require further research.

The results of the present study will be included in current and future projects within Wij & Wadvogels and dike improvement projects. Within this framework, Vogelbescherming Nederland will translate the results into concrete actions in the field.

1 Introduction

The Wadden Sea is one of the most important wetlands for migratory shorebirds in the world. Its unique appearance with vast, productive intertidal mudflats and saltmarshes forms an important breeding, staging and wintering area for numerous birds. Many shorebird species breed in the Artic region and use the Wadden Sea to refuel on their way to their winter grounds in the south and in spring on their northward migration or use it to stay during winter (van de Kam *et al.*, 2004; Reneerkens *et al.*, 2005; Blew *et al.*, 2017). Other species use it as a staging site after breeding in Europe or use it as a gathering site during moult. It therefore forms an important site within the network of staging sites along the eastern coast of the Atlantic Ocean, also named the East Atlantic Flyway (Figure 1).

Unfortunately, many shorebird species are declining in the Wadden Sea. Long term trends (1987/1988 to 2013/2014) show that out of 34 species, 16 species are declining. Notable examples are the Common Eider (*Somateria mollissima*), Eurasian Oystercatcher (*Haematopus ostralegus*), Pied avocet (*Recurvirostra avosetta*), Spotted redshank (*Tringa erythropus*) and Common redshank (*Tringa totanus*) (Blew *et al.*, 2017). Reasons for these declines are diverse and changes in foraging conditions and/or environmental conditions can strongly affect survival and/or reproduction of species. Declines are also most pronounced in benthivore populations, especially for shellfish-eating species (van Roomen *et al.*, 2012). In total, 468,000 bird individuals have disappeared from the Wadden Sea comparing between the two recent ten-year periods ('93/'94-'03/04 and '04/'05-'13/14) (Blew *et al.*, 2017).

Roosting Red knots. Photo by Hanneke Dalmeijer

Furthermore, human pressure has intensified and is still increasing over time in the Wadden Sea (Lotze, 2005; Lotze *et al.*, 2005). Beside activities as fisheries, air traffic and gas drilling, also recreational activities have increased in the Wadden Sea (De Jong *et al.*, 1999; Bjarnason *et al.*, 2017; van der Tuuk *et al.*, 2019). Especially outdoor activities like kite surfing, canoeing, tidal flat walking and recreational boating along the coast have increased considerably in the past decades (De Jong *et al.*, 1999). This increase in activities can form a potential risk for birds at their foraging grounds and high tide roosts. In addition to these human disturbances, also natural disturbance from Peregrine Falcon (*Falco peregrinus*) has increased due to an increase in the number of Falcons in the Wadden Sea

(Van den Hout, 2009; van Roomen *et al.*, 2012). Both the increase in human and natural disturbances increases the pressure on the number of available safe foraging and roosting sites.

To support shorebirds populations, Vogelbescherming Nederland, partner of BirdLife International (VBN), would like to have insight into the barriers and opportunities to improve roosting possibilities in the Dutch part of the Wadden Sea. This research aims to provide that insight by analysis of the availability and quality of roosts in relation to the foraging opportunies. Such insight is expected toprovide opportunity for policy and management to support the shorebird populations.

During high tide, shorebirds gather in high concentrations on roosts. These roosts are often located at the edges of salt marshes, on high sandy tidal flats and beaches or, if natural site are lacking, at dikes. Roost site choice is of great importance for these birds: best foraging grounds may be of no use to shorebirds if they are not associated with good roost sites (Dias *et al.*, 2006). A good roost should therefore be safe from disturbance and predation and close to foraging grounds to optimize the energy management of (migratory) shorebirds during moult and migration.

In this study, we investigated the use of high tide roosts by shorebirds in relation to nearby foraging areas and site conditions. First, we analyzed the numbers and trends of a broad spectrum of twelve selected shorebird species (Avocet, Bar-tailed Godwit, Oystercatcher, Curlew, Red knot, Dunlin, Spotted redshank, Common redshank, Greenshank, Turnstone, Grey plover and Ringed plover) in the Dutch Wadden Sea. Second, we analyzed the numbers at the roosts as a function of the availability of food resources in the vicinity of the roosts using Structural Equation Models (SEM). And third, we related this to the quality and availability of nearby roosts. With these analyses, we indentified opportunities for the improvement of high-tide roost usage in the Wadden Sea. These findings can be used to create an action perspective for policy makers, conservation and nature managers in the Dutch Wadden Sea region to improve high tide roost usage.

Figure 1: Overview of the East Atlantic Flyway. Breeding birds of the Arctic tundra and European coast use a network of staging and wintering sites along the coast of NW Europe and Africa. (Image from CWSS, Van Roomen *et al.* (2017)).

2 Methods

2.1 Study area

This study was conducted in the Dutch part of the Wadden Sea which is is a large coastal area bordering the north of the Netherlands. It is part of the international Wadden Sea which stretches from Den Helder, in the northwest of the Netherlands, past the western coastline of Germany to its northern boundary at Skallingen in Denmark. The Wadden Sea is considered as one of the largest (8000 km^2) and most important tidal ecosystems in the world (Wolff, 1983; Reise, 2005). The Wadden Sea is under protection by international agreements such as the Ramsar Convention on Wetlands (1971), the Joint Declaration of the Protection of the Wadden Sea (1982) and Natura 2000 (2003). In 2009 the Wadden Sea became one of the UNESCO Natural World Heritage sites.

A range of inhabited and uninhabited barrier islands separates the Dutch Wadden Sea from the North Sea. The barrier islands consist of sandy beaches, dunes, saltmarshes, and polders (reclaimed land) with meadows, fields and villages. In between, there are smaller uninhabited sand flats, some of which also have dunes and saltmarshes. The southern mainland border of the area consists of inhabited polders which are mainly used for agriculture. Between the dikes protecting the polders from flooding, are summer polders, that can flood during extremely high tides in winter, and saltmarshes, often man-made, that developed from active land reclamation. The areas bordering the intertidal flats are used for roosting during high tide by the huge numbers of migratory birds feeding on the exposed mudflats during low tide. There are clear differences in the type of habitat preferred by the different species for roosting: saltmarshes, or the edges of salt marshes, sand flats and beaches, inland fields and meadows or, when foreland is lacking, also at dikes and breakwaters in harbours (Koffijberg *et al.*, 2003).

The Wadden Sea itself consists of intertidal and subtidal flats, deep tidal inlets, channels and drainage gullies. Tidal currents and exposure to waves strongly differ between regions due to differences in tidal range, geomorphology, fetch and the occurrence of barrier islands. The intertidal flats consist of sand mixed with finegrained muddy sediments; the fractions of fine-grained particles increase towards the shores and the tidal divides (Folmer *et al.*, 2017). The tidal flats are extremely productive (Herman *et al.*, 1999) and the densities of benthos and the numbers of shorebirds that they sustain, are exceptionally high (Folmer *et al.*, 2017).

2.2 Benthos

To assess the quality of the foraging landscape for the twelve species of shorebirds, we made use of Synoptic Intertidal Benthic Survey (SIBES) which is carried out by the Netherlands Institute for Sea Research (NIOZ) and the MosKok program, carried out by Wageningen Marine Research (WMR). The survey programs and the way the data were used, is described in the sections below. Table 1 presents the scientific species names and the abreviated codes and classes of the benthos species occurring within this report. The surveys are carried out once a year during spring in summer and do not capture the seasonal changes in densities and biomass. The seasonal dynamics are complex which is mainly due to temporal changes in metabolism and spatio-temporal variation in predation. Nevertheless, the surveys are expected to be reasonably representative for the entire year due to the large spatial and annual variation.

species	code	class
Abra alba	abralb	bivalve
Abra tenuis	abrten	bivalve
Cerastoderma edule	ceredu	bivalve
Ensis leei	enslee	bivalve
Limecola balthica	macbal	bivalve
Macomangulus tenuis	macten	bivalve
Mya arenaria	myaare	bivalve
Mytilus edulis	mytedu	bivalve
Scrobicularia plana	scrpla	bivalve
Alitta succinea	alisuc	polychaete
Alitta virens	alivir	polychaete
Arenicola marina	aremar	polychaete
Capitella sp.	capitsp	polychaete
Hediste diversicolor	heddiv	polychaete
Heteromastus filiformis	hetfil	polychaete
Lanice conchilega	lancon	polychaete
Marenzelleria viridis	marvir	polychaete
Nephtys hombergii	nephom	polychaete
Scoloplos armiger	scoarm	polychaete
Carcinus maenas	carmae	crustaceans
Corophiidae	corosp	crustaceans
Crangon crangon	cracra	crustaceans
Gammarus sp.	gammar	crustaceans
Littorina littorea	litlit	gastropoda
Peringia ulvae	hydulv	gastropoda

Table 1: Scientific species names, abreviated code names and class of the benthos species mentioned in this report. The coding convention is taken from the SIBES program.

2.2.1 SIBES

Within SIBES, sediment and benthos was sampled throughout the entire intertidal Dutch Wadden Sea (Figure 2). Most of the sampling takes place between June and August but in some years sampling started in April and lasted until October. Sampling was performed over 500 m grids. The grid sampling is supplemented with randomly located sites to improve fine-scale accuracy of spatial interpolations Bijleveld *et al.* (2012). Sampling sites were visited by foot during low tide and by boat during high tide. In the current study data for the period 2008-2014 and 2019 are used.

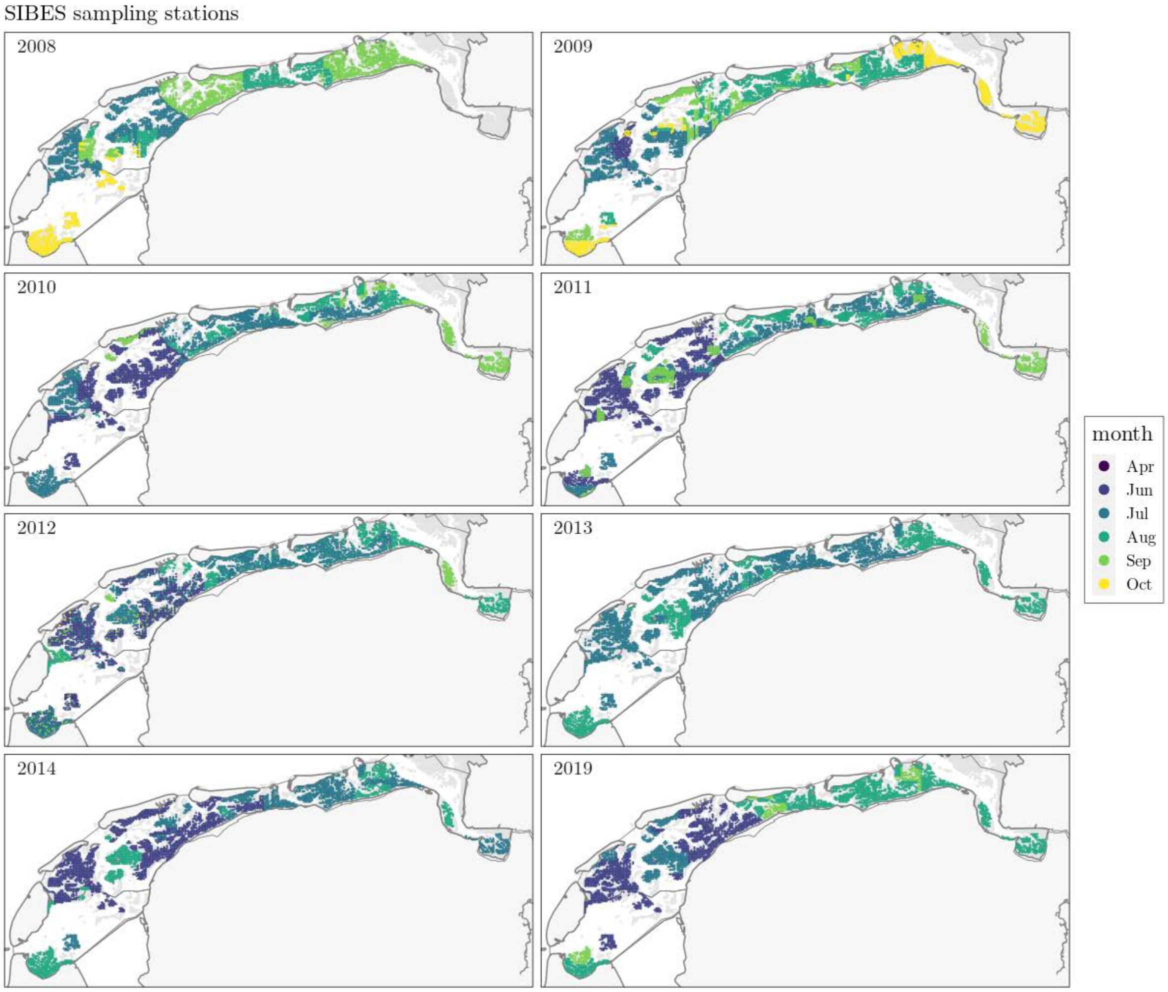


Figure 2: SIBES sampling stations in the period 2008-2019. Each point represents a sampling station and the colour represents the month in which the benthos sample was taken.

At the sites sampled by boat, two cores were taken to a depth of approximately 25 cm (total area of 0.0173 m^2). At the sites sampled by foot, a core of 0.0177 m^2 was taken. The samples taken by foot were split into a top (0–4 cm) and a bottom (4-25 cm) layer and separately sieved in the field over 1 mm round mesh. Bivalves were separated from the other macrofaunal species and stored frozen until laboratory analysis. The remaining species were preserved using a 4% formaldehyde solution.

Molluscs were identified to species level. Other organisms (mainly crustaceans, polychaetes, oligochaetes) were identified to the highest taxonomic level possible. Polychaetes and crustaceans were identied to either genus or species level; oligochaetes were identied to class level. The lengths of all molluscs, crabs and shrimp were measured to the nearest 0.1 mm and the biomasses were determined to the nearest 0.1 mg. Some polychaete species are divided into large and small size classes. In the cases that there were multiple individuals of the same mollusc species with shell length less than 8 mm in one sample, the total weight of the small, same-sized individuals was determined. The flesh of molluscs with shell length larger than 8 mm was separated from the shell and dried for 2 to 3 days at 60 °C in a ventilated stove. The dried flesh was weighed to the nearest 0.1 mg after which it was incinerated at 560 °C for 5 h. After incineration, the weights of the ashes were measured again (to the nearest 0.1 mg). In this way species and length-specific values for ash-free dry mass (AFDM) were obtained. For further details concerning sampling and handling of benthos we refer to other sources (Bijleveld *et al.*, 2012; Compton *et al.*, 2013; Folmer *et al.*, 2017).

2.2.2 MosKok

The purpose of the MosKok survey is to estimate the biomass and the spatial distributions of cockles (*Cerastoderma edule*) and mussels (*Mytilus edulis*) for fishery purposes. Though the program focuses on cockles and mussels, densities of Baltic tellin (*Limecola balthica*) are also estimated. It should be noted, however, that a sieve with a mesh size of 5 mm is used and that spatfall of Baltic tellins tends to be missed.

The survey is based on a stratified sampling method where the sampling density is increased when high densities of cockles and mussels are expected (Figure 3). The stratification needs to be taken into account when computing the total stocks or average densities. The total stock or the average density can be computed by taking into account the size of the area for which each sampling point is representative. This is done by multiplication with a weight factor which is based on the area A_i for which the sample is representative[1], i.e. $w_i = \frac{A_i}{\sum_{i=1}^{N} A_i}$. The weighted mean and standard deviation of the stocks are computed as follows: $\bar{B}_w = \sum_{i=1}^{N} w_i B_i$ and $sd_w = \sqrt{\sum_{i=1}^{N} w_i (B_i - \bar{B}_w)^2}$

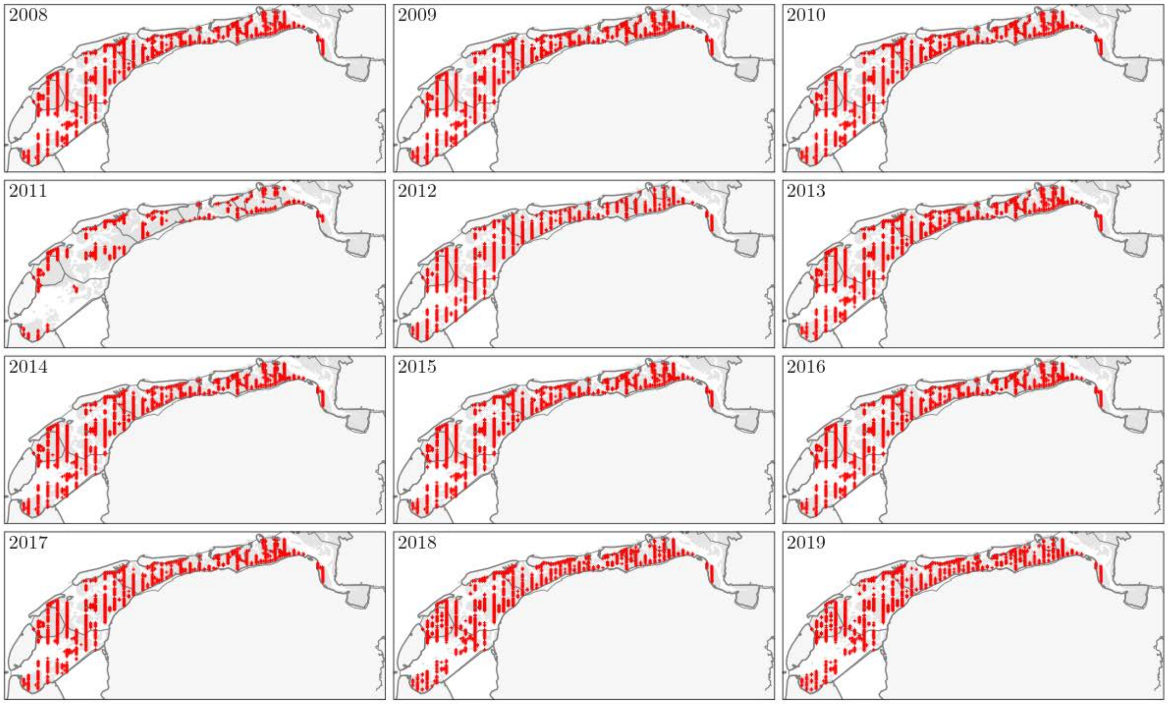
2.2.3 Comparing SIBES and MosKok

We compared the density estimates of Common Cockles and Baltic Tellins from the SIBES and MosKok surveys in order to assess possibile differences between the programs. An important difference between the programs is the timing of the sampling. SIBES mainly runs between July and September and Moskok takes place in May. During the sampling period of SIBES spatfall is encountered but this is not the case during the sampling of the Moskok program. Another difference is that growth of bivalves takes place between the sampling in spring and (late) summer. To adjust for spatfall in SIBES, it is filtered out. Beukema and Cadée (1991) show that typical growth rates of Baltic Tellins are around 9 mm per year. Given that spatfall takes place in spring and most of the growth is in summer we removed the Baltic Tellins that were smaller than 7 mm from the SIBES dataset.

---

[1] In some years extra points were sampled; those points are not used to compute the stocks

MosKok - cockle sampling stations



MosKok - mussel sampling stations

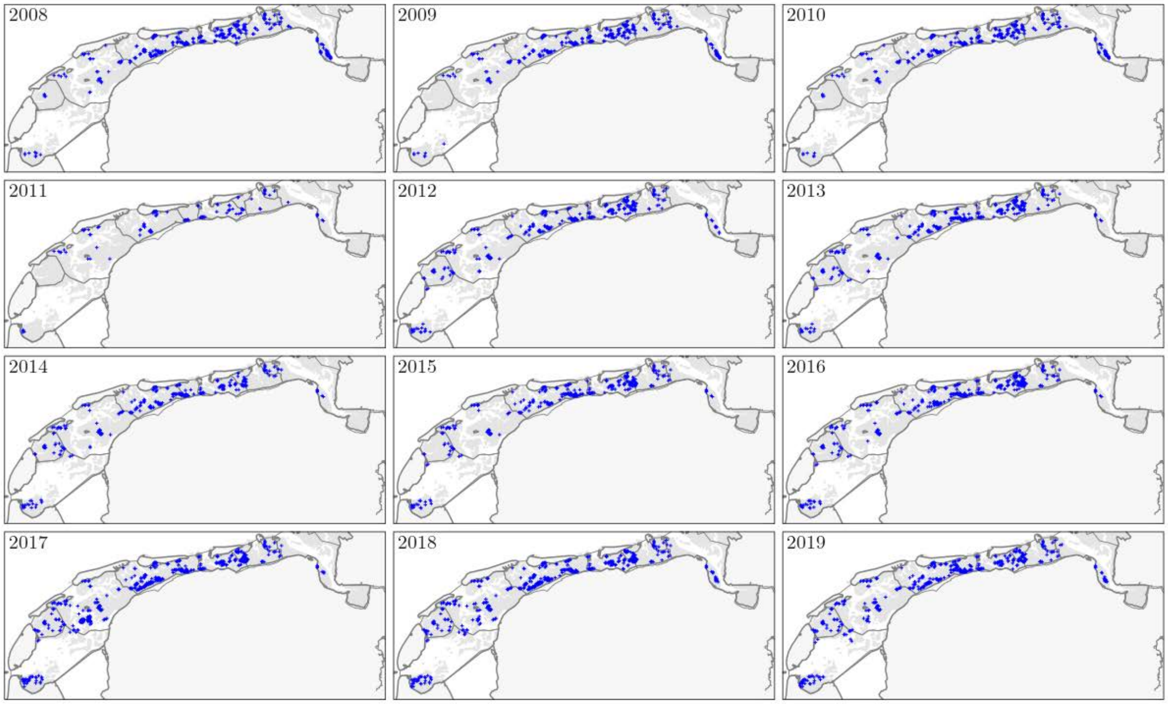


Figure 3: Cockle and blue mussel sampling stations from the MosKok survey in the period 2008-2019.

2.2.4 Mussel and oyster beds

The coverage and distribution of mussel and oyster beds is monitored with a combination of aerial inspections and field research. In spring, prior to the field surveys, aerial inspection is carried out to assess whether the beds that were mapped in the previous year were still present, whether significant parts of beds had disappeared, and whether there were any new seed beds. Locations where large changes are observed are prioritized during the field surveys. In the field the contour of mussel and oyster beds are mapped with handheld GPS receivers. The available time is usually not sufficient to map all mussel beds by means of GPS. For beds not visited it is assumed that the contour is the same as in the preceding year if the aerial survey confirmed the presence. For further details regarding mussel and oyster bed mapping we refer to (Folmer *et al.*, 2014; van den Ende *et al.*, 2020).

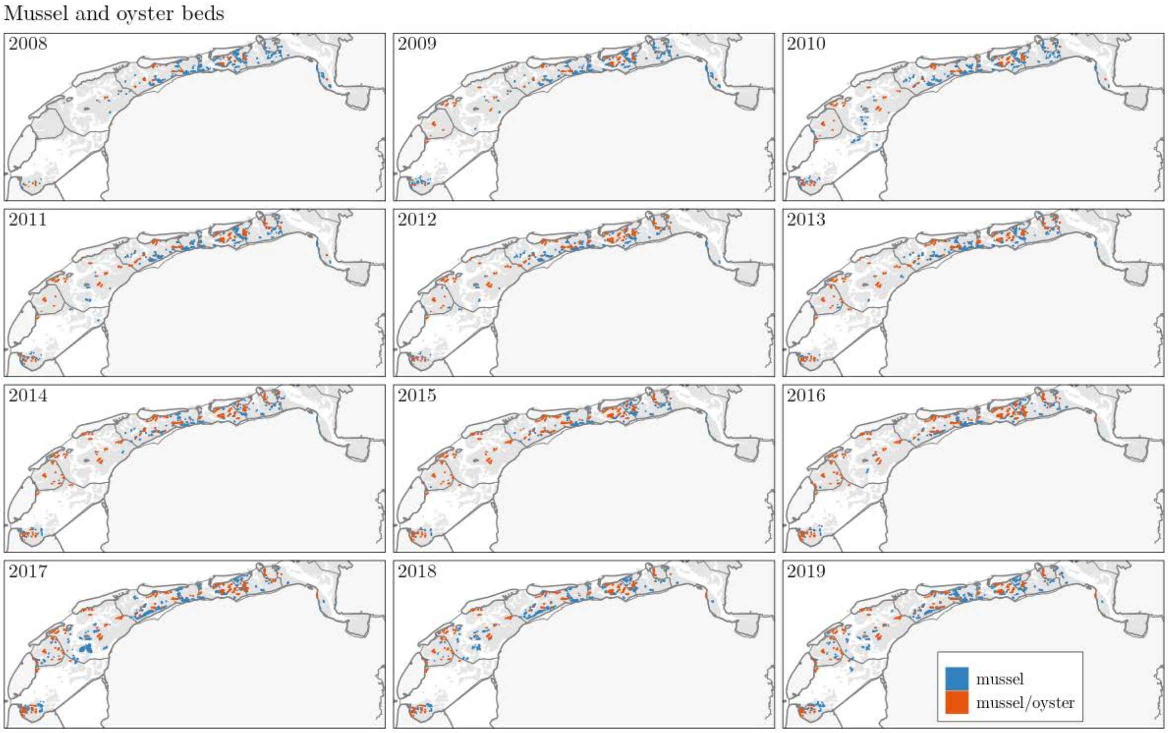


Figure 4: Distribution of mussel and oyster beds in the period 2008-2019.

Relationship between length and mass of intertidal mussels

To compute the harvestable biomass for different bird species, the ash-free dry mass (AFDM, g) of their food items is required. In the MosKok survey only the total number of individual mussels per size class and the total fresh mass of samples is measured, but not the AFDM of individual mussels. Three size classes are used: juvenile (<20 mm), half-grown [20, 45 mm) and adult ($\geq$ 45 mm) (van den Ende *et al.*, 2017). Based on 348 individual mussels, Ens & Kats (2004) have established the following relationship between AFDM (mg) and length (L, mm) for littoral mussels: $AFDM = 5.97 \cdot 10^6 \cdot L^{2.9}$. The relationship describes 95% of the variation. To compute the representative AFDM of each size class we assume that all juvenile mussels are between 8 and 20 mm and that the maximum length in the adult size class is 55 mm. Using the relationship above and assuming a uniform distribution of lengths within size classes, we computed the following AFDM values per size class: juvenile (13.4 mg) half-grown (157.7 mg) and adult (510.2 mg).

2.3 Bird counts

Shorebirds are counted during high tide when they concentrate on high tide roosts. All areas in and around the Wadden Sea that remain dry during high water, and where high tide roosts may be located, belong to the study area and are divided into counting areas (Figure 9). Sovon Dutch Centre for Field Ornithology coordinates the counts that are mainly conducted by highly trained volunteers, nowadays referred to as citizen scientists. Sovon also manages and curates the database with the results of the counts. Since 1994/95, four to five integral high tide counts are carried out in the Wadden Sea each year. Integral counts are carried out in September, November, January, May and an annually changing month. In addition to these integral counts, ten sub-areas have been counted more frequently for years, usually on a monthly basis. In addition, a large number of additional counts are available, often for individual islands. As far as possible, all these counts are stored at the level of the counting areas. The resulting dataset consists of a matrix of year, month and counting area, in which the integral counts, area counts, and sample counts are included. This matrix contains missing values, because there are areas where during a particular month no count was conducted. To correct for this variation in counting effort, missing counts are estimated with the Uindex program (Bell, 1995). The number of birds per species is modeled depending on the counting area, the month and the season (year), using the non-missing counts (Underhill & Prys-Jones, 1994). This is referred to as imputing and yields an estimated number for each bird species, for each counting area in each month. Imputing introduces errors in the estimated number. These errors must be added to the unavoidable errors in large scale shorebird counts during counting. These counting errors have been investigated by Rappoldt *et al.* (1985). Errors average out for species that occur in many counting areas, like the Oystercatcher. However, when we reduce the number of counting areas, because we are interested in local trends, this averaging process is less effective. Thus, we should take care when studying trends, that we do not reduce the size of the local areas and the time periods too much.

Trends are calculated using the program trendspotter (Visser, 2004). The arguments for this approach are provided by (Soldaat *et al.*, 2007). To study trends in different parts of the Wadden Sea, we divided the Dutch Wadden Sea into 14 major areas by lumping local counting areas. We also took into account that species differ in the way they use the Wadden Sea in the course of the year, including migratory populations joining a resident population to spend the winter, and different subspecies where one subspecies only occurs during migration, whereas the other subspecies spends the winter in the Wadden Sea. Furthermore, we are especially interested in the holiday season, as this is the period where we expect most conflict between roosting birds and recreational activity. The seasonal patterns are depicted in appendix B. These patterns were combined with knowledge on the distribution of different age classes, subspecies and subpopulations during summer and winter (Van Roomen *et al.*, 2018) to identify one or more time periods. The resulting classifications of time periods are given in Table 2.

Bird species			**Period**		**Interpretation**
English name	**Latin name**	**abbr.**	**months**	**1/2**	
Oystercatcher	*Haematopus ostralegus*	oyc	Apr - Jul	1	mainly summering immature individuals
			Aug - Mar	2	local breeders and inland breeders from the Netherlands and breeders from Scandinavia
Red Knot	*Calidris canutus*	knot	Aug - Oct	1	migration subspecies canutus
			Nov - Jul	2	wintering birds from subspecies islandica and summering immature individuals
Curlew	*Numenius arquata*	curlew	Jul - Apr	1	wintering birds from Scandinavia, Baltic states, Finland and Russia
			May - Jun	2	mainly summering immature individuals
Dunlin	*Calidris alpina*	dunlin	Jul - Jun	1	no periods distinguished because of complicated flyway population/subspecies structure
Grey Plover	*Pluvialis squatarola*	gplov	Aug - Apr	1	mainly wintering birds
			May	2	birds passing on spring migration
Bar-tailed Godwit	*Limosa lapponica*	btgod	Oct - Apr	1	wintering birds of the subspecies lapponica
			Sep - May	2	birds from subspecies taymyrensis passin on migration in spring and autumn
Turnstone	*Arenaria interpres*	tstone	Jul - Jun	1	numbers too low to distinguish between subpopulations
Ringed Plover	*Charadrius hiaticula*	rplov	Oct - Apr	1	wintering birds of the resident subspecies *hiaticula*
			Aug - Sep	2	mainly passing migrants of subspecies *psammodroma*
Redshank	*Tringa totanus*	rshank	Jul - Sep	1	locally breeding subspecies *totanus*, preparing for their southward migration
			Oct - Jun	2	wintering birds of subspecies *robusta*
Avocet	*Recurvirostra avosetta*	avocet	Jul - Dec	1	birds breeding in the international Wadden Sea migrating south at the start of winter
			Jan - Jun	2	local breeding birds
Greenshank	*Tringa nebularia*	gshank	Jul - Oct	1	birds on passage in autumn
			Apr - Jun	2	birds on passage in spring
Spotted Redshank	*Tringa erythropus*	sshank	Jul - Nov	1	birds on passage in autumn
			Apr - Jun	2	birds on passage in spring

Table 2: English and Latin names, abbreviations and description of the different time periods used for the study species to study the time trend in the use of local areas in the Dutch Wadden Sea. **abbr.** is the abbreviated English name used in some figures. The dash in the column months means up until and including. **1/2** is the index used to distinguish between periods.

2.4 Bird diets

One of the most astonishing feats of the bird species that feed on the intertidal mudflats of the Wadden Sea is the wide variety in their bill shapes (Figure 5). These are clear adaptations to capture and handle different prey, or to capture the same prey differently. The longer the bill, the deeper the birds can probe into the mud, so birds with short bills hunt for prey on or close to the surface, which may include worms that spend most of their time deep down in their burrow. Bills of equal length may be used differently. Whereas the Bar-tailed Godwit probes deep into sandy sediment, the Avocet uses it delicate upward curved bill to sweep through soft sediment. But the bill is not the only adaptation. Some birds use mainly sight to find their prey, whereas others rely heavily on touch, which may include detecting buried prey at some distance from the bill tip (Piersma *et al.*, 1998). To overcome the prey defense of bivalves, i.e. their thick shell, Oystercatchers use their strong bill to hammer or stab the bivalves, whereas Knots swallow the shellfish whole and crack the shells in their stomach.

Ideally, we would calculate for each species and site the optimal prey choice and the intake rate that could be achieved using prey choice models developed as part of optimal foraging theory (Stephens & Krebs, 1986). To this should be added a distribution model, which requires knowledge on how the birds compete for food (Goss-Custard, 1980; Meer & Ens, 1997), resulting in an individual-based model predicting the diet (as well as the distribution, condition and mortality) of the entire population (Stillman & Goss-Custard, 2010). However, sufficient knowledge is only available for Oystercatchers (Goss-Custard, 1996) and Knots (van Gils *et al.*, 2006).

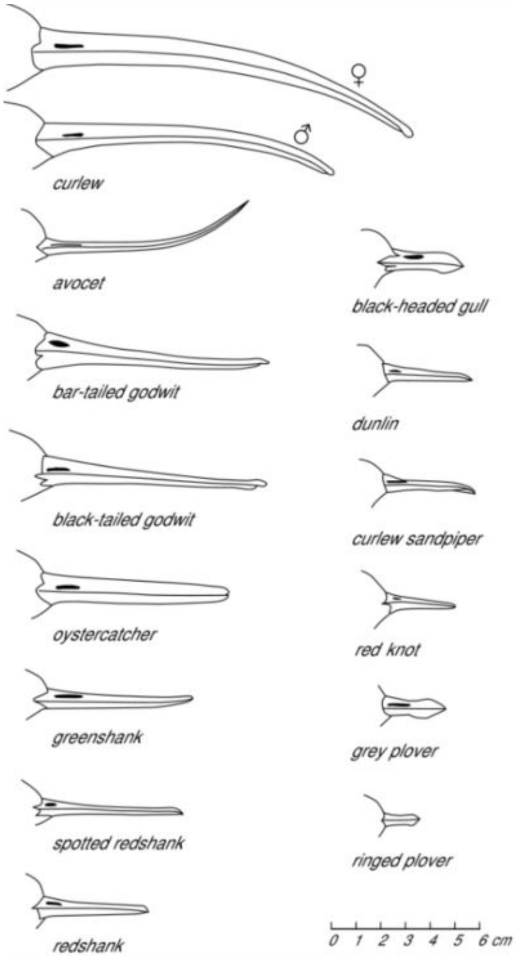


Figure 5: Bill shapes of shorebirds feeding on the intertidal mudflats of the Wadden Sea. Taken from van de Kam *et al.* (2004).

For this study, we relied on reviews of the literature on the diet of shorebirds in the Wadden Sea and comparable areas. Leopold *et al.* (2004b) go so far as to present the diet as fixed percentages of prey. Given the large spatiotemporal variation in the populations of benthic animals (Beukema & Dekker, 2020) this seems unwarranted because shorebirds will respond to this variability. The temporal variability includes both annual variation and seasonal variation, due to changes in burying depth, prey activity, spatfall, growth or loss of body condition, and migration to and from the mudflats (Zwarts & Wanink, 1993). We did not correct for seasonal changes. For instance, Shorecrabs are a highly preferred and important prey for Curlew, but only in summer and early autumn, because after early autumn crabs are unavailable because they move to deeper and warmer water. Nor did we directly correct for burying depth in most cases. However, for many burying benthic species, burying depth increases with size and by setting a maximum size based on the literature, we implicitly included a maximum burying depth. In the case of Knot, which has a relatively short bill and is not able to reach prey that is buried too deeply, we could make use of the fact that the SIBES program is designed for Knots. On the basis of the by-foot samples in which the bottom and top layers were separated, we estimated the probability that an individual specimen was in the top or bottom as a function of species, length and the interaction between species and length using a logistic regression model. In a similar vein as Folmer *et al.* (2010), the model was used to correct the fraction of individuals in the top for the samples collected by boat by multiplying the total number of individuals by the probability that it would occur in the top layer.

Ens *et al.* (2016; 2017) included new literature on shorebird diet that appeared since the review by Leopold *et al.* (2004b) and classified prey as staple food, supplemental food and rarely taken prey. In this study, staple foods and supplemental foods were lumped as primary prey species and distinguished from prey that were rarely taken (Figure 6). When available, we also included the best estimates of the minimum and maximum size of a prey species taken by a shorebird species.

Which prey can be harvested by a shorebird may also depend on the sediment. Benthic animals occur in different substrates, but their niche is very broad (Beukema, 1976; Folmer *et al.*, 2017). Sometimes the foraging niche of shorebirds is less wide than that of their prey when it comes to sediment, but despite many studies (Zwarts, 1988; Ens *et al.*, 1993; Yates *et al.*, 1993; Brinkman & Ens, 1998; Granadeiro *et al.*, 2004; Ens *et al.*, 2005; Granadeiro *et al.*, 2007), it is hard to derive sharp boundary values that can be used in calculations. Sanderlings and Bar-tailed Godwits prefer sandy mudflats, Knots mudflats of intermediate composition and Oystercatchers can be found on almost any type of sediment. The species that is most clearly adapted to a particular type of sediment is the Avocet that uses its delicate bill to sweep through muddy sediments. For this species, we excluded all prey on mudflats with less than 20% mud.

2.5 Analysis

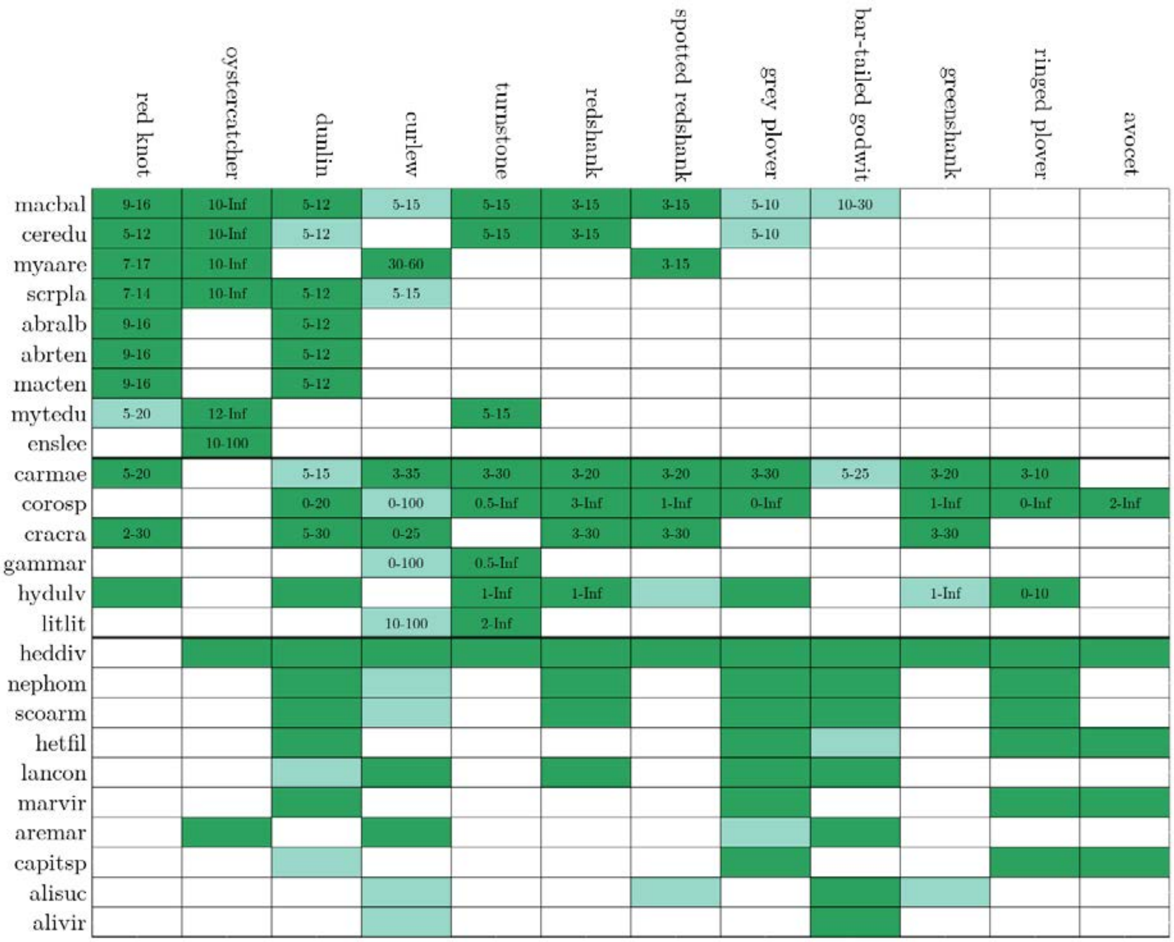
2.5.1 Linking roost counts with abiotic variables and benthos

The quality of the food landscape can be assessed in different ways. We chose the biomass density of prey that is part of the diet, taking size limits into account (Figure 5). We did not correct for growth or loss of condition, or changes in depth distribution or activity of the prey. The most important dataset to compute available prey was the SIBES dataset as it covers most of the benthos species. The WMR mussel dataset was required for Oystercatcher, Red knot and Turnstone as they forage on musselbeds which are not well represented in the SIBES dataset.

We obtained exposure time data from the PACE project in which the hydrodynamics were simulated for the entire Wadden Sea on a 200×200 m grid during the period 2009-2011with the GETM[2] model Burchard & Bolding (2002). Modelling details and postprocessing are described in (Gräwe *et al.*, 2016;

---

[2] GETM is designed for coastal ocean simulations with drying and flooding of intertidal flats



	red knot	oystercatcher	dunlin	curlew	turnstone	redshank	spotted redshank	grey plover	bar-tailed godwit	greenshank	ringed plover	avocet
macbal	9-16	10-Inf	5-12	5-15	5-15	3-15	3-15	5-10	10-30			
ceredu	5-12	10-Inf	5-12		5-15	3-15		5-10				
myaare	7-17	10-Inf		30-60			3-15					
scrpla	7-14	10-Inf	5-12	5-15								
abralb	9-16		5-12									
abrten	9-16		5-12									
macten	9-16		5-12									
mytedu	5-20	12-Inf			5-15							
enslee		10-100										
carmae	5-20		5-15	3-35	3-30	3-20	3-20	3-30	5-25	3-20	3-10	
corosp			0-20	0-100	0.5-Inf	3-Inf	1-Inf	0-Inf		1-Inf	0-Inf	2-Inf
cracra	2-30		5-30	0-25		3-30	3-30			3-30		
gammar				0-100	0.5-Inf							
hydulv	🟩		🟩		1-Inf	1-Inf	▨	🟩		1-Inf	0-10	
litlit				10-100	2-Inf							
heddiv		🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
nephom			🟩	▨		🟩		🟩	🟩		🟩	
scoarm			🟩	▨		🟩		🟩	🟩		🟩	
hetfil			🟩					🟩	▨		🟩	🟩
lancon			▨	🟩		🟩		🟩	🟩			
marvir			🟩					🟩			🟩	🟩
aremar		🟩		🟩				▨	🟩			
capitsp			▨					🟩			🟩	🟩
alisuc				▨			▨		🟩	▨		
alivir				▨					🟩			

Figure 6: The diets of the investigated shorebirds based on literature. For the molluscs and crustaceans the numbers represent the minimum and maximum length (mm) that the shorebird species select. Dark green cells represent primary prey species and the light green cells represent prey species that are rarely selected.

Folmer *et al.*, 2016). We used the average inundation time during 2009-2011. This model underestimates exposure time near tidal divides, probably because the bathymetry map is not sufficiently detailed so that the runoff of water is too slow (Wang pers. comm.). Evidence of underestimation is presented in the appendix on the amplitude map Rappoldt *et al.* (2019).

For each bird species, the quality of the (virtual, see point 3 below) roosts was computed with the following sequence of steps:

1. We constructed a grid with cell size $750 \times 750\ m$ to link the abiotic variables exposure time and mud content to the prey densities (Figure 9). The reason to "resample" the abiotic and biotic variables to a common grid was to be able to link data from various sources with different sampling schemes.
2. The SIBES dataset was subsetted on the basis of prey and size selection of the different bird-species (Figure 6). For most benthos samples, the number of specimens per species and the

individual lengths (mm) and AFDMs ($g\ m^{-2}$) were given. In cases that AFDM values were missing, they were imputed using species-specific relationships between length and AFDM (on the basis of the subset). Using cases where length and AFDM were both available, we estimated linear regression models where the cubic root of AFDM was the response variable and the predictor variables were length, year and the interaction between length (l) and year, i.e. ($AFDM^{1/3} = year + l + l \cdot year$). With these species-specific models the missing AFDM values were imputed. In the cases where both AFDM and length were missing, we first imputed length by taking the average of all the measured specimens (again, for the subset only). For Oystercatcher, Red knot and Turnstone, the musselbed data had to be included in the analysis. Because the heterogeneity in the MosKok mussel points is high, a large number of samples is required to reliably estimate the numeric density and biomass of mussels inside a bed. Instead of linking the area of mussel beds in each grid cell to a limited number of samples inside or near that grid cell, we use the average density of all points per year but distinguished between the eastern and western Wadden Sea. On the basis of the relationship between AFDM and length given in section 2.2.4, we computed the density and total biomass of mussels per gridcell. The total AFDM per benthosspecies and gridcell was computed by summing individual AFDMs.

3. The counting areas vary in size which makes it difficult to link bird numbers at the roosts to the foraging areas. To obtain a spatially balanced distribution of virtual roosts we defined 33 equidistant points on a line along the Wadden Sea coast (Figure 9). The island of Griend (number 34) was added manually. We also defined virtual roosts along the the Ems and on Borkum in Germany to avoid the assignment of intertidal foraging area that is near to roosts in Germany, to roosts in the Netherlands; there are no bird counts for these virtual roosts.

4. Based on the assumption that shorebirds minimize travel costs, foraging areas are connected to the virtual roosts on the basis of shortest distance[3]. This "central place foraging" strategy results in Voronoi tessellation of space in which shorebirds occupy nonoverlapping feeding zones (Cairns, 1989; Aarts *et al.*, 2021). As predicted by the ideal-free distribution (Fretwell, 1969), the number of birds at the virtual roosts is a function of the prey availability in these zones. For each "bird season", we computed the average number of birds over the months described in section 2.3. Because there are no SIBES data for the Ems-Dollard estuary in 2008, the virtual roosts 31-33 are discarded for that year (Figure 9).

5. For each year, and each prey species, the prey availability (P) at the virtual roosts is computed as a function of the prey biomass in the grid cells within the feeding zones, their exposure time and distance to the virtual roost.

$$P_{jst} = \sum_i b_{ist} \cdot w(d_{ij}) \cdot \tau_i \cdot g(s_i) \tag{1}$$

---

[3] This assumption is unrealistically strict and different bird species follow different foraging movements during low tide. For instance, Red Knots roosting at Richel may forage at the Frisian coast. One reason for maintaining this assumption is that for most of the species the exact movement patterns are unknown and constructing species level roost-foraging demarcations would be unwieldy, impossible to do right and counterproductive. Instead, interpretation of the results based on our strict assumption should be done with available ecological knowledge regarding low tide movements. Particularly, the mismatch observed at one particular roosting site should be considered in relation to mismatches at nearby roosting sites. Using the Red Knot example, the roosting sites Griend and Richel tend to be both used by large numbers of birds, which may forage near Griend, Richel or the Frisian coast. This means that a possible negative mismatch at Griend could be explained by a positive mismatch at Richel or the Frisian coast.

where b_{ist} is the AFDM (g) of benthos species s in cell i in year t. Weighing for distance is based on the negative exponential function; $w(d_{ij}) = e^{-\lambda d_{ij}}$ where d_{ij} is the distance between cell i and roost j. We used the values 0.15, 0.1 and 0.05 for λ to investigate the sensitivity of the analysis for this parameter (Figure 7). In the main results we present the outcome on the basis of $\lambda = 0.10$ and note here that the conclusions would not be different if another choice was made (though slight differences were observed). τ_i is the average exposure time of the cell (between 0-1; 0 is never exposed, 1 is always exposed). $g(s_i)$ describes the foraging suitability of the mudflats for Avocets on the basis of mud content. Because Avocets can only forage in soft and muddy sediments $g(s_i) = 0$ when mud content is < 20% and $g(s_i) = 1$ when mud content > 20%.

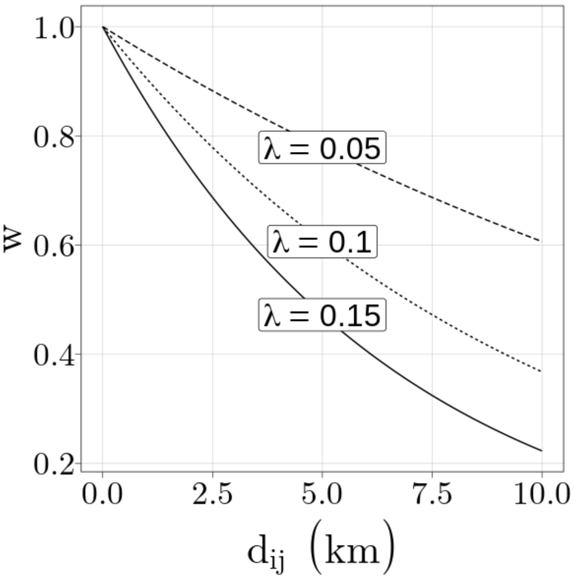


Figure 7: Relationship between the weight (for devaluing foraging value) and distance between roost and foraging area.

Flight distances Oystercatcher Weighing prey availability with a negative exponential function of distance to roost amounts to increasingly reducing the value of the prey availability with increasing distance to the roost for the birds using that particular roost. The rationale is that the greater the distance between food and roost, the higher the energetic cost of traveling between food and roost is, and hence affects the choice for foraging and roosting areas. Including this travel cost in our model calculations would have required developing an individual-based model, which was outside the scope of our regression approach. Furthermore, modeling foraging decisions requires detailed knowledge about the cost of flight in relation to the overall energetics. We therefore chose to devalue the food with distance in a way which we thought was reasonable.

The only data with which we could compare our choice are the flight distances between roost and feeding area for Oystercatchers. Studies with GPS-trackers indicate that for this species, the maximum distance between roosting area and foraging area is usually only a few kilometers (Ens *et al.*, 2015;

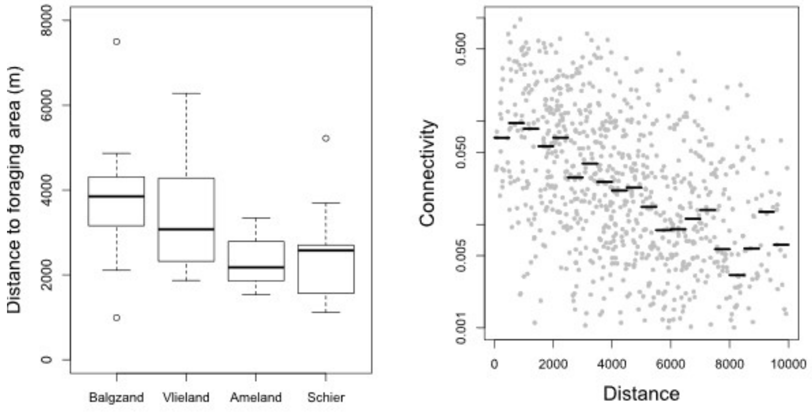


Figure 8: Travel distances from roosts to foraging areas in each tidal basin (A) and the relationship between the connectivity and the distance (m) between roosts and foraging areas (B). Black stripes are the median connectivity on a distance interval (m) indicated by the stripe width. Connectivity is on a log scale in this graph. From Bakker *et al.* (2021).

Dokter *et al.*, 2017; van der Kolk *et al.*, 2020). Thus, we expect that shorebirds will roost in the vicinity of their foraging areas which may be achieved by significant devaluation of food value over a distance of several kilometers. Bakker *et al.* (2021) conducted a very sophisticated analysis of travel distance between foraging sites and roosts. They analysed movement data from several tracking studies of Oystercatchers equipped with UvA-BiTS Global Positioning System (GPS) transmitters (Bouten *et al.*, 2013). The studies were conducted between 2008 and 2017 in four areas, namely Balgzand, Vlieland, Ameland and Schiermonnikoog. For a detailed description of the calculations, we refer to the original paper. Apart from travel distance, a connectivity table was obtained with values ranging from 0 to 1, where a 1 indicated that all birds using a particular roost foraged at one particular area, whilst a 0 indicated that no birds from the roost used a particular foraging area. From this, the travel distance could be obtained in each area (Figure 8 A.) as well as the relationship between connectivity and distance between roost and foraging area (Figure 8 A.). Very few Oystercatchers foraged further than 10 km from the roost, so a high devaluation of food value at that distance seems reasonable.

2.5.2 Structural equation modelling

Structural eqation modelling (SEM) is a general modelling framework in which factor analysis can be combined with multi-equation regression modelling Bollen (2014). Factor analysis attempts to determine which sets of variables share common variance-covariance characteristics that define the (latent) factors. A factor represents the common variation among a set of observed variables. Using SEM it is possible to study the relationships of latent variables to other observed measures. An advantage of this method compared to multiple regression, is that the individual benthos effects can be judged by considering the factor loadings and that elimination of predictors or model selection is not necessary. Here, overall foraging potential is modelled as a latent variable (F measured by P_{jst}) and its effect on the number of birds at the virtual roosts (N) is estimated. The relationship between the latent variable F(ξ in Lisrel notation) and the prey specific foraging potential P_s can be written

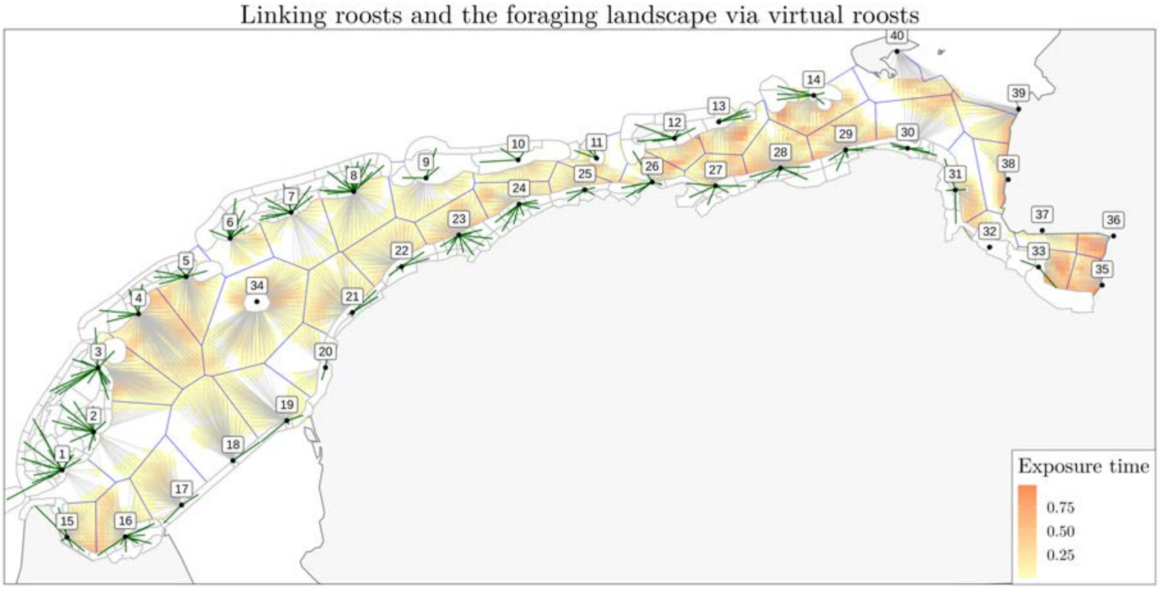


Figure 9: The spatial system consisting of the intertidal foraging landscape, counting areas (grey lines), and virtual roosts (black, numbered dots). Table 3 gives the geographic names that are related to the IDs of the virtual roosts. The green lines connect the counting areas to the virtual roosts. The blue lines represent borders between feeding zones and are based on Voronoi tessellation of the area around the virtual roosts. Virtual roosts 35-40 are placed along the Ems in Germany and on Borkum to avoid that intertidal foraging areas near roosts in Germany are allocated to roosts in the Netherlands. We have no data for the roosts in Germany and therefore virtual roosts 35-40 are not included in the analyses.

in matrix algebra terms as follows [4].

$$\begin{bmatrix} P_1 \\ P_2 \\ P_3 \end{bmatrix} = \begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \end{bmatrix} + \begin{bmatrix} 1 \\ \lambda_{P_2} \\ \lambda_{P_3} \end{bmatrix} \begin{bmatrix} F \end{bmatrix} + \begin{bmatrix} \delta_1 \\ \delta_2 \\ \delta_3 \end{bmatrix} = \alpha_P + \Lambda_P F + \delta_P \tag{2}$$

where P_s is the total weighed prey availability for each benthos species (eq. 1), α_P is the intercept vector, Λ_P is the matrix of factor loadings and F is the latent variable describing the overall foraging potential (per virtual roost and year) and δ_P is the factor for P_s. The coefficient of λ_{P_1} is set to one to provide a measurement scale for the latent variable F (λ_{P_2} and λ_{P_3} are multiples/fractions of λ_{P_1}) . The relationship between the number of birds as a function of F is given by

$$N \quad = \alpha_N + \Lambda_N F + \epsilon \tag{3}$$

where Λ_N is the regression coefficient describing the effect of F on N.

Before estimating a structural equation model the identification problem must be resolved. A SEM is identified when it is possible to uniquely estimate values of all of the parameters of the theoretical

---

[4] For simplicity, the indices for year and virtual roost are not included.

ID	Name	ID	Name	ID	Name
1	Texel - south	13	Schiermonnikoog - east	25	Frisian coast - Wierum
2	Texel - mid	14	Rottums	26	Frisian coast - Paezemerlannen
3	Texel - north	15	Noord-Holland - Balgzand	27	Groningen coast - west
4	Vlieland - west	16	Noord-Holland - Stroe	28	Groningen coast - mid
5	Vlieland - east	17	Afsluitdijk - west	29	Groningen coast - east
6	Terscheling - west	18	Afsluitdijk - mid	30	Eems-Dollard - Eemshaven
7	Terscheling - mid	19	Afsluitdijk - east	31	Eems-Dollard - North - Watum
8	Terscheling - east	20	Frisian coast Zurich - Harlingen	32	Eems-Dollard - Mid - Delfzijl
9	Ameland - west	21	Frisian coast Harlingen - Westhoek	33	Eems-Dollard - South - Dollard
10	Ameland - east	22	Frisian coast Westhoek - Zwarte Haan	34	Griend
11	Engelsmanplaat	23	Frisian coast Buitendijks west		
12	Schiermonnikoog - west	24	Frisian coast Buitendijks east		

Table 3: The ID numbers of the virtual roost and the related geographic names.

model (i.e. the implied covariance structure) with the sample data contained in the sample variance-covariance matrix. All models estimated in this report are identified because they meet the necessary and sufficient condition for identification Bollen (2014).

The fit of the model is based on the difference between the implied (Σ) and measured (S) covariance structure. The fit of the model is $F_{ML} = trace(S\Sigma^{-1}) - ln|S\Sigma^{-1}| - p$ and $\chi^2 = nF_{ML}$ where n is the number of observations. Another measure of the fit is the root mean square error of approximation ($RMSEA = \frac{\sqrt{(\chi^2-df)}}{\sqrt{(df(n-1))}}$) which for a good fitting model is lower than 0.1.

R^2 is the proportion of variance in an outcome that is explained by all predictors of that outcome. In the case of the number of birds, it is the proportion of variance that is explained by the latent variable F; it is computed as $R^2 = 1 - \frac{\hat{\sigma}}{\sigma_y}$ where $\hat{\sigma}$ is the estimated residual variance and σ_y is the model-implied variance of the data. We log-transformed the bird numbers and the prey biomass prior to estimation. To avoid taking the log of zero, we added 1 to the bird numbers and prey biomass. Log-transformed variables are denoted with a prime (e.g. $N' = log(N+1)$).

In the appendix we present the model residuals on log-scale which is the difference between the observed and the implied covariance matrices. In the results section we present the mismatch (M) between N and F in absolute terms. It is computed as $M = N - \hat{N}$, where N is the observed[5] number of birds and $\hat{N} = e^{\alpha_N + \Lambda_N F} - 1$.

Illustration

We did a very simple simulation to illustrate the principle and the SEM methodology for computing the mismatch. First we generated a dataset consisting of correlated random variables $P_1 = 1, 2, ..., 25$, $P_2 = 2P_1$, and $P_3 = 4P_1$ representing correlated food predictors (akin to the biomass of benthos linked to the roosts). N represents the observed number of birds and is a function of food density,

---

[5] More accurately, it is the mean of the *imputed* number of birds (see 2.3).

i.e. $N = P_1 + P_2 + P_3$. Random Gaussian noise was added to each of the random variables. Then we estimated the structural equation model depicted in figure 10 showing the factor loadings $\lambda_{P_1} = 1.00, \lambda_{P_2} = 2.27, \lambda_{P_3} = 4.25$ and the regression coefficient $\lambda_N = 7.83$. These results correspond well with the simulation parameters.

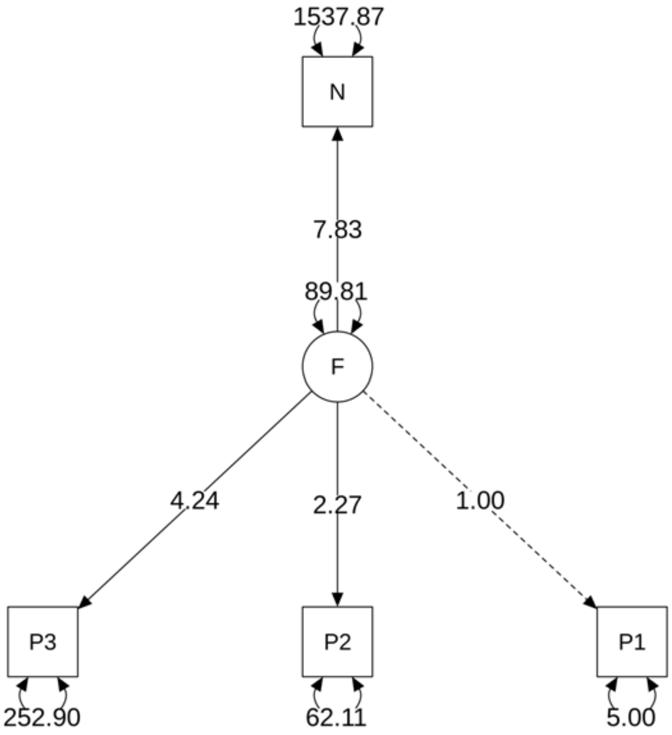


Figure 10: Stuctural Equation Model with prey availability P_1, P_2, P_3 and latent variable F describing the overall foraging potential and the number of birds (N). The data underlying this graph are simulated to provide an illustration of the principle of estimating the model and computing mismatches.

The estimated model is used to compute $\hat{N} = \alpha_N + \lambda_N F$. In figure 11 $\hat{N}$ is plotted against the simulated N. The difference between the two is the mismatch ($M = N - \hat{N}$). If it is positive, there are more birds than expected on the basis of food (“overutilization”, green lines). If it is negative, there are fewer birds than expected on the basis of food (“underutilization”, red lines).

2.6 Characteristics of roosting areas

Natural and human disturbance An important requirement for high tide roosts is that the levels of disturbance by predators and humans are low. In recent years, more and more information is collected on disturbance, but standardized quantitative data is still largely lacking. In addition, the available data about disturbance is at a spatially and temporally coarser level than the counts at the actual roosting sites. We therefore decided not to incorporate the disturbance pressure quantitatively

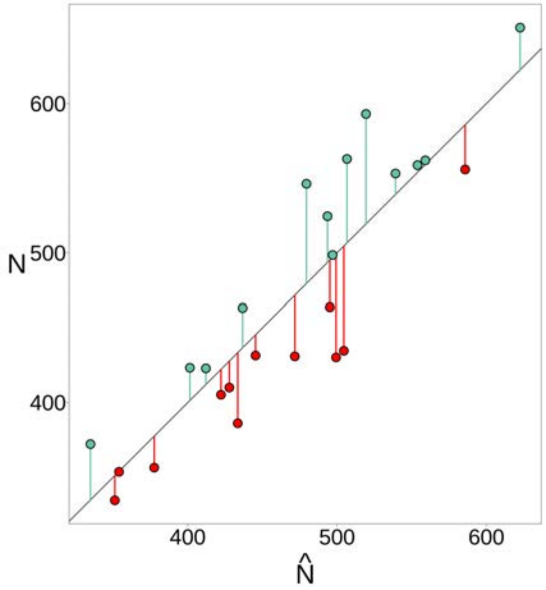


Figure 11: Illustration on the basis of the simulation: scatterplot of the predicted ($\hat{N}$) and observed (N) number of birds and the mismatch depicted by red (“underutilization”) and green (“overutilization”) lines.

in the spatial analyses. However, in order to interpret the results of our mismatch analyses, we made maps of natural and human disturbance based on field knowledge of experts and predator counts. To investigate if underutilization was due to high disturbance levels, we compared the maps of mismatches in bird numbers with the disturbance maps.

We interviewed the (voluntary) birdcounters of Sovon and asked them about their specific observations with regard to disturbance and other characteristics at the counting areas. This enabled us to calculate semi-quantitative measures of disturbance, i.e. *Frequency of disturbance* (with classes low-1, medium-2, and high-3) and *Intensity of disturbance* (with classes low-1, medium-2, and high-3) (see table 4 for the explanation of these classes). Total human disturbance was calculated by multiplying frequency and intensity (values ranging 1 till 9) per roosting area.

To get insight in the levels of natural disturbance by air predators, average Peregrine numbers were calculated based on bird counts done by volunteers of Sovon in each counting area. Other birds of prey species can also cause disturbance of waders, but to interpret the results of our mismatch analyses we only use Peregrine numbers. Detailed information about the distribution of foxes and their role in natural disturbance is lacking. In general, we assume that foxes only occur on the mainland.

Other characteristics In addition to disturbance, we also made an investigation of the general characteristics such as vegetation height, available area in relation to high tides and local specific issues. This was done on the basis of literature research and field knowledge of employees and volunteers of Sovon and site managers.

Characteristics Roosting area	**Type**	**Classes**
Human disturbance	Frequency	1. low: next to the counting crew few or no other people in the area 2. medium: next to the counting crew with some regularity also other people in the area 3. high: next to the counting crew almost always many other people in the area
	Intensity	1. low: the disturbances by humans affect a small part of the birds present 2. medium: the disturbances by humans affect part of the birds present 3. high: the disturbances by humans affect all or almost all birds present
	Sources	(mostly) cyclists and/or walkers (with dog), and/or tourist by boat and/or water sporters (mud walking, surfers, canoeists)
	Closed nature area art. 2.5	yes/no
	Nature area	Permanent or closed in breeding season
	Comments	
Natural disturbance	Peregrines	average number (Sep - Mar)
	Intensity disturbance by peregrine/birds of prey	1. minor: a few birds fly up 2. moderate: some of the birds fly up 3. large: all or almost all birds fly up
	Fox	yes/no
	Comments	
Other characteristics	High vegetation in autumn and winter	yes/no
	Roost still in use with (very) high tides	yes/no
	Comments	

Table 4: Overview of the parameters used to define the characteristics of counting areas.

3 Results

3.1 Benthos

Figure 12 shows the importance and the annual variation of the different benthos prey species in terms of biomass ($g\ m^{-2}$), numeric density (specimens m^{-2}), and the percentage of occupied sites (occupancy, %) for the twelve studied shorebird species (Table 2). In this figure, the mean values are based on all specimens of all sizes; in the shorebird-specific analyses selections on the basis of size and burying depths are made. It shows that the common cockle (*Cerastoderma edulis*) has the highest average biomass followed by lugworm (*Arenicola marina*) sandgaper (*Mya arenaria*), razor clam (*Ensis leei*) and baltic tellin (*Limecola balthica*). The numeric density of these relatively large species are small compared to e.g. the mudsnail (*Peringia ulvae*), armored bristleworm (*Scoloplos armiger*) and *Corophium sp*. Species for which the occupancy is high, tend to occur throughout the Wadden Sea. For a detailed description of relationships with abiotic factors we refer to Folmer *et al.* (2017).

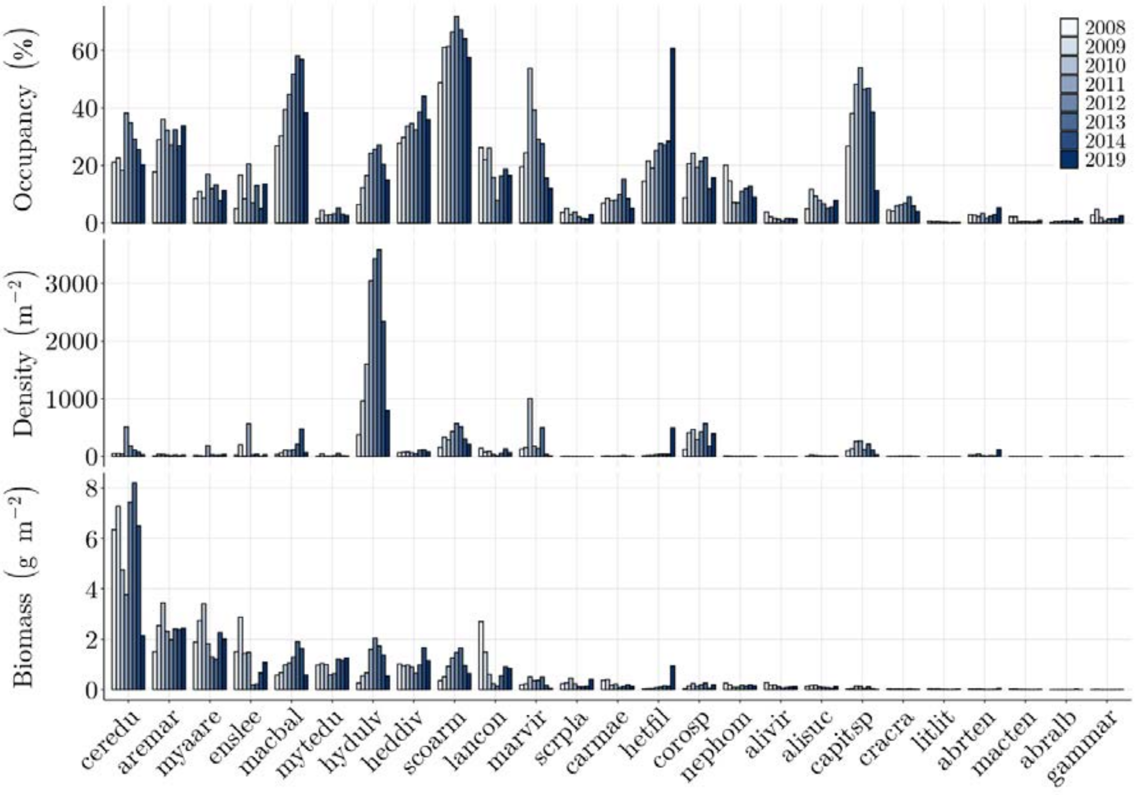


Figure 12: Average biomass ($g\ m^{-2}$), numeric density (specimens m^{-2}) and occupancy (%) for the benthos species in the Dutch Wadden Sea in the period 2008-2014 and 2019 that are consumed by the twelve shorebird species studied in this report. See Table 1 for abbreviations and species names.

3.1.1 Comparing surveys: cockles and Baltic tellin

Overall, the spatial distributions of both species are similar between the SIBES and MosKok surveys (Figure 31). This pattern also shows up when the data are aggregated per tidal basin (Figure 32). Both programs show that the density of cockles is higher in the eastern Dutch Wadden Sea and that the highest densities of Baltic Tellins occur near the shores.

3.2 Birds

In this section trends are shown for each of the twelve shorebird species. Trends are presented for the entire Dutch Wadden Sea for 14 subareas by lumping local counting areas. We also took into account that species differ in the way they use the Wadden Sea in the course of the year, including migratory populations joining a resident population to spend the winter, and different subspecies where one subspecies only occurs during migration, whereas the other subspecies spends the winter in the Wadden Sea.

3.2.1 Oystercatcher

The Dutch Wadden Sea is an important wintering area for the minority of Dutch Oystercatchers that breed in the area itself, as well as for a large part of the majority of Dutch Oystercatchers breeding inland. During winter, these residents and inland migrants are supplemented with birds breeding in Scandinavia, Finland and Russia. The juveniles and immatures of these northernpopulations do not migrate to the breeding areas until three years old, so comprise the bulk of the birds counted in spring. The overall numbers of juveniles and immatures are slightly declining, and this slight decline is also evident in many local areas. In contrast, the total number of wintering Oystercatchers has almost halved since 1995 (Figure 13), which is in line with the continuing decline of the winteringpopulation in the Dutch and German Wadden Sea (Blew *et al.*, 2016), and many other parts of Europe (van de Pol *et al.*, 2014). This population decline occurs in nearly all local areas, except for three areas in the western part of the Dutch Wadden Sea: Westhoek – Harlingen, Griend – Richel, and Balgzand, where the numbers are relatively stable.

Photo by Tom Voortman

Many different factors contribute to the decline of the Oystercatcher population. It includes overexploitation of shellfish (blue mussels and cockles) which mainly took place in in the 1990s (Ens, 2006). However, since then these shellfish stocks have recovered (Troost *et al.*, 2021)). Other important factors underlying the decrease include the increased risk of flooding of nests and chicks of saltmarsh breeding Oystercatchers (van de Pol *et al.*, 2010), agricultural intensification affecting the large number of inland breeding Oystercatchers (Kampichler *et al.*, 2013), which also suffer from an increase in predation of nests and chicks. Human disturbance of roosts may have impacts locally, but it is not likely a major cause of the population decline.

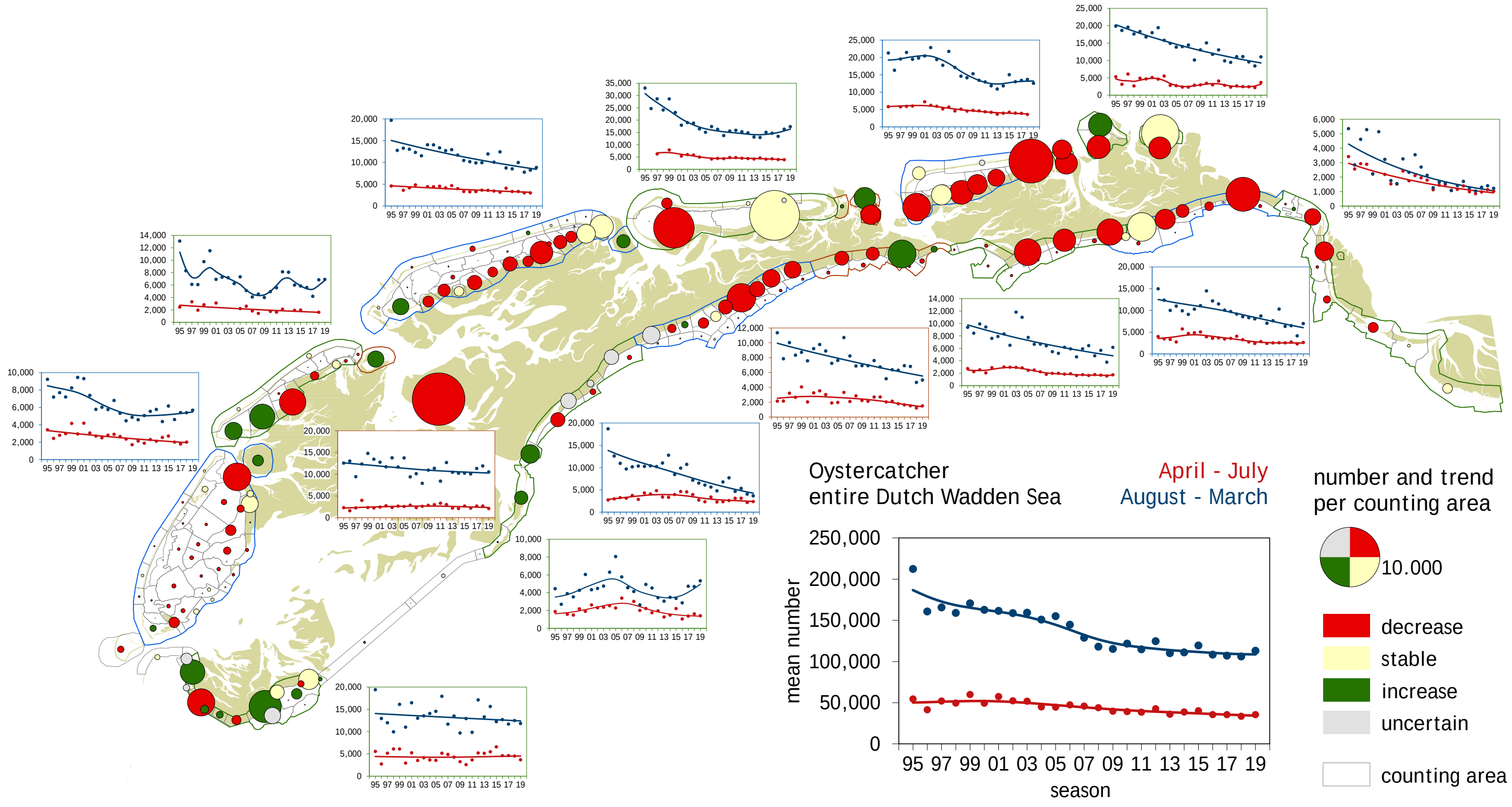


Figure 13: Oystercatcher - spatial distribution and population trends along the high tide roosts in the Dutch Wadden Sea.

3.2.2 Red Knot

The Dutch Wadden Sea is used by two subspecies of Red Knot (Van Roomen *et al.*, 2018). The subspecies *canutus* breeds on the arctic tundra in Siberia and winters in Africa and uses the Wadden Sea as a stopover. The subspecies *islandica* breeds on the tundra in Canada and Greenland and winters in the Wadden Sea and other estuaries in western Europe. *Canutus* only migrates through the Dutch Wadden Sea in late summer, early autumn. In spring, it uses the German Wadden Sea as a stopover. Overall, numbers in late summer – early autumn have increased in the Dutch Wadden Sea (Figure 14) while the numbers in the German Wadden Sea have declined (Blew *et al.*, 2016). The largest concentrations of Knots are found on Griend-Richel. On Balgzand, Terschelling, Amelandand east Friesland the numbers have increased since the beginning of this century. On Griend-Richel, Schiermonnikoog and the Rottums there are strong fluctuations in the numbers. From November to July numbers (mainly islandica) are lower and fluctuating for the Dutch Wadden Sea as a whole. In areas with large numbers, the trends resemble each other. This is not the case for Balgzand, where wintering numbers are stable in contrast to a strong increase in numbers during late summer – autumn. In the major stronghold Griend-Richel, wintering numbers have declined since 2012.

Photo by Hanneke Dalmeijer

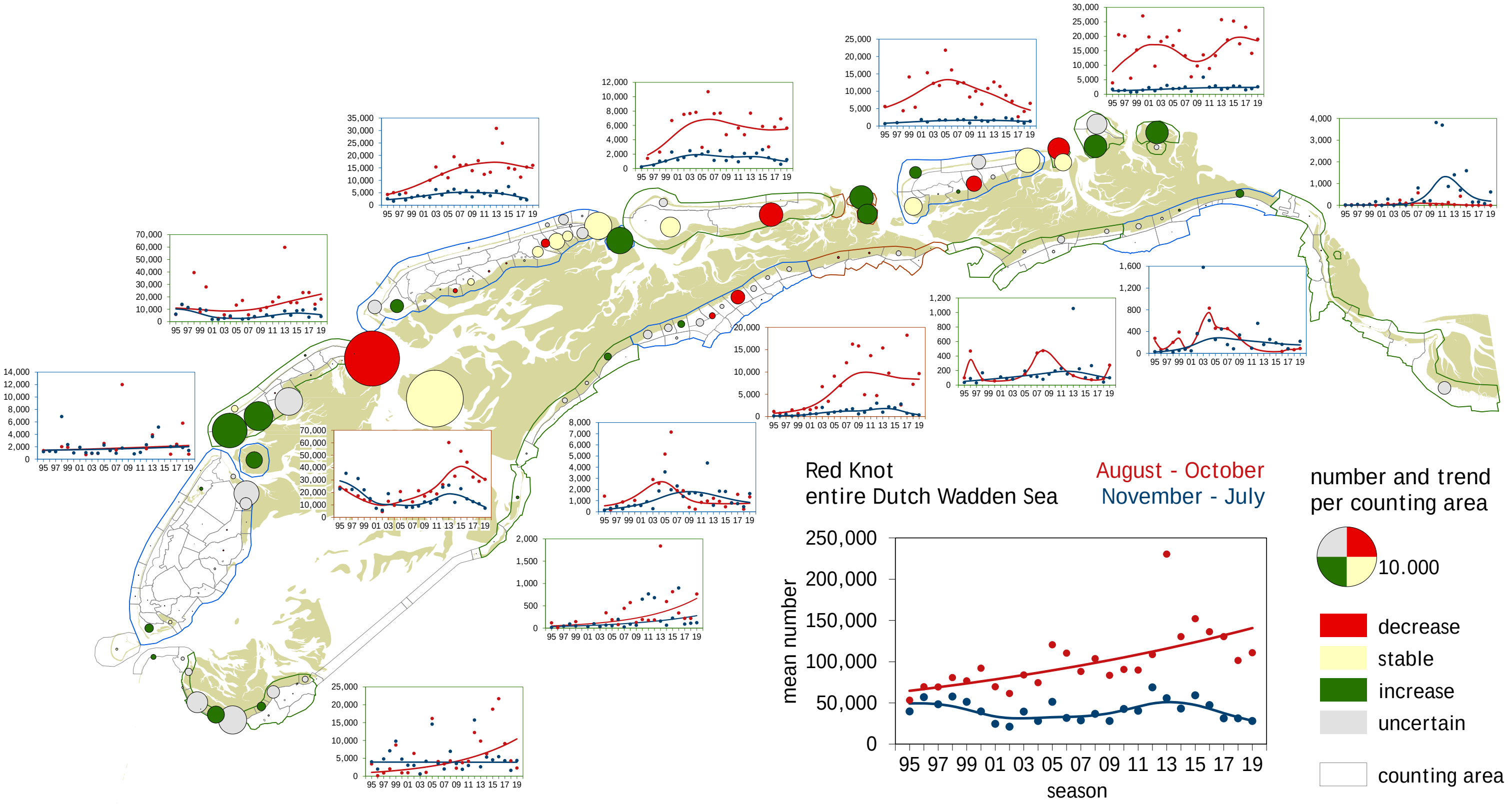


Figure 14: Red Knot - spatial distribution and population trends along the high tide roosts in the Dutch Wadden Sea.

3.2.3 Curlew

Curlews wintering in the Dutch Wadden Sea arrive in July and depart in April to their breeding grounds in Scandinavia, Finland, the Baltic states and Russia. The nonbreeding immatures stay in the Dutch Wadden Sea during summer, so comprise the bulk of the population counted in May and June. There is no clear overall trend during May & June, nor are there clear differences in trends between areas (Figure 15). About 100.000 Curlews winter in the Dutch Wadden Sea. There is an indication that the number of wintering Curlews increased between 1995 and 2005 and slightly decreased since then. The latter decline is also observed for the entire European population (Van Roomen *et al.*, 2018). Curlews are distrubuted quite evenly throughout the Dutch Wadden Sea. The declines in wintering numbers since the beginning of the century occurred along the Frisian and Groningen coast, on Ameland and on Texel. Wintering numbers show an increase on Balgzand, Harlingen-Westhoek, Dollard and Vlieland since 1995 after which they stabilize around 2005. Wintering numbers are relatively stable on Terschelling and the Rottums and fluctuate on Schiermonnikoog.

Photo by Hanneke Dallmeijer

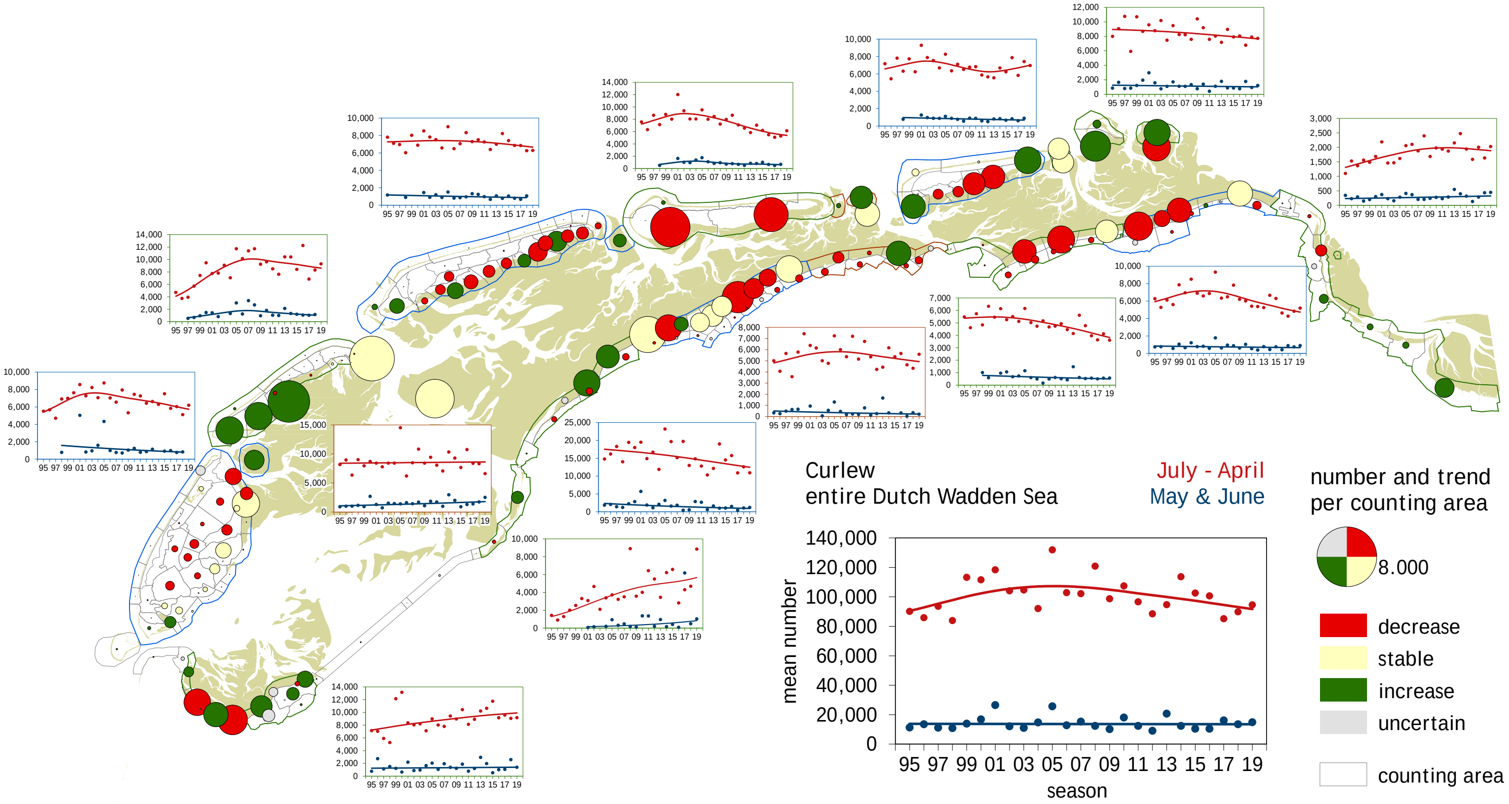


Figure 15: Curlew - spatial distribution and population trends along the high tide roosts in the Dutch Wadden Sea.

3.2.4 Dunlin

In contrast to the German and Danish Wadden Sea, where Dunlins continue to decline (Blew *et al.*, 2016), average numbers in the Dutch Wadden Sea have increased from 170.000 to 250.000 during 1995-2019 (Figure 16). The main regions where Dunlins concentrate are Vlieland (including Richel), Frisian coast east, Schiermonnikoog east, the Rottums and the Dollard. There are clear increases in numbers on Balgzand, Frisian coast, western Groningen coast, Texel, Vlieland and Terscheling. A decline is visible on Griend, Ameland and the eastern Groningen coast. There are no cleartrends on Schiermonnikoog and the Rottums.

Photo by Jeroen van Wijk

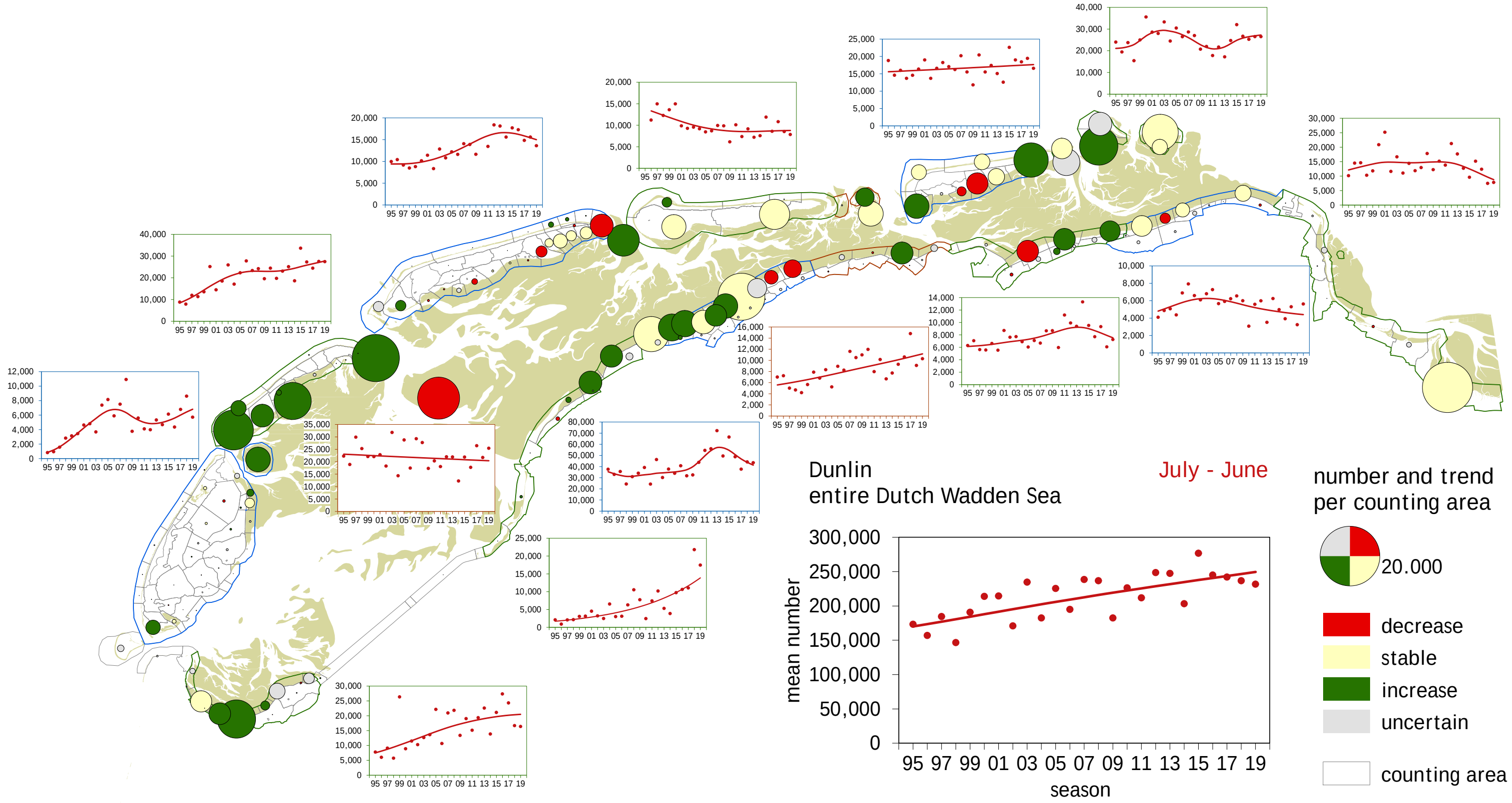


Figure 16: Dunlin - spatial distribution and population trends along the high tide roosts in the Dutch Wadden Sea.

3.2.5 Grey Plover

Grey Plovers breed on the Siberian tundra and spend the winter in European and African estuaries. Some Grey Plovers use the Dutch Wadden Sea as a stopover during autumn and spring migration, whereas others spend the whole winter in this area. Especially during spring migration in May the numbers are high in the Dutch Wadden Sea during which time they varied between 40,000 and 80,000 in the period 1995-2019. These numbers during spring migration slightly increased and are much higher than the numbers from August to April, which include the wintering birds (Figure17). The number of wintering birds are also slightly increasing.This general pattern is different from the German Wadden Sea, where numbers decline (Blew *et al.*, 2016). The increase in numbers in the Dutch Wadden Sea occurs evenly across most areas. On Texel, Terschelling and Schiermonnikoog average numbers do not differ much between the two time periods. On the Rottums the numbers during spring migration have declined steeply and are now lower than the number of wintering birds.

Flock of waders including Red Knots, Dunlins and Grey Plovers. Photo by Stephan Sprinz

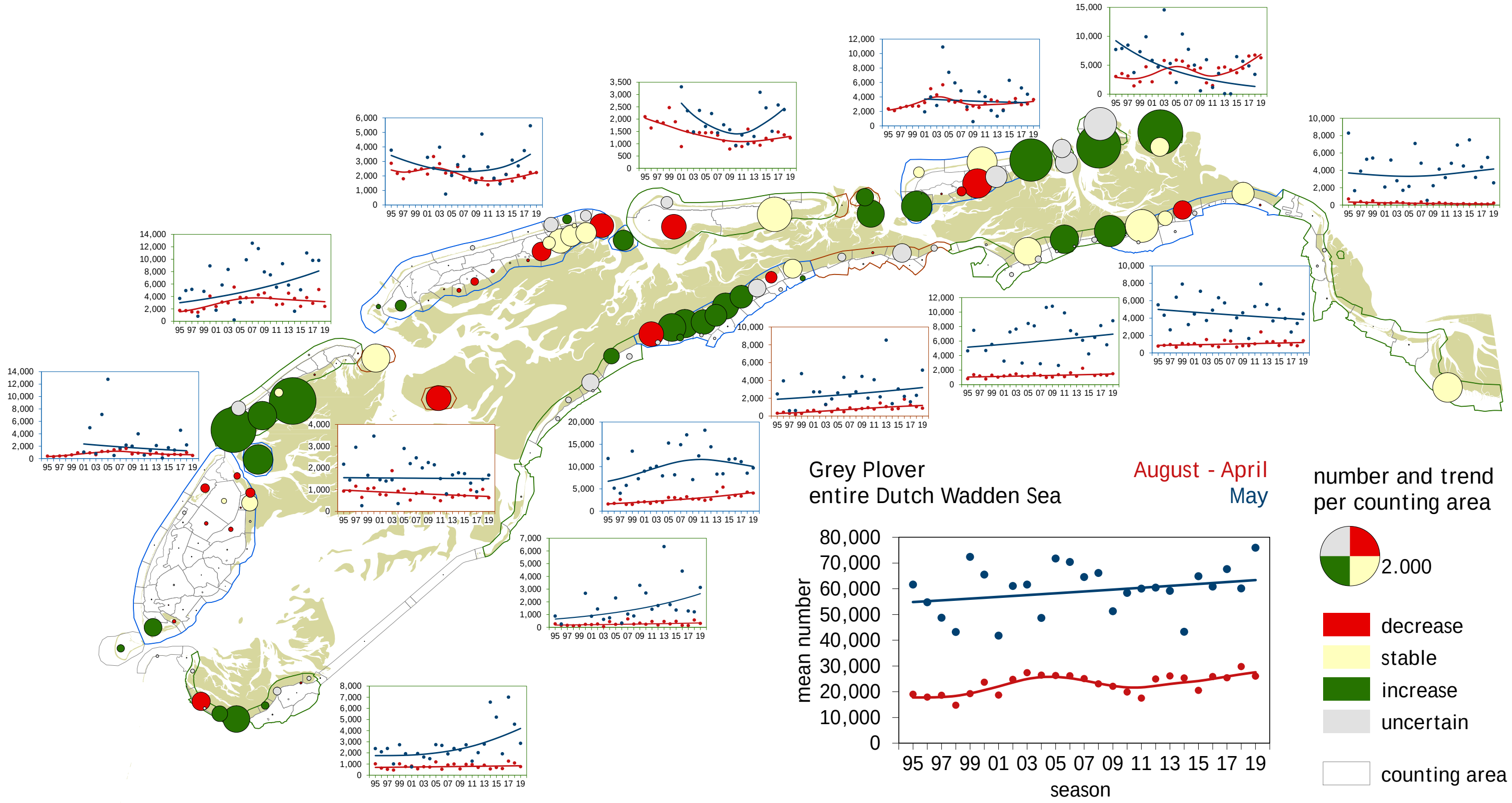


Figure 17: Grey Plover - spatial distribution and population trends along the high tide roosts in the Dutch Wadden Sea.

3.2.6 Bar-tailed Godwit

Two subspecies of Bar-tailed Godwit depend on the Wadden Sea (Van Roomen *et al.*, 2018). *Lapponica* breeds in northern Fennoscandia east to the Kanin Peninsula and winters in western Europe. The *taymyrensis* subspecies migrates through western Europe (mainly the Wadden Sea) to winter in western and southern Africa. The numbers of wintering *lapponica* (October to April) have inceased from 20,000 in 1995 to 40,000 in 2005 and are currently fairly stable. The numbers are higher in spring and late summer, when taymyrensis uses the Wadden Sea as a stopover. The numbers during the migration months also show a moderate increase in the Dutch Wadden Sea (Figure 18). The largest concentrations of Bar-tailed Godwits are found on Griend-Richel and Vlieland. There is considerable variability in densities and trends between local areas. Declines during the migratory period are evident along the central Frisian and Groningen coast, Dollard and Schiermonnikoog. In contrast, numbers increased on Balgzand, Texel and Vlieland during the migratory period. Wintering numbers increased on Balgzand, Texel, Vlieland, Terschelling and Rottum. In contrast, wintering numbers declined on Griend-Balgzand. Remarkably, on Griend and Balgzand during winter, numbers are higher than during the migratory period. On Texel and Vlieland, numbers are similar.

Photo by Harvey van Dieck

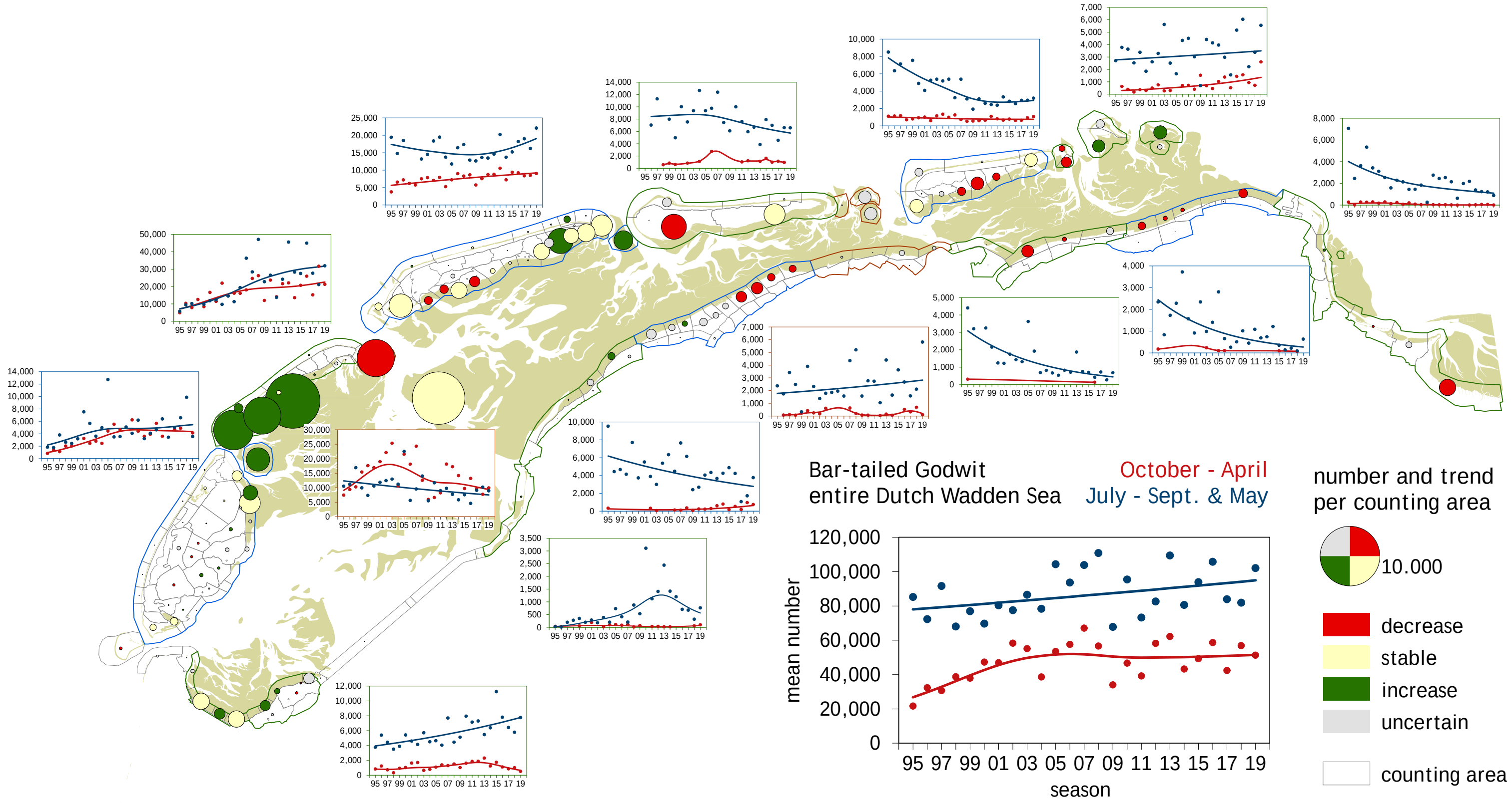


Figure 18: Bar-tailed Godwit - spatial distribution and population trends along the high tide roosts in the Dutch Wadden Sea.

3.2.7 Turnstone

Turnstones have subpopulations showing similar migratory behaviour to the subspecies of the Red Knot. Turnstones breeding in Northeast Canada and Greenland spend the winter in the western Europe, whereas Turnstones breeding in the high arctic of northern Scandinavia and Russia winter in western Africa (Van Roomen *et al.*, 2018). The number of Turnstones passing through the Dutch Wadden Sea is much higher than in the other parts of the international Wadden Sea (Blew *et al.*, 2016). Yet, only a few thousand Turnstones occur in the Dutch Wadden Sea. The numbers show a non-constant increase (Figure 19) which corresponds to the trends in most local areas holding a relatively large number of Turnstones. In contrast, along the East Frisian coast – Engelsmanplaat, numbers have declined. Numbers appear stable on Balgzand and the Frisian coast near Harlingen.

Photo by Jurgen Hamann

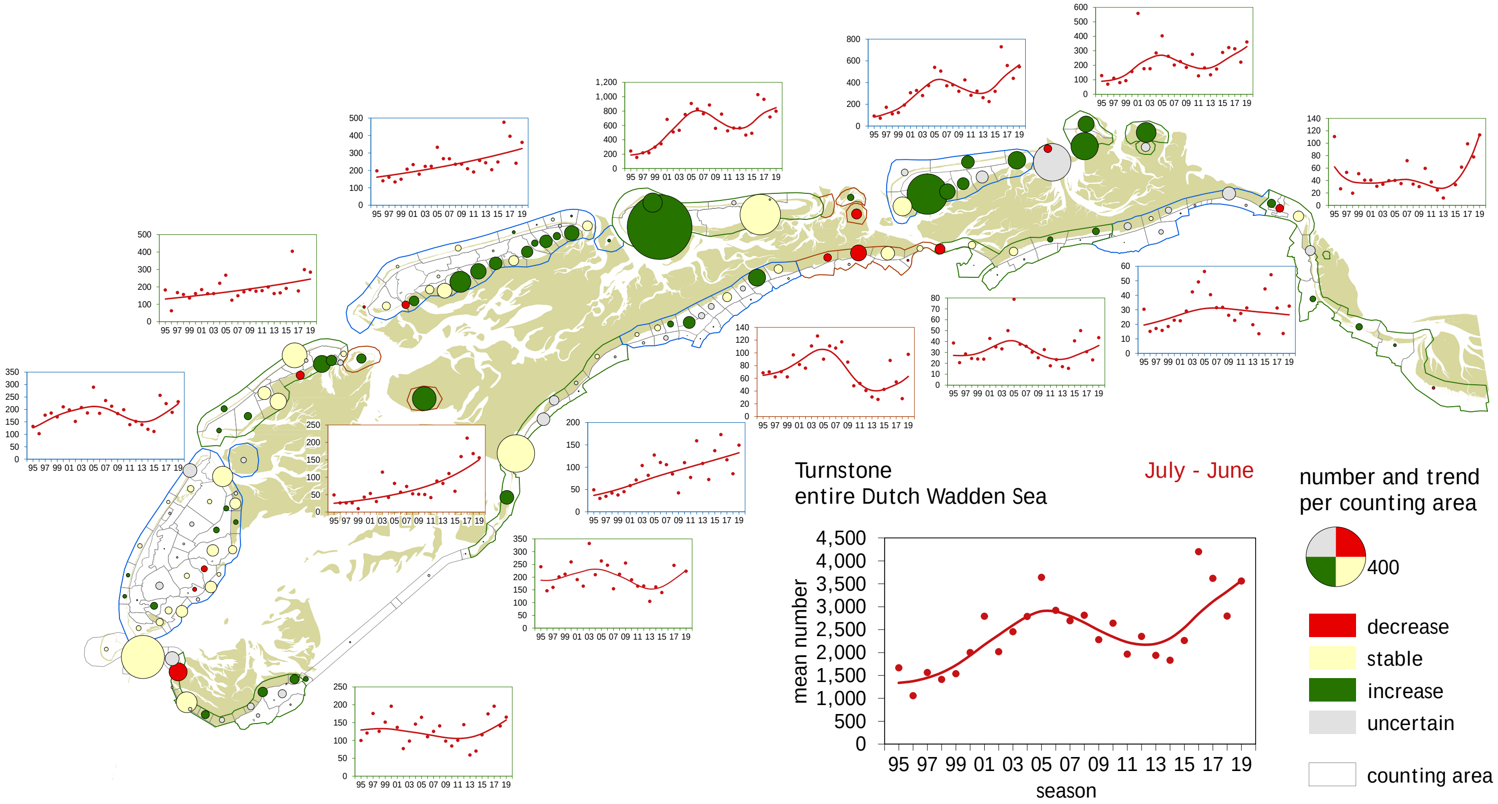


Figure 19: Turnstone - spatial distribution and population trends along the high tide roosts in the Dutch Wadden Sea.

3.2.8 Ringed Plover

In the Wadden Sea, large numbers of Ringed Plover only occur during autumn migration in August - September and during spring migration in May (Figure 20). A very small number stays to spend the winter. Numbers have increased in all parts of the international Wadden Sea, except for Lower Saxony where numbers have declined. The most pronounced increase has occurred in the Dutch Wadden Sea (Blew *et al.*, 2016). The Ringed Plover is distributed relatively evenly across the roosting sites but the largest concentrations are found at the Rottums. The increase is evident in all local areas holding a sizable number of Ringed Plover.

Photo by Jeroen van Wijk

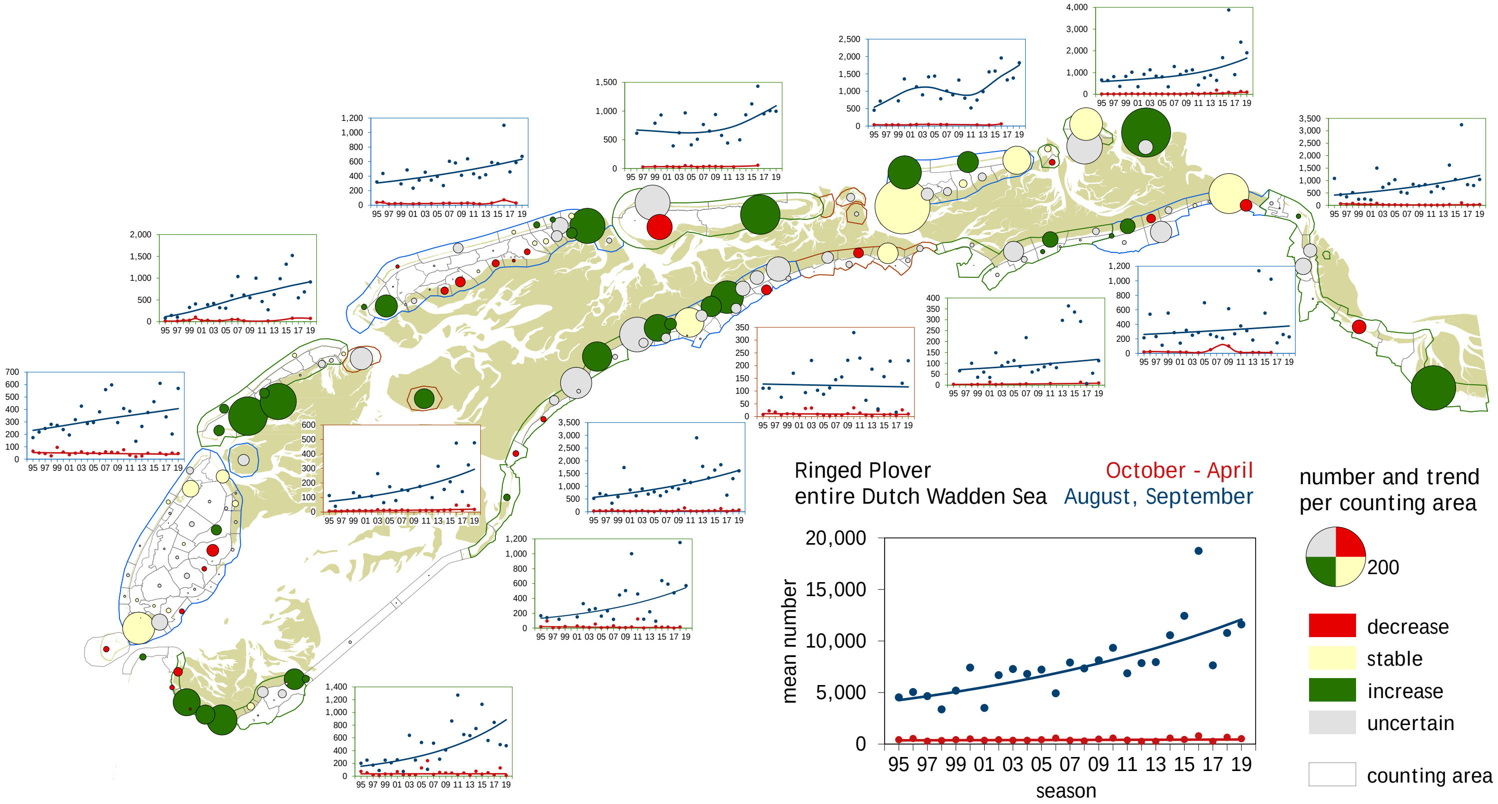


Figure 20: Ringed Plover - spatial distribution and population trends along the high tide roosts in the Dutch Wadden Sea.

3.2.9 Redshank

Two subspecies of Redshank depend on the Wadden Sea (Van Roomen *et al.*, 2018). *Totanus* breeds in or near the Wadden Sea and gathers in the area during late summer before southward migration. *Robusta* breeds in Iceland and winters in the Wadden Sea and other estuaries around the North Sea. In the Dutch Wadden Sea as a whole, numbers during late summer (*totanus*) are considerably higher than numbers in winter and spring (mainly *robusta*) (Figure 21). Both the late summer and the winter/spring numbers have remained relatively constant during the period 1995-2019. [kan ook niet anders]. For both late summer and winter, numbers seem first to go up and then go down on Texel, Vlieland, Schiermonnikoog and the central Frisian coast. In contrast, numbers increase on Balgzand and the Frisian coast near Harlingen. A continuing decline is evident on Ameland, east Frisian coast, Groningen coast and Dollard. Numbers of Redshank are low and relatively stable in the Danish Wadden Sea, but high and declining in the German Wadden Sea (Blew *et al.*, 2016).

Photo by Bruno Ens

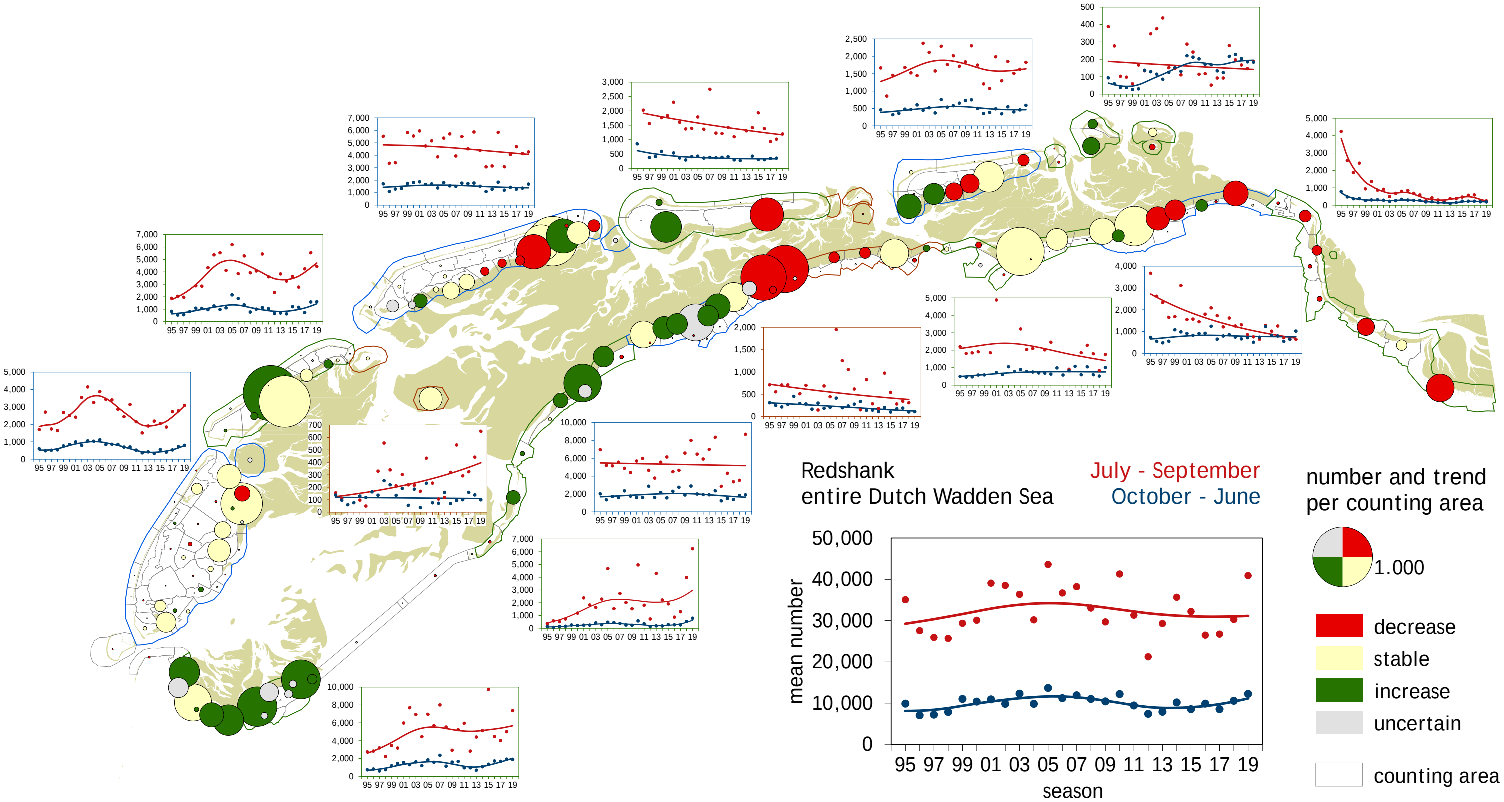


Figure 21: Redshank - spatial distribution and population trends along the high tide roosts in the Dutch Wadden Sea.

3.2.10 Avocet

The Wadden Sea is the northern limit of the breeding range of the Avocet (Van Roomen *et al.*, 2018). During late summer and autumn, the birds breeding around the Wadden Sea gather in large flocks in the Wadden Sea. Many migrate south during winter and numbers are much lower at that time of year. In spring, numbers increase, but are much lower than in late summer and autumn (Figure 22). The bulk of the Avocets in the Dutch Wadden Sea occur at the Frisian mainland coast and in the Dollard. The seasonal differences are also evident in the local populations, except for the Dollard, where numbers in winter and spring sometimes exceed the autumn numbers. Whereas the European population as a whole shows a slight increase (Van Roomen *et al.*, 2018), the numbers in all parts of the international Wadden Sea show a decline (Blew *et al.*, 2016). This decline is also evident in the autumn numbers, and to a lesser degree in the wintering numbers, in the Dutch Wadden Sea as a whole and in many local areas. Again, the Dollard is different as both autumn numbers and wintering numbers don't show a clear trend. The decline of the Wadden Sea population of Avocets is linked to a low reproductive success (Koffijberg *et al.*, 2017). This is probably due to an increased risk of predation on the mainland, where most Avocets breed. Furthermore, Avocets breeding in the saltmarshes suffer from an increased risk of flooding (van de Pol *et al.*, 2010).

Photo by Koos Dansen

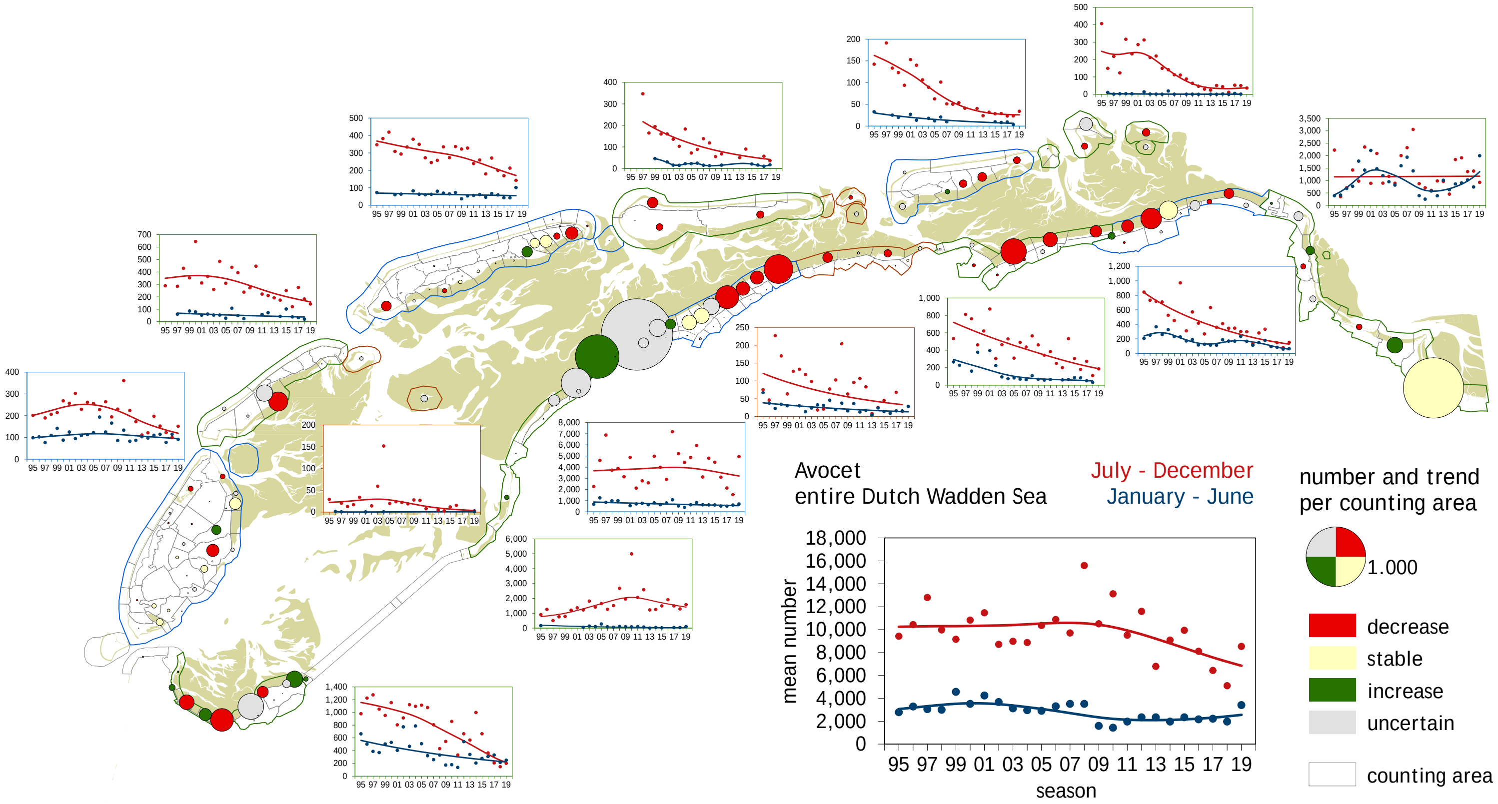


Figure 22: Avocet - spatial distribution and population trends along the high tide roosts in the Dutch Wadden Sea.

3.2.11 Greenshank

The Greenshank breeds in boreal and arctic habitats in the north of Europe and mainly winters in Africa (Van Roomen *et al.*, 2018). The population is judged as stable (Van Roomen *et al.*, 2018). The Wadden Sea is used as a stopover site during spring and autumn migration. In the Dutch Wadden Sea, the Greenshank is not very numerous, but numbers during autumn are much higher than during spring. This pattern is also clear in local areas (Figure 23). In recent years, autumn numbers show a decline in the Dutch Wadden Sea. This recent decline is evident in most local areas, except for the Dollard. Along the Groningen coast, the numbers increased in the period 1995-2009 after which they declined. Numbers also declined in the German Wadden Sea, but increase in the Danish Wadden Sea (Blew *et al.*, 2016). Thus, what we observe may be mainly a redistribution within the international Wadden Sea.

Photo by Hans Hillewaert

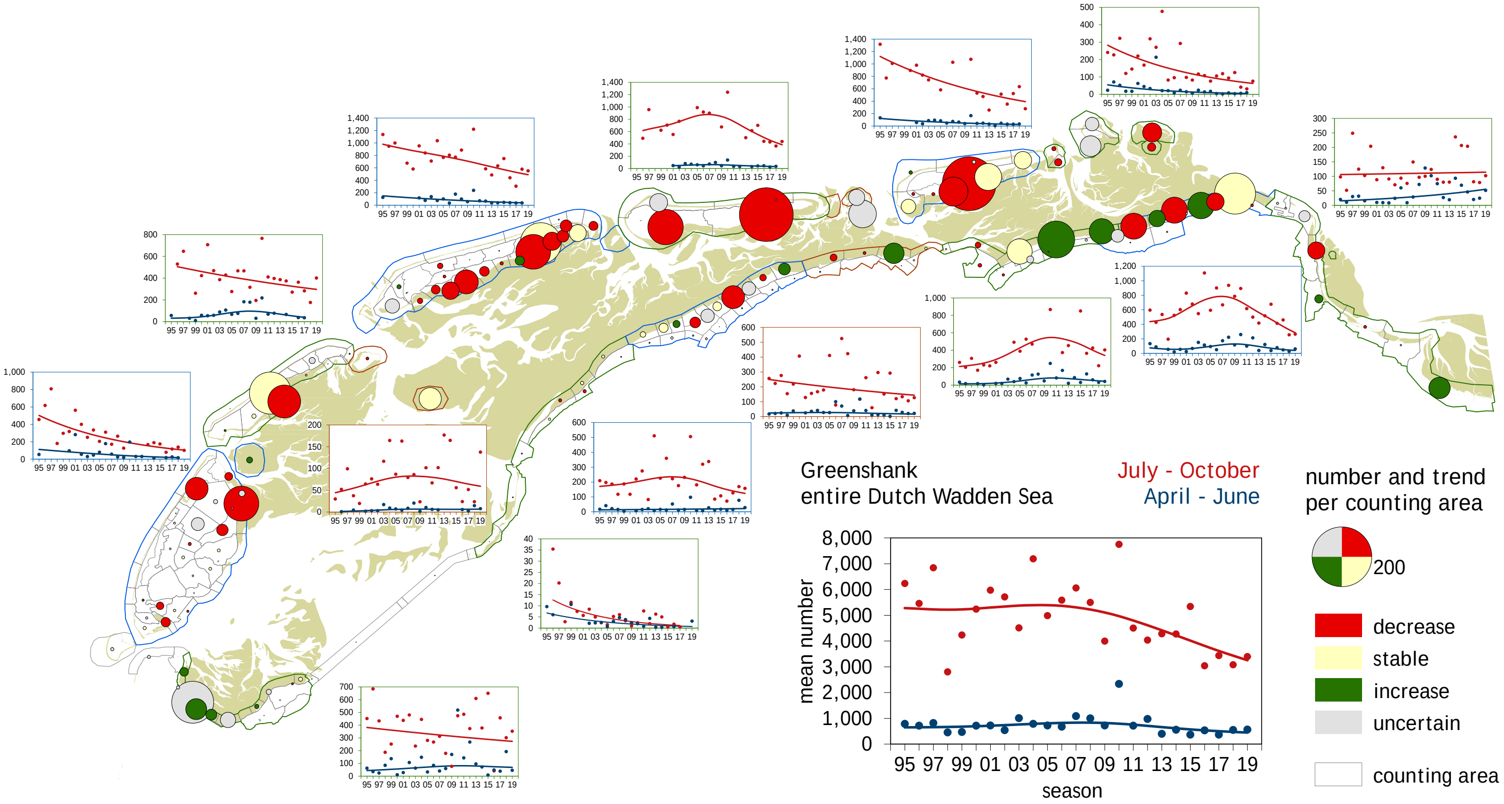


Figure 23: Greenshank - spatial distribution and population trends along the high tide roosts in the Dutch Wadden Sea.

3.2.12 Spotted Redshank

The Spotted Redshank breeds in northern Fennoscandia and northern Russia, and winters in Africa. It uses the Wadden Sea as a stopover site during spring and autumn migration (Van Roomen *et al.*, 2018). Numbers are declining in all parts of the international Wadden Sea (Blew *et al.*, 2016). The numbers of Spotted Redshanks in the Dutch Wadden Sea are low and numbers are higher during autumn migration than during spring migration (Figure 111). Declines are evident for both periods and this general pattern is clear in nearly all local areas where relatively high numbers of Spotted Redshank occur. The one exception being the Dollard, which is the major stronghold in the Netherlands. Numbers are higher during autumn migration, but after an initial decline, numbers have increased during both spring and autumn. As a result, the trend for the Dollard is classified as stable for the period 1995-2019.

Photo by Ian Kirk

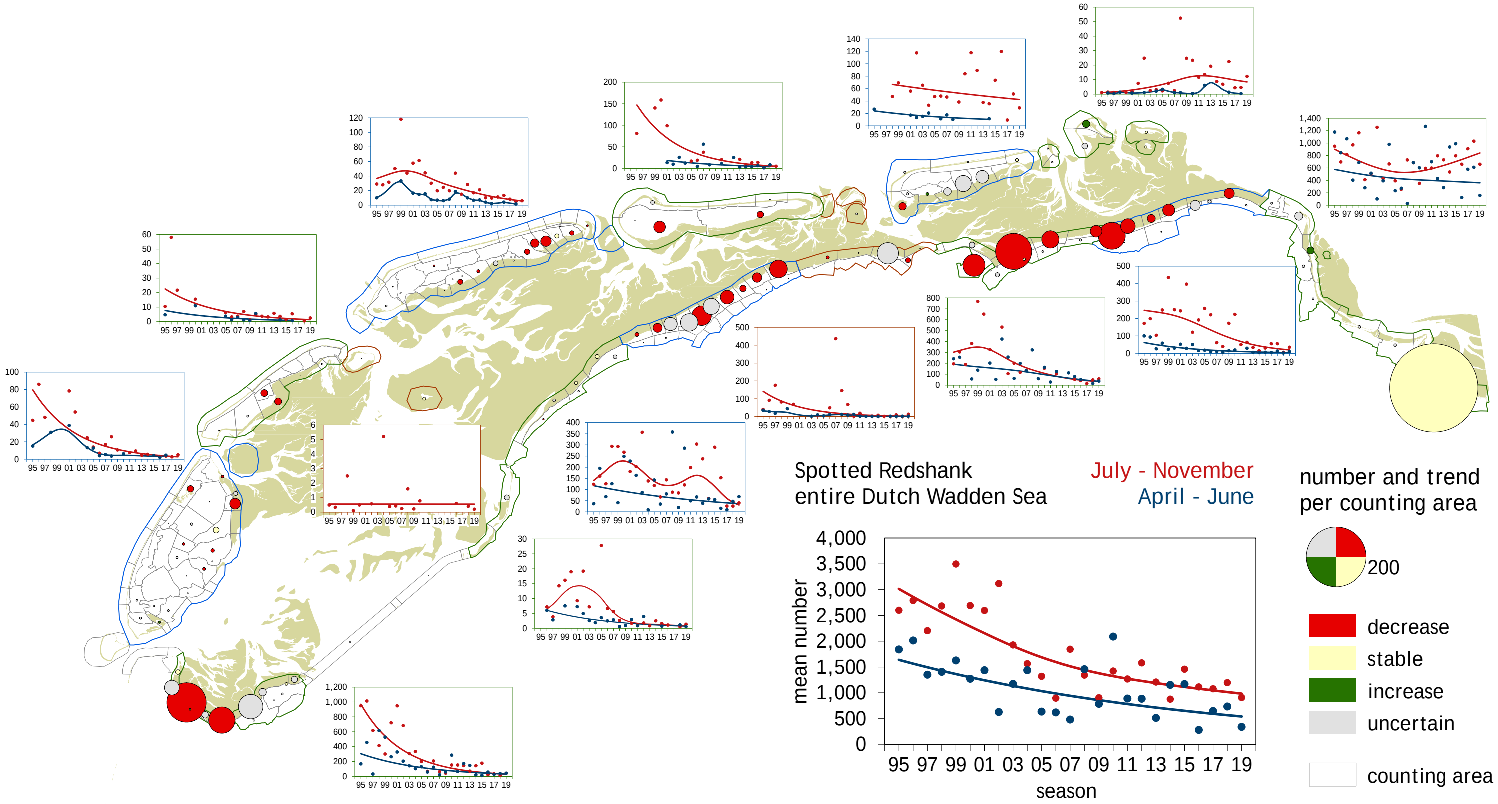


Figure 24: Spotted Redshank - spatial distribution and population trends along the high tide roosts in the Dutch Wadden Sea.

3.3 SEM - mismatch

In this paragraph, we present the results of the statistical analyses. For each shorebird species and for each virtual roosting site, we calculated the foraging potential (i.e. the nearby food supply based on diet, habitat and distance) and the number of birds and analyzed the relation between the two. The difference between the modelled and the actual counted number of birds provides an estimate of the mismatch which is used to identify areas that are “underutilized” (fewer birds are found than expected on the basis of the food supply) and areas that are “overutilized” (more birds are found than expected on the basis of the food supply). In the Mismatch plots (Figures 25 and 26), red dots are cases of under-utilization (negative mismatch) and green dots are cases of over-utilization (positive mismatch).

Oystercatcher The foraging potential (i.e. the amount of available food nearby, eqation 2) for Oystercatchers is highest around roosts at the western part of Vlieland, Griend and in the eastern part of the Wadden Sea (Figure 25 and 38). This is partly reflected in Oystercatcher numbers and in the mismatch between numbers and food: numbers are relatively high and utilization of roosts is generally better on the islands (e.g positive mismatch at Griend, Terschelling, Ameland and Rottums) than on the mainland coast. Exceptions are Vlieland, where numbers are lower then expected based on food, and the southern part of Balgzand, where numbers are higher than expected based on food.

Red knot The foraging potential for Red knots is highest around roosts at Balgzand, Griend and in the eastern part of the Wadden Sea (Figure 25, 44 and 48). Knot numbers are higher and the utilization of roost is generally better on the western islands (e.g Griend, Vlieland including Richel, Ameland) than on the mainland coast. For both subspecies, utilization of the Groninger mainland coast is lower than expected. On Vlieland numbers are higher than expected based on food. Knots prefer to roost in large flocks on large open sand flats with a clear view. It is believed that this preference is linked to minimizing the risk of predation by Peregrines. Social aggregation (i.e. aggregation independent of the clustering of food) leads to a mismatch with the ideal-free distribution and thus a mismatch with the food distribution (Folmer *et al.*, 2010, 2012).

Curlew The foraging potential for Curlews is highest around roosts at Balgzand, the Western part of Vlieland, Griend and in the eastern part of the Wadden Sea (Figure 25 and 54). Curlew numbers are widely distributed across the Wadden Sea. Utilization of roosts is lower than expected in the eastern part of the Wadden Sea and at Griend. Roosting areas with higher numbers than expected, are Balgzand, Zwarte Haan and Friesland Buitendijks.

Dunlin The foraging potential for Dunlins is highest around roosts at the Western part of Vlieland, Griend and in the eastern part of the Wadden Sea (Figure 25 and 60). Large numbers of Dunlins can be found at the Northern part of Texel and the western part of Vlieland, Friesland Buitendijks and at the Rottums. Utilization of roosts is lower than expected in the eastern part of the Wadden Sea and at Griend. Roosting areas with higher numbers than expected, are Vlieland, Zwarte Haan, Friesland Buitendijks, western part of Ameland and the Dollard.

Grey plover The foraging potential for Grey plovers is highest around roosts at the western part of Vlieland, Griend and in the eastern part of the Wadden Sea (Figure 25 and 66). Grey plover numbers are higher and utilization of roost is generally higher at the northern part of Texel and the western part of Vlieland, Friesland Buitendijks, Rottums and middle part of the Groningen coast. Roosting areas with lower numbers than expected, are Balgzand, Griend and several parts of the mainland coast, such as the area around Wierum and the eastern part of the Groningen coast.

Bar tailed godwit The foraging potential for Bar tailed godwits is highest around roosts at Vlieland including Richel, Griend and in the eastern part of the Wadden Sea (Figure 25, 72 and 76). Large numbers are found in the western part of the Wadden Sea, mainly on Vlieland, Richel and Griend. The general trend is that numbers are higher than expected at roosts on the islands in the western part of the Wadden Sea. Numbers are lower than expected in the eastern part of the Wadden Sea. There are no large differences in numbers and utilization of roosts between the two periods.

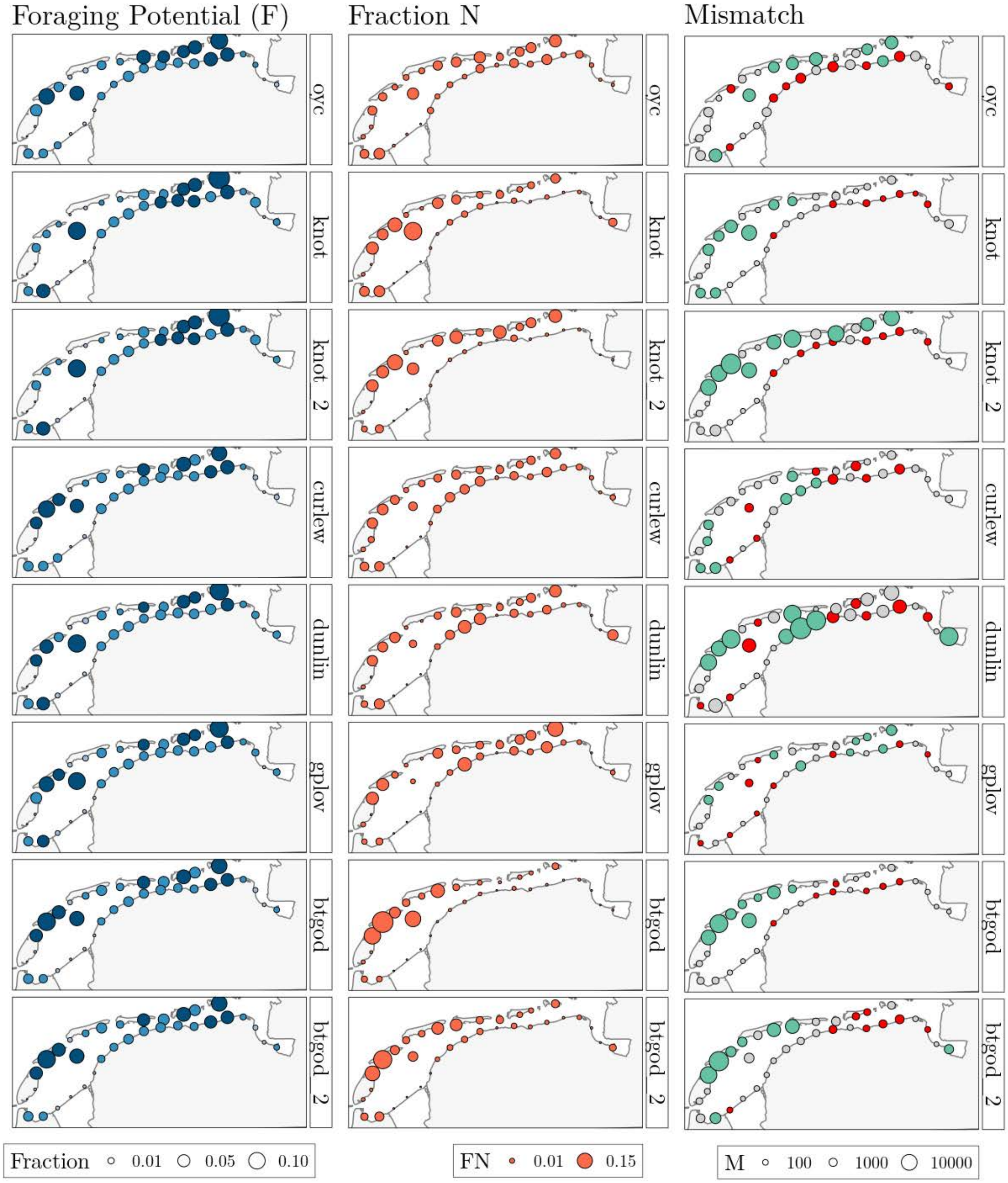


Figure 25: Foraging Potential (left), Fraction of birds (middle) and mismatch (right) between bird numbers and their food. When in the right margin "_2" is added to the shorebird species, it refers to the second period as defined in section 2.3. In the Foraging Potential plots the light blue dots are the roosts with the lowest 1/3 foraging potential; blue are the 1/3 intermediate roosts and darkblue are the 1/3 roosts with highest foraging potential. In the Mismatch plots, the dots are red in the case of under-utilization (negative mismatch, fewer birds than expected) and green in the case of over-utilization (positive mismatch, more birds than expected).

Turnstone The foraging potential for Turnstones is highest around roosts at Balgzand, western part of Vlieland, Griend and in the eastern part of the Wadden Sea (Figure 26 and 82). This is partly reflected in Turnstone numbers and in the mismatch between numbers and food: numbers are relatively high and utilization of roosts is generally higher on Balgzand and on the islands Ameland, Schiermonnikoog and Rottums. Utilization of roosts is lower than expected across the Frisian and Groningen coast.

Ringed plover The foraging potential for and numbers of Ringed plover are more or less evenly distributed across the Wadden Sea, with relatively high numbers at the Rottums (Figure 26 and 88). Utilization of roosts is higher at Vlieland, Ameland, Rottums, Westhoek, Peazemerlannen and the Dollard. Roosting areas with lower numbers than expected are Griend, Wierum, Engelsmanplaat and the Groningen coast.

Redshank The foraging potential for Redshank is good in many parts of the Wadden Sea and Redshanks also occur throughout the Wadden Sea (Figure 26, 94 and 98). Numbers are relatively high on the eastern part of Terschelling and at Friesland Buitendijks. Roosting areas with higher numbers than expected, are Balgzand, western part of Vlieland, eastern part of Terschelling, Zwarte Haan and Friesland Buitendijks. Utilization of roosts is lower than expected in the eastern part of Vlieland and Griend and in general in the eastern part of the Wadden Sea. Because the food supply calculations do not correct for season, and because the distributions during the two periods (representing different subspecies of Redshank) are rather similar, the utilization is also very similar.

Avocet The foraging potential for Avocets is highest across the relatively muddymainland coast (Figure 26 and 104). Yet, the majority of birds aggregate in only two areas: the area Westhoek - Zwarte Haan - Friesland Buitendijks and the Dollard. Roosting areas with higher numbers than expected, are the southern part of Balgzand, western part of Vlieland, the area Westhoek-Zwarte Haan-Frieslandbuitendijks and the Dollard. Utilization of roosts is lower than expected at the eastern part of Ameland, Schiermonnikoog, Wierum, Peazemerlannen, middle part of the Groningen coast and northern part of the Eems-Dollard.

Greenshank The foraging potential for and number of Greenshanks are more or less evenly distributed across the Wadden Sea (Figure 26 and 110). Yet, the birds are nearly absent from the Frisian west coast. The general trend is that numbers are higher than expected based on food at roosts on the islands and on parts of the Groningen coast. Number are lower than expected on the eastern part of Vlieland, southern part of Balgzand, Griend, parts of the Frisian coast and the Rottums.

Spotted redshank The foraging potential is evenly distributed throughout the Wadden Sea, yet the large majority of Spotted Redshank occur in the Dollard (Figure 26 and 116). Roosting areas with higher numbers than expected based on food, are the northern part of Balgzand, Friesland Buitendijks, western and middle part of the Groningen coast (saltmarshes), western part of Schiermonnikoog and the Dollard. Utilization of roosts is lower than expected at Vlieland, Griend, western part of the Frisian coast and parts of the eastern islands.

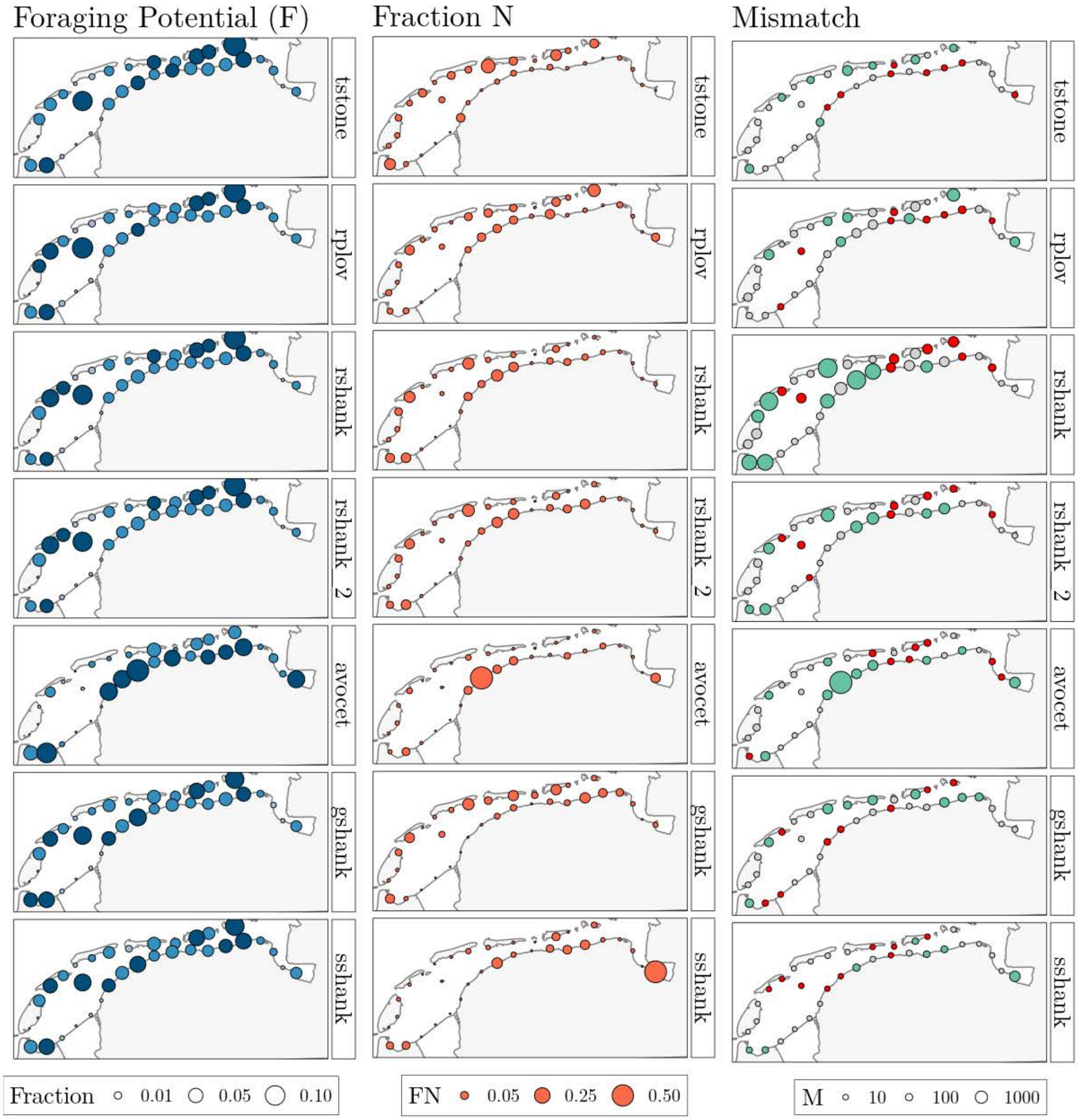


Figure 26: Foraging Potential (left), Fraction of birds (middle) and mismatch (right) between bird numbers and their food. See the caption of figure 25 for further details.

3.4 Disturbance

3.4.1 Peregrine

Three raptor species regularly cause disturbance of roosting shorebirds in the Wadden Sea: Marsh Harrier (during summer), Hen Harrier (during winter) and Peregrine (Polwijk *et al.*, 2018). Among these three, Peregrines are probably the most dangerous for shorebirds. Although large shorebirds, like Oystercatchers can be killed, especially mid-sized shorebirds like Knot and Bar-tailed Godwit are vulnerable to predation by Peregrines (van den Hout *et al.*, 2008). Peregrines will also take small shorebirds, like Dunlin, when these are easy to catch after a long migratory flight (Bijlsma, 1990). In the 1970s, Peregrines were very rare due to poisoning with DDT, but following the ban on DDT in Europe, there numbers increased. Nowadays, dozens of Peregrines are counted in the Wadden Sea during high tide, especially in winter. Probably, the actual mortality that they inflict on the shorebirds is not very high, but their primary impact may be through disturbance and the avoidance behaviour that they induce among the mid-sized species (Van den Hout, 2009). It has been suggested that Knot avoid the eastern Wadden Sea in winter in response to the relatively high number of Peregrines wintering there (Buiter *et al.*, 2016). It is certainly the case that Peregrines are more common in the eastern part of the Wadden Sea (Figure 27). There is little variation in their distribution between years, which may be related to their territorial behaviour.

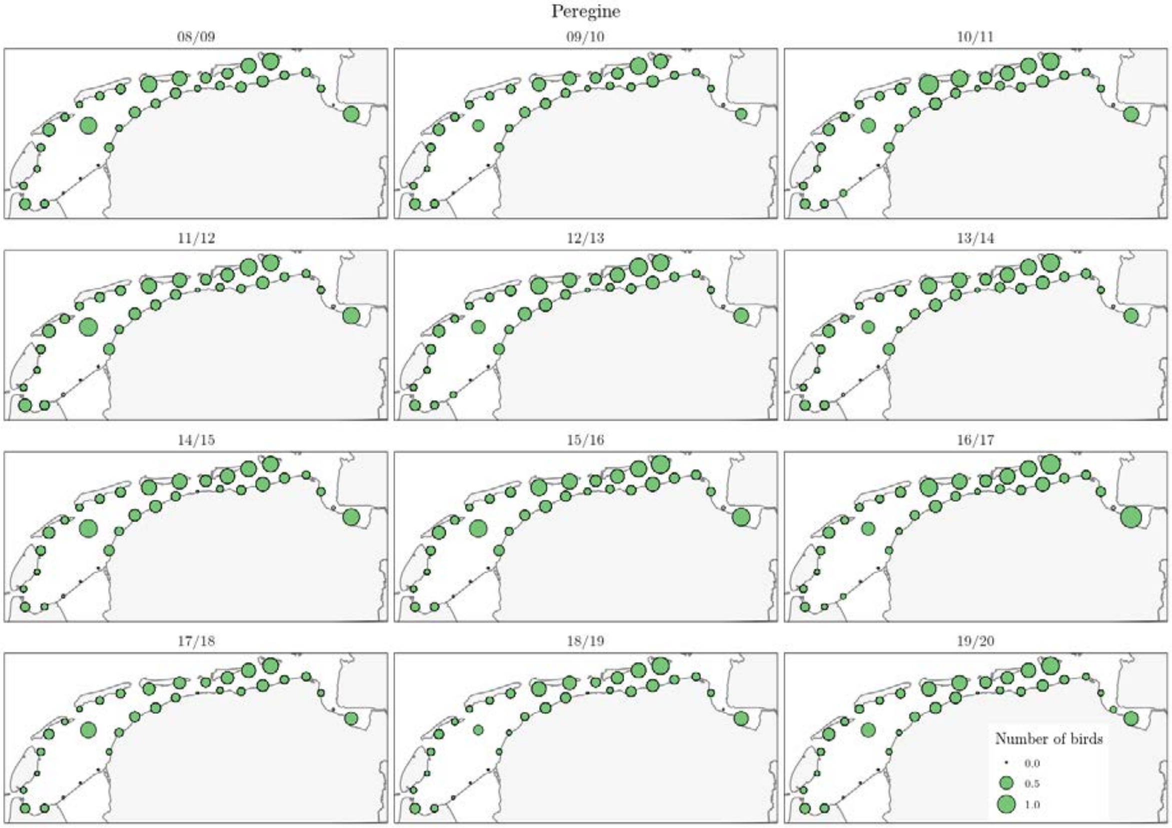


Figure 27: The distrubution of Peregrine along the virtual high tide roosts during the period 2008-2020.

3.4.2 Human disturbance

In this paragraph, general patterns with respect to human disturbance are described. A detailed description of the roosting areas and local disturbance, based on the input of the volunteers who counted these areas, is given in Appendix C (in Dutch).

Figure 28 shows that human disturbance is more frequent and more intense in the western part of the Wadden Sea than in the eastern part of the Wadden Sea. Human disturbance is also higher on the islands Texel, Vlieland, Terschelling and Ameland than on the island Schiermonnikoog and the mainland coast.

Specific areas on the islands with relatively much human disturbance are: the North Sea beaches of the islands Texel, Vlieland, and Ameland, part of the Vliehors, the eastern part of Vlieland, Groene Strand at Terschelling and the east point of Terschelling.

Specific areas along the mainland coast with relatively high levels of human disturbance are: the area Koehool-Westhoek- Zwarte Haan and the area Holwerd-sluices Lauwersmeer in Friesland and the saltmarshes near the Westpolder in Groningen.

Very specific sites within counting areas that do not pop up in these maps (figure 28), but are classified as areas with specific disturbance issues, are specific parts of the Noordsvaarder (e.g. by walkers (with dogs), mountainbikers and watersport activities), Vogelpolle and Westhoek (e.g. by cyclists and walkers close by or in the area, which is especially a problem with very high tides), Nieuwlandsreid-Zoute weide (e.g. by mountainbikers crossing the area), Engelsmanplaat (e.g. by surfers from the mainland) and Paezemerlannen (e.g. by cyclist, walkers, crossmotors and surfers) (see Appendix C for more details).

The main sources of (severe) human disturbances are cyclists (including mountainbikers), walkers (with dogs) and locally, (kite)surfers.

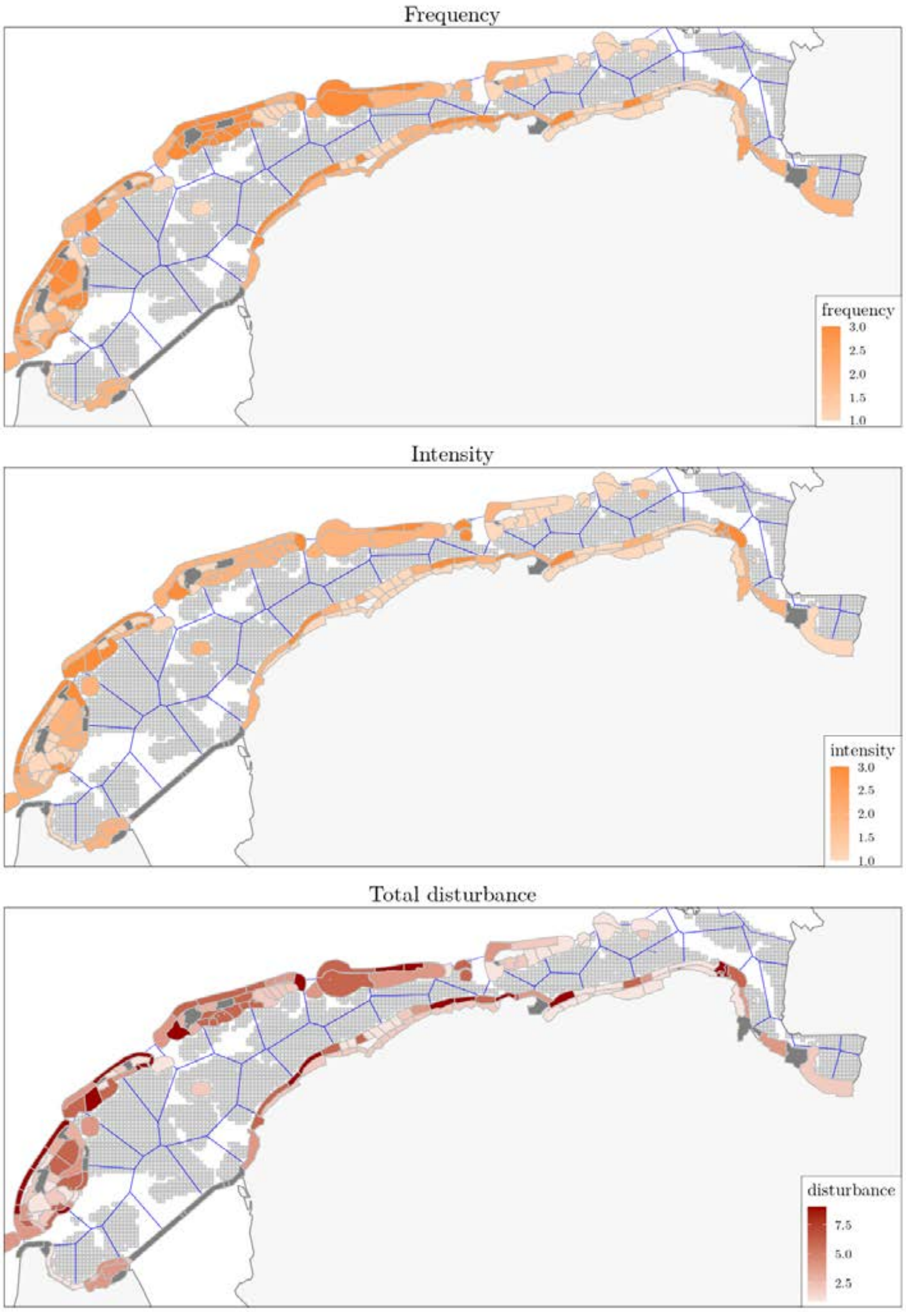


Figure 28: Frequency of disturbance, intensity of disturbance, and total disturbance (frequency × intensity)

3.4.3 Roost site characteristics

Besides natural and human disturbance, we also investigated environmental characteristics of roost sites to get further insight in roost quality. We qualitatively investigated four factors that may influence a wader's choice where to roost: 1) presence of tall cover or vegetation succession, 2) spatial limitations (i.e. surface area), 3) nearby alternative roosts and 4) risk of flooding during high tides. We interviewed the birdcounters of Sovon and asked them about their specific observations with regard to these environmental characteristics at the counting areas. In this paragraph, general patterns are described. A detailed description of the counting areas is given in Appendix C (in Dutch).

Presence of tall cover or vegetation succession

Vegetation succession is locally an issue, for example on Griend, Westhoek (Friesland), Karhoek (Texel), and parts of the Groningen coast. On Griend, birds move to Richel when very high tides forces them towards the vegetation. The Westhoek area has a narrow zone with low pioneer vegetation, but the remaining area of the saltmarsh consists of high reed vegetation. The limiting space on the saltmarsh, in combination with regular disturbance of cyclists and walkers on the dike, makes the whole area unsuitable for roosting. Wadden Sea wide, tall cover and roughening of the vegetation seems not to be a structural issue for roosting birds. But locally, vegetation conditions may be improved and the effects are expected to differ per species. Large species like Curlew readily roost in high saltmarsh vegetation, whereas small species are often reluctant to do so. Further research into the effects of vegetation on roosts is required.

Spatial limitations

Some roosting areas are relatively small, like several saltmarshes along the coast. Examples are Westerse Veld-Vlieland, Striep-Terschelling, Vogelpolle-Ameland, Stroe-Noord Holland and Wierum-Friesland. The small size is not directly an issue for the roosting site, apart from the fact that it can accommodate fewer birds. The size becomes particularly problematic during very high tides and when the levels of disturbance are high. Roosting birds are then forced to move elsewhere. For example, the Westerse veld is the only suitable roosting area at the east point of Vlieland. In summer, when the levels of disturbance caused by walkers is high, birds move away from the Westerse veld.

Large roosting areas that are surrounded by rich foraging grounds and experience relatively low human disturbance are important for roosting birds. Examples of these areas are Vliehors, Griend, Rottums, the saltmarshes of Terschelling, Ameland and Schiermonnikoog, Friesland Buitendijks, Groningen saltmarshes and the Dollard. In these areas, birds have the opportunity to move to nearby areas. At other locations, roosting sites may be more isolated, like Westhoek and Vogelpolle. At Westhoek it has been observed that during extremely high tides, roosting birds will fly to Zwarte Haan or Griend, the latter with a distance of 19 km.

Almost all roosts that border directly to the Wadden Sea are not (or less) in use during very high tides. Birds move inland and to higher areas like beaches, high tidal flats and high saltmarshes like Rif, Richel and Rottums. Less space during very high tides in roosting areas in itself seems no structural issue for roosting birds, if nearby alternatives are available.

In summary, quality of roosts rapidly declines when roosting space is limited or becomes limited during (very) high tides in combination with high levels of disturbance and no suitable roost nearby. This is the case at a.o. Westhoek, Vogelpolle, saltmarshes Striep and Wierum. Birds are then forced into a small area between the water and the source of disturbance and move away. In some cases, like the Vogelpolle on Ameland, birds leave or even avoid this area when disturbance by humans is too high. At Ameland it is even observed that birds stay in the air during high tide.

3.5 Synthesis

In this study, we analyzed the trends and spatial distributions of a broad spectrum of selected shorebird species (i.e. Avocet, Bar-tailed Godwit, Oystercatcher, Curlew, Red knot, Dunlin, Spotted redshank, Common redshank, Greenshank, Turnstone, Grey plover and Ringed plover) in the Dutch Wadden Sea. Subsequently, we analyzed the numbers at the roosts as a function of the availability of food resources in the vicinity of the roosts and related the mistmatches to possible sources of disturbance at the roosts. Our analyses reveal several common and striking patterns regarding high tide roost usage by the twelve selected species. Figure 29 gives per species an overview of the overall trend in the Wadden Sea, the foraging potential and the local roost usage for each species per virtual roosting site.

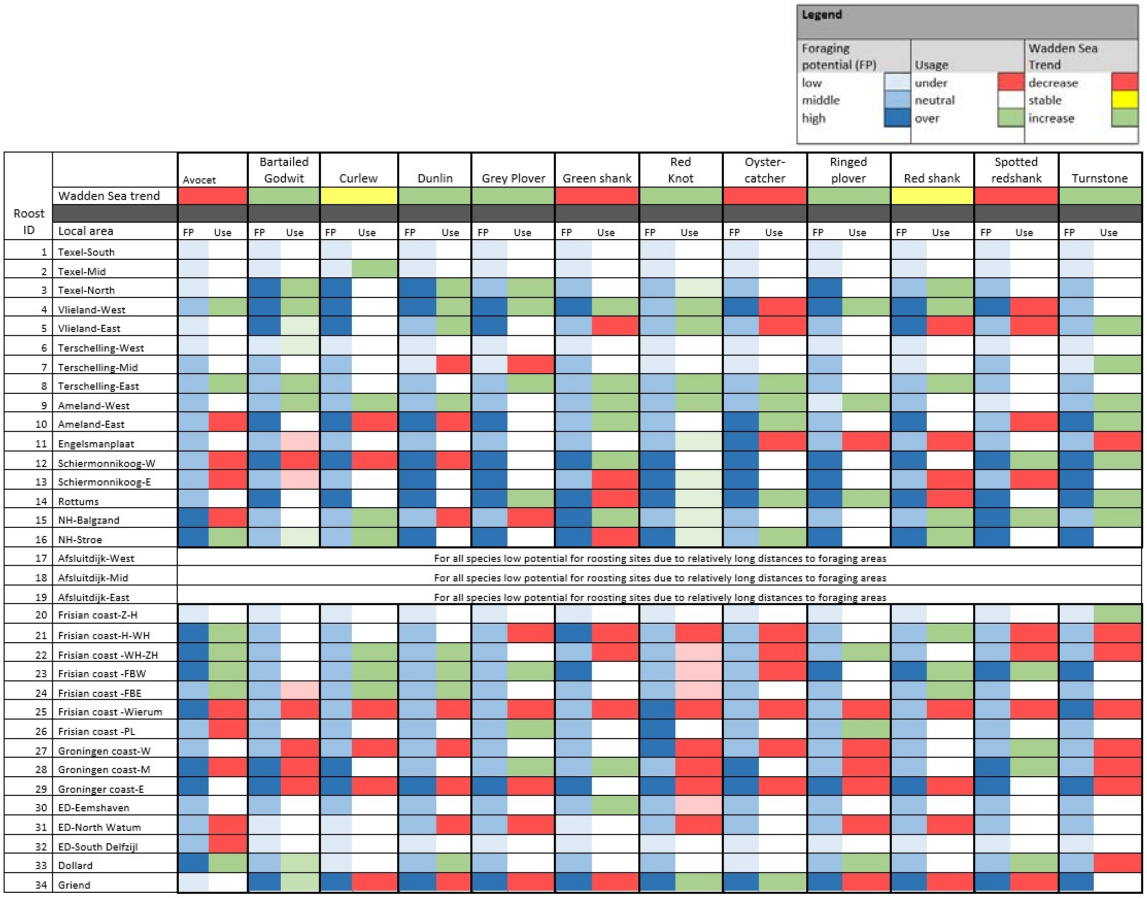


Figure 29: Overview of trends, foraging potential and usage per bird species in each virtual roost-region. Trends, foraging potential and usage are classified based on sections 3.2 and 3.3 and appendix C. Colours pink and light green are used when utilization differs between subspecies (i.e. neutral-under and neutral-over).

Important roosting areas in the Dutch Wadden Sea

Several areas are exceptionally important for the majority of the species. In general, the numbers of birds per species are higher in the eastern part of the Wadden Sea than in the western part (Ens *et al.*, 2009). This is probably due to higher food availability, shorter distances to the foraging grounds and less human disturbance (Figure 28). In the eastern Dutch Wadden Sea, Ameland, Engelsmanplaat, Schiermonnikoog, the Rottums and the saltmarshes along the Frisian and Groningen coast (including the Dollard) are of great value. In the western Wadden Sea, Balgzand, the western part of Vlieland, the area around Vlieland-Richel, eastern part of Terschelling and Griend are locations of great value as roosting area to the majority of species. For a few species, a geographical shift is currently visible: numbers of Redshanks, Bar-tailed Godwits and Curlews are increasing in the western part and decreasing in the eastern part of the Wadden Sea. This shift in numbers might be due to shifts in food supply.

Foraging potential

For nearly all shorebird species, the overall foraging potential (eqation 2) is relatively high in the eastern part of the Wadden Sea (Figures 25 and 26, left panels). Areas with particulary high foraging potential are the tidal flats around Schiermonnikoog, the Rottums and parts of the Frisian and Groningen coast. In the western part of the Wadden Sea, areas with high foraging potential are Griend, Vlieland and Balgzand. For several species such as Avocet, Greenshank and Spotted Redshank also the Dollard has a relatively high foraging potential. Roosts that are related to areas with relatively low foraging potential are the southern and middle part of Texel, the western part of Terschelling, the Afsluitdijk, the area around Zurich and the area around Delfzijl. This is mainly due to the longer distances between roosts and tidal flats in these areas.

Roosting areas that perform well

Roosting areas that perform well have a positive trend, relatively high foraging potential and/or high utilization. For most of the species, these patterns are visible in the following areas (Figure 29):

- Northern part of Texel - western part of Vlieland;
- Rottums;
- Balgzand-Stroe;
- Westhoek-Zwart Haan;
- The western part of Friesland Buitendijks;
- Griend is especially important for Red knots, Oystercatchers and Bar-tailed godwits. Most trends are stable but declining trends are observed for Dunlin, Grey Plover and Oystercatcher.

Our mismatch analyses show that for most of the shorebird species, the number of individuals at these roosting areas are higher than expected. These areas have in common that they have plenty of space for roosting, are surrounded by rich foraging grounds and experience relatively low disturbance or regulated disturbance. The latter means that these roosting areas cannot be closely approached by humans, that acces to the area is guided by paths and signs or that birds can avoid disturbance by moving to nearby undisturbed areas.

Roosting areas that perform poorly

Roosting sites that perform poorly show negative, uncertain or varying trends and they are underutilized. Our analyses demonstrate that most of the species show an uncertain or declining trend and an under-utilization at the following areas.:

- Middle part of Terschelling
- Eastern part of Ameland and the western part of Schiermonnikoog
- The area around Wierum at the Frisian coast
- The Groningen coast (mainly the western and eastern part)
- The area Watum - Delfzijl in the Eems-Dollard. For Oystercatcher the trend is declining but utilzation is (still) good.
- At Griend, Dunlin and Grey Plover show negative trends and underutilization.
- At the trajectory Harlingen-Westhoek, Grey Plover, Greenshank, Knot, Oystercatcher, Spotted Redshank and Turnstone show negative or uncertain trends and underutilization

The area around Delfzijl is probably unsuitable for roosting because nearby (rich) foraging areas are limited, leading to a low foraging potential. Most of the feeding area allocated to these Delfzijl roosts is located on the German side of the Eems. It could be that there are good roosting sites on the German side as well. Along the middle part of Terschelling, Wierum, east part of the Groninger coast and Watum, the foraging potential is high, but suitable roosting sites are lacking. In these areas, waders can only roost on small areas close to the dike or behind the dikes on farmland because extended saltmarshes are missing. Most species will roost on dikes if these are undisturbed (Koffijberg *et al.*, 2003), but there are clear differences between species in their preference to roost on dikes. Oystercatchers and Turnstones regularly roost on dikes, whereas Curlew rarely do so. Very often dikes are disturbed by humans. In this case, the nearby intertidal flats may remain relatively underutilized.

Other striking patterns

In addition, several areas draw the attention due to declining trends or underutilization. At the eastern part of Terschelling, the western part of Ameland and the eastern part of Friesland Buitendijks, trends for most of the species are declining. However, based on the mismatch analyses, the number of birds present are as expected or even higher than expected. So, despite the fact that the roosts are (still) utilized well, the declining trends suggest issues. A possible cause of the declines is a changing foraging landscape related to food or disturbance on the mudflats. Disturbance might influence these trends as the levels of human disturbance on Terschelling and Ameland are relatively high. The Vogelpolle, for example, is the most important high-water refuge west of the Ameland ferry dam. This area experiences high disturbance, because walkers and cyclists are often close by or even in the area as a newly built dam directly links the dike to the roosting area. At higher tides, most of the roosting area floods and birds move towards the area close to the dike. Disturbance at the dike will then result in large numbers of birds leaving the area. This situation is aggrevated by the recent construction of walking paths between the dike and the salt marsh. Via these paths, people (with dogs) can easily reach the salt marsh and the surrounding mudflats. On the east side of Ameland, in the area Nieuwlandsreid-Zoute weide, walking and especially cycling (mountain bikers) through the area is an increasing problem. In contrast, human disturbance in the eastern part of Friesland Buitendijks is low. Reasons for the declines in this area are unknown.

4 Discussion

4.1 Approach

In this study, we have analyzed the use of high tide roosts by shorebirds in relation to nearby foraging areas and site conditions. We applied structural equation modeling to link bird numbers to food supply and to identify roosting areas that are "underutilized" and "overutilized", i.e. where fewer and more birds are found than expected on the basis of the foraging potential (Figure 10). We also collected other environmental information of the roosting sites. We did not include this information in the SEMs, but used it to interpret the mismatches. In summary, we showed that in some cases disturbance provided a reasonable explanation for the mismatch and in other cases the amount of available space provided a reasonable explanation. At some of the sites, the combination of limited space due to high tides and disturbance was reason for concern.

However, in some cases modeling results have to be interpreted with caution because the underlying assumptions might be too general and do not reflect species specific patterns. The reliability of our modeling depends heavily on the extent to which the underlying assumptions are justified. At least three important assumptions underlie explicitly or implicitly our calculations:

1. That we properly link low tide feeding areas to high tide roosts.
2. That we properly describe the food landscape.
3. That the value of food on the low tide feeding areas should be devalued with the distance to the roost.

4.1.1 Linking food supply to high tide roost counts

This study deals with bird species that feed on the muflats during low tide and aggregate in large roosting flocks along the edges of the Wadden Sea during high tide. The birds are counted during high tide but not while feeding during low tide. Linking bird numbers to food supply therefore requires correct identification of feeding and roosting areas of the tidal populations, i.e. the geographically distinct areas where subpopulations of birds feed and rest. Depending on amongst others species, time of year and expected foraging conditions, these areas may differ. However, ecological knowledge to robustly demarcate such areas is not available. The best way to identify such areas is to study habitat use of many individuals with transmitters that track the location of these individuals with high precision at a high frequency. For most species, such information is lacking. However, for Oystercatchers, the tidal movements of a large number of birds were studied with GPS-trackers in different parts of the Wadden Sea (Bakker *et al.*, 2021). The virtual tidal populations, as used in our analyses, correspond rather well with the real tidal populations (Ens *et al.*, 2021). Another well studied species is the Knot (van Gils & Piersma, 1999; van Gils *et al.*, 2006). Here, the fit between the virtual tidal areas of the subpopulations and the actual tidal movement of this species is less good. Knots follow the tidal movement over longer distances and use larger geographically distinct areas, which will most likely result in larger and fewer tidal subpopulations than what we used in the analyses (i.e. 34 virtual subpopulations). However, as explained in the methods section, constructing species level roost-foraging demarcations would be unwieldy and counterproductive and instead we interpreted the mismatches in relation to mismatches at other nearby virtual roosts. Nonetheless, it would be good to study tidal movements in the other focal species as well to improve the model output. The WATLAS- tracking system, currently operational in the western Wadden Sea (Bijleveld, NIOZ) seems ideal to collect more detailed information on this in the future.

4.1.2 Characterizing the food supply – proxies for carrying capacity

In our study, we assume that we were able to characterize the foraging landscape of the selected study species on the basis of the benthos surveys by NIOZ and WMR combined with information on prey choice of the various bird species derived from the scientific literature. Properly characterizing the food supply is, however, a difficult task.

For instance, it is assumed that the benthos densities measured during spring and summer are representative for the entire year. This is a strong assumption because seasonal changes in metabolism and spatio-temporal variation in predation of benthos cause spatially variable seasonal dynamics. Although the surveys provide a reasonably representative estimate of the relative food conditions for the entire year (because the spatial variation is high), it should be possible to obtain better seasonal estimates by using data from benthos surveys where data are collected throughout the year.

In previous studies, different proxies were used to estimate the carrying capacity. For example, the harvestable prey biomass, i.e. prey that are both profitable and available (Zwarts & Wanink, 1993), is an important parameter to characterize the food supply, but is not easily defined. In an extremely detailed long-term study along the Frisian coast, Zwarts *et al.* (1996b) succeeded in defining and measuring the harvestable biomass for Oystercatchers after parameterizing the multi-species functional response equation (Charnov, 1976) on the basis of the many studies on prey size selection and intake rate of Oystercatchers (Zwarts *et al.*, 1996a). This study showed, that large numbers of Oystercatchers occurred in the area, when harvestable biomass was high. In years when predicted intake rates were too low to maintain energy balance, very few Oystercatchers occurred in the study area. However, harvestable biomass should not be confused with carrying capacity itself. According to Goss-Custard (1996) the carrying capacity of an area is reached when, as a result of a density-related feedback process such as competition for food, no more birds can establish themselves, however large the number of potential settlers to do so. Harvestable biomass can be called a proxy of carrying capacity, as it is not measured in number of birds, but correlates with the number of birds that an area can sustain. In a similarly detailed and long-term study on Knots in the western Wadden Sea Kraan *et al.* (2009) arrived at a different proxy for carrying capacity, namely the suitable foraging area measured in ha. They did not use the multi-species functional response equation (Charnov, 1976) to predict intake rates, because in their view this equation has been developed for ‘handling-limited’ foragers. Knots swallow their shellfish prey whole and the resulting digestive constraints are taken into account in the digestive rate model (van Gils *et al.*, 2005). Hence, this digestive rate model was used to predict intake rates.

Apart from total prey biomass, harvestable prey biomass and suitable feeding area, more proxies for carrying capacity can be thought of. For instance, emersion time can be included in the proxy, so that the longer an area is exposed during low tide and available for feeding, the more it contributes to the proxy (Ens *et al.*, 2016). In addition, also sediment conditions can affect the proxies for carrying capacity. Sediment composition may impact whether or not prey is harvestable to birds feeding there. However, in most studies, the preference for a particular sediment type is rather crudely characterized and even then, these crude classifications may differ between studies (Zwarts, 1988; Yates *et al.*, 1993; Brinkman & Ens, 1998; Granadeiro *et al.*, 2004; Ens *et al.*, 2005). Hence, we decided not to take this factor into account, except for the Avocet, whose delicate bill is most clearly adapted to sweep through muddy sediments. All prey on mudflats with less than 20% mud were excluded from the calculations. Despite this correction for sediment, the SEM fitted the data poorly. The criterion of 20% mud was based on a guesstimate and another criterion might have yielded a better fit. Alternatively, the preferred prey of Avocet may differ from the assumed prey, or disturbance and other factors have an overriding influence on the distribution of this bird.

In summary, one would think that there is a best way to characterize the food supply for each bird species, i.e. that there is one carrying capacity proxy showing a high positive correlation with bird numbers when comparing areas, exceeding the correlation of other proxies. This amounts to the assumption that also underlies this study, namely that food is the prime determinant of how birds distribute themselves in the Wadden Sea. Disturbance at the roost, or other confounding factors such as sediment compostion, may make an area less attractive, but the effect is never so big that it could make the correlation between bird numbers and food supply disappear. However, it could lead to low correlations (Ens *et al.*, 2019). Further research is necessary to define the best predictive proxy for the carrying capacity. This requires detailed studies on prey choice of the various bird species in different parts of the Wadden Sea.

4.1.3 The impact of the distance between the roosting area and the feeding area

It is generally believed that the larger the distance between a feeding area and the roost, the less profitable it is for the roosting birds to go and feed there. This assumption makes sense because travel costs increase with travel distance and a higher daily energy expenditure must be compensated with a higher daily energy intake, requiring higher intake rates and/or longer foraging times. In the Tagus estuary, the density of feeding Dunlin decreased with distance from the roost, and calculations suggested that parts of the estuary were underused because suitable nearby roosting areas were lacking (Dias *et al.*, 2006). Similarly, Black-tailed Godwits were observed to select as foraging grounds flooded, rolled pans that minimized their movements between the roosting and foraging grounds (Santiago-Quesada *et al.*, 2014). Yet, birds may sometimes cover large distances to reach a safe roosting area. For instance, Whimbrels occasionally covered distances of more than 50 km to reach a safe night roost, so the daily commuting distance exceeded 100 km for these birds (Watts *et al.*, 2021).

To include the effect of travel cost, we devalued the prey biomass with a negative exponential function, starting with 1 at a travel distance of 0 km and declining at a decelerating rate to 0 with increasing distance. We chose $\lambda = 0.1$ which resulted in a weight of slightly less than 0.4 at 10 km. We did not derive this value from energy budget considerations, but guesstimated it. However, we also estimated the full set of SEM models for $\lambda = 0.05$ and $\lambda = 0.15$. Within this (considerable) range, the impact on the results was small (Figure 30). However, it would be good to study this function between distance, harvestable biomass and travel cost to improve the model output. The WATLAS- tracking system seems ideal to collect information on the selection of combinations of roosts and foraging grounds.

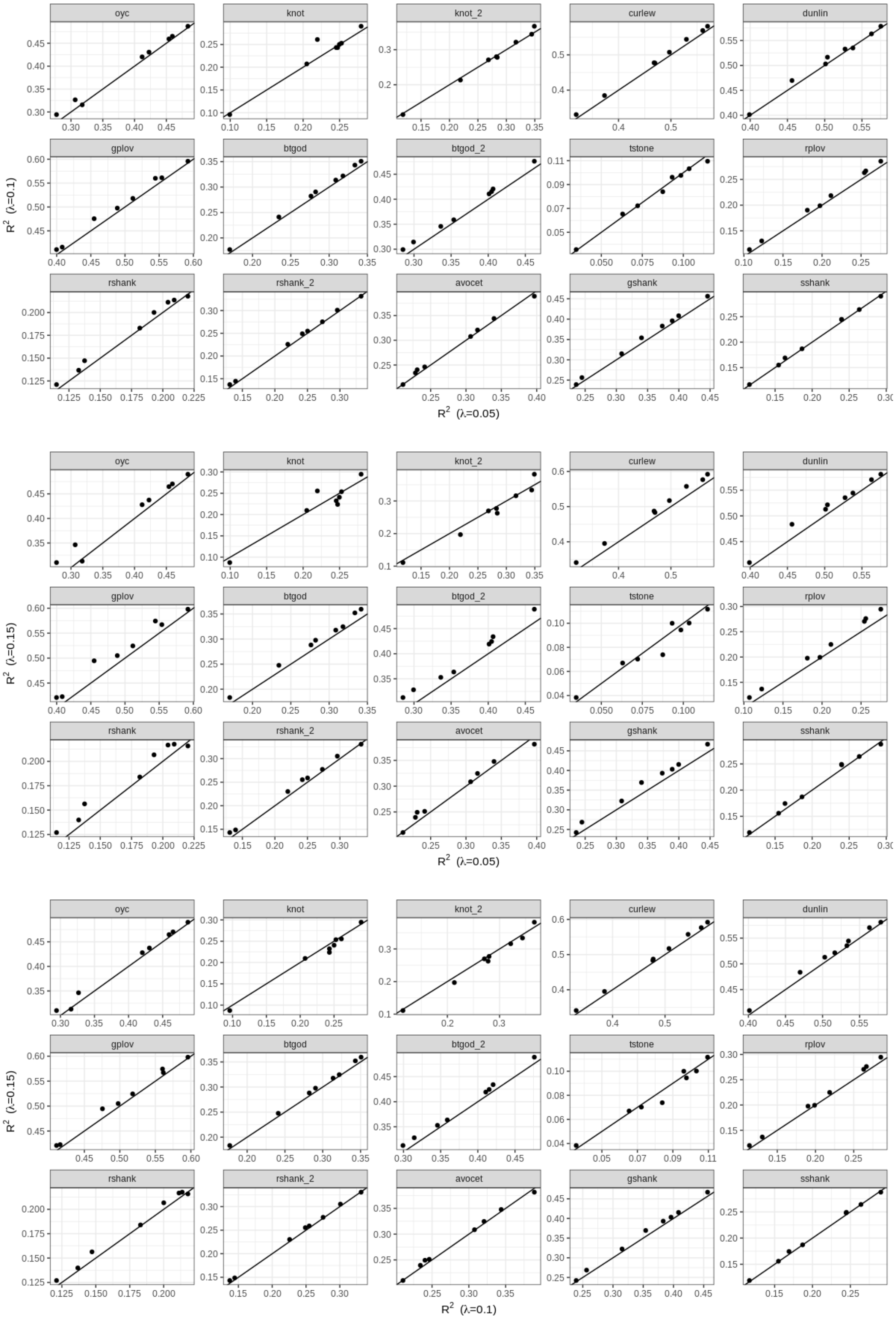


Figure 30: Scatterplots of the R^2 values from the regression models $\hat{N}' = f(N')$ for the different values of λ. The black line has intercept 0 and slope 1.

4.2 Trends at the scale of roosts vs Wadden Sea trends

In species that are declining throughout the Wadden Sea, a decline in numbers at a particular (virtual) roost need not be due to conditions at the roost or the adjoining feeding area. Over a thirty-year period, quite a few shorebird species show a significant decline in the international Wadden Sea (Kleefstra *et al.*, 2019). Fewer species show a significant decline over a more recent and shorter ten-year period (Kleefstra *et al.*, 2019).

Oystercatcher, Avocet, Redshank and Dunlin show a significant decline in the international Wadden Sea both in the long term and in the short term. However, in all these species, Figure 29 shows that there are areas in the Dutch Wadden Sea, where numbers are significantly increasing: 1 area for Avocet, 15 areas for Dunlin, 4 areas for Oystercatcher and 9 areas for Redshank. Instead of focusing on the absolute value of the trend at a particular virtual roost, one might consider investigating if the trend is more negative than average at that particular roost.

5 General conclusions & recommendations

5.1 Conclusions

The aim of this study was to investigate high tide roost usage by shorebirds in relation to nearby foraging areas and site conditions across the Dutch Wadden Sea. To get insight in high tide roost usage, we calculated for twelve shorebird species and for 34 virtual roosting sites across the Wadden Sea, the foraging potential (i.e. the nearby food supply based on diet, habitat and distance) and the number of birds and analyzed the relation between the two. Furthermore, we provided an overview of the spatiotemporal trends of these shorebird species. Our main conclusions are:

- Specific roosting areas in the Wadden Sea are of exceptional importance to migratory shorebirds. These roosts accommodate high numbers, show positive or stable trends, have a relatively high foraging potential, and are utilized as expected or better. These areas are the western part of Vlieland (i.e. Vliehors), the saltmarshes near Balgzand and Stroe, Westhoek-Zwarte Haan, Friesland Buitendijks-West and the Rottums.
- Griend is also extremely important as a high tide roost, because it is undisturbed and surrounded by rich mudflats and it generally accommodates high numbers, especially of Oystercatchers, Bar-tailed Godwits, Red knots and Dunlins. However, overall trends are stable, uncertain or declining and for some species the utilisation is lower than expected. On Griend, succession of the vegetation may be a problem. In addition, the sand suppletion in 2016 seems to fulfill an important role as roosting site at Griend.
- The Dollard is specifically important for Spotted Redshanks, Avocets and Dunlins. In general, other shorebirds also do quite well in this area, but numbers and foraging potential are generally lower than the rest of the Dutch Wadden Sea.
- The eastern part of Ameland, the western part of Schiermonnikoog and the Groningen saltmarshes are important for shorebirds in terms of numbers and foraging potential. But trends are largely declining and utilization is lower then expected. Disturbance and/or vegetation succession might play a role and needs to be further investigated.
- Specific areas on the islands with relatively high levels of human disturbance are: the North Sea beaches of Texel, Vlieland, and Ameland, part of the Vliehors, the eastern part of Vlieland, Groene Strand at Terschelling and the east point of Terschelling. Specific areas along the mainland coast with relatively high levels of human disturbance are: the area Koehool - Westhoek - Zwarte Haan and the area Holwerd-sluices - Lauwersmeer in Friesland and the saltmarshes near the Westpolder in Groningen.
- Specific sites within counting areas that do not show up in our disturbance maps due to its resolution, but are classiffied as areas with disturbance issues, are parts of the Noordsvaarder, Vogelpolle and Westhoek, Nieuwlandsreid- Zoute weide, Engelsmanplaat and Paezemerlannen.
- The main sources of (severe) human disturbance are cyclists (including mountainbikers), walkers (with dogs) and locally, (kite)surfers.

- Wadden Sea wide, vegetation succession and disturbance by raptor species seems no structural issue for roosting birds. Locally, however, vegetation conditions can probably be improved but the effects may differ per species. Further research is required.
- In general, issues with roost usage by shorebirds seem to arise when space at roosting sites is limited during (very) high tides, and/or when people enter the area. Birds are then forced into a small areas between the water and the source of disturbance and often tend to move away.

5.2 Recommendations

With our analyses, we identified opportunities for the improvement of high-tide roost usage, which gives an action perspective for improvement of policy and conservation in the Dutch Wadden Sea region. Based on our analyses, the following recommendations can be made:

- Maintain or or improve the conditions at important roosting sites. Protection in these areas can exist of measures that prevent or regulate human disturbance. Closing areas at times when birds are vulnerable is an example of regulating disturbance by human visitors (i.e. dynamic zonation). In most of the areas, the access of human visitors is already regulated or (partly) prohibited, but it is important to maintain and to improve this. Information of ground predators is largely lacking and this requires further investigation.
- More specific, human disturbance can be reduced by (better) informing visitors with signs, by guidance of visitors which makes their occurrence and movementmore predictable to birds, by closing off specific areas and/or by using dynamic zonation. This is particularly importantfor sites where disturbance is high or recently increasing, often in combination with limited space of the roost:
    - Stroe, Noord Holland, the frequency of disturbance here is higher than at Balgzand and increasing.
    - East part of Vlieland, currently mainly important for Oystercatchers, Turnstones and Redshanks. Oystercatchers that forage under the eastern part of Vlieland during the tourist season avoid this area during high tide and fly to Richel, which is further away (Van der Kolk 2021).
    - Striep-De Ans, Terschelling
    - Vogelpolle, Ameland
    - Nieuwlandsreid-Zoute weide, Ameland
    - Westhoek-Zwarte Haan, Friesland
    - Holwerd-Wierum-Moddergat, Friesland
    - Westpolder, Groningen
- In some areas, suitable roosting sites are lacking or small. Limited size is not necessarily problematic. However, small sites can accommodate fewer birds and birds on small roosts are more sensitive disturbance due to the absence of a bufferzone. There might be opportunities for creating or increasing undisturbed and suitable roosting areas, like at the middle part

of Terschelling (Striep-De Ans), the area Harlingen-Westhoek, the area around Wierum, the eastern part of the Groninger coast and the area around Watum. This may locally strengthen the roosting function for most of the species. However, space for roosting areas is limited at the seaside in most of these locations. Inland there might be more opportunities for creating roosts, for example via the use of the 'Dubbele dijken' or 'Wisselpolder' concept or undisturbed farmland. At some sites, like Harlingen-Westhoek and the east part of the Groningen coast, the dikes can also function as roosting site, if undisturbed. This requires that the trend to increase accessibility of seaward parts of dikes for walkers and cyclists should be reversed.

- Some sites, like the saltmarshes of Ameland and Schiermonnikoog, Simonszand and the eastern part of Friesland Buitendijks show a decline in numbers for several species, while the utilization of the roost is (still) neutral or good. It is recommended to further investigate the causes of the declines in these areas in a more detailed way, like the research that has been done for Westhoek (Ens *et al.*, 2021). Reasons for the decline are uncertain and varying. At the eastern saltmarshes of Ameland for example, the increasing number of mountain bikers across the salt marsh is a concern. At Simonszand, the roosting function has declined rapidly since the morphology of the tidal flat changed enormously about six years ago.
- The Oystercatcher, Greenshank, Avocet and Spotted redshank show a decline in numbers throughout the entire Dutch Wadden Sea. It is possible that the food supply in the Wadden Sea, or external factors such as the reproduction are so decisive in controlling numbers that measures aimed to improve roosting sites have little effect on their numbers. It is important to identify the factors that underlie the decline of these species.
- Our analysis depends on assumptions and the quality of the available data. A general recommendation is therefore to instigate research that will endorse our assumptions and improve the quality of the available data. In this context, we address the following specific recommendation:
  - Instigate studies with WATLAS to improve knowledge on the connectivity between low tide feeding areas and high tide roosts for Knot and other species.
  - Instigate studies that substantiate our current description of the food landscape of different species, i.e., find the best proxy for carrying capacity by studying site choice and prey choice of selected shorebirds throughout the Wadden Sea. WATLAS might provide the proper infrastructure for such studies.
  - Instigate studies that allow a quantitative estimation of the factor by which food has to be devalued with distance from the roost.
  - Instigate studies on the relationship between harvestability of the food and sediment composition for shorebird species where this may be an issue.
  - Improve the quantitative monitoring of the disturbance landscape, especially for the following sources of disturbance:small boats without AIS transponders, humans (including fishermen, holiday makers, runners, bird watchers etc) walking on the mudflats, saltmarshes or dikes, cyclists coming close to roosts and (kite)surfers.

Acknowledgements

Shorebirds are counted by a large number of volunteer bird counters. We are very grateful for their efforts. For responding to the questionnaire on disturbance at the high tide roosting areas, special thanks go to: Dieko Alting, Ruud van Beusekom, Peter de Boer, Roeland Bom, Bert Brinkman, Anja Cervencl, Jan de Jong, Adriaan Dijksen, Lieuwe Dijksen, Arjen Dijkstra, Eelke Sybren Dijkstra, Meinte Engelmoer, Rob Hammer, Roelf Hovinga, Theo Jager, Leon Kelder, Romke Kleefstra, Jan Kostwinner, Johan Krol, Petra Manche, Ron Mes, Floris Mulder, Gerard Nieuwland, Leendert Oudman, Jelle Postma, Kees Rappoldt, Cor Smit, Harry Smit, Henry Soyer, Vincent Stork, Wim Tijsen, Margriet Timmer, Vasco van de Boon, Marc van Roomen, Kees van Scharenburg, Dick Schermer, Bernard Spaans, Jan Veen, Dick Veenendaal, Hans Witte. We would like to acknowledge the NIOZ and WMR for providing data and Allert Bijleveld for commenting the report and Karin Troost for advice regarding the use of the MosKok dataset.

References

Aarts, G., Mul, E., Fieberg, J., Brasseur, S., Gils, J.A.v., Matthiopoulos, J. & Riotte-Lambert, L. (2021). Individual-level memory is sufficient to create spatial segregation among neighboring colonies of central-place foragers. *The American Naturalist*. Publisher: The University of Chicago Press.

Bakker, W., Ens, B.J., Dokter, A., van der Kolk, H.J., Rappoldt, K., van de Pol, M., Troost, K., van der Veer, H.W., Bijleveld, A.I., van der Meer, J., Oosterbeek, K., Jongejans, E. & Allen, A.M. (2021). Connecting foraging and roosting areas reveals how food stocks explain shorebird numbers. *Estuarine, Coastal and Shelf Science*, 259, 107458.

Bell, M. (1995). UINDEX4: a computer programme for estimating population index numbers by the Underhill method. Report.

Beukema, J.J. (1976). Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. *Netherlands Journal of Sea Research*, 10, 236–261. Publisher: Elsevier.

Beukema, J.J. & Cadée, G.C. (1991). Growth rates of the bivalve *Macoma balthica* in the Wadden Sea during a period of eutrophication: relationships with concentrations of pelagic diatoms and flagellates. *Marine Ecology Progress Series*, 68, 249–256.

Beukema, J.J. & Dekker, R. (2020). Half a century of monitoring macrobenthic animals on tidal flats in the Dutch Wadden Sea. *Marine Ecology Progress Series*, 656, 1–18.

Bijleveld, A.I., van Gils, J.A., van der Meer, J., Dekinga, A., Kraan, C., van der Veer, H.W. & Piersma, T. (2012). Designing a benthic monitoring programme with multiple conflicting objectives. *Methods in Ecology and Evolution*, 3, 526–536.

Bijlsma, R.G. (1990). Predation by large falcons on wintering waders on the Banc d'Arguin, Mauritania. *Ardea*, 78, 75–82.

Bjarnason, J., Günther, K. & Revier, H. (2017). Tourism. In: *Wadden Sea Quality Status Report 2017* (ed. Kloepper, S.).

Blew, J., Guenther, K., Haelterlein, B., Kleefstra, R., Laursen, K. & Scheiffarth, G. (2016). Trends of Migratory and Wintering Waterbirds in the Wadden Sea 1987/1988 - 2013/2014. Report.

Blew, J., Günther K., K., Hälterlein, B., Kleefstra, R., Laursen, K., Ludwig, J. & Scheiffarth, G. (2017). Migratory birds. In: *Wadden Sea Quality Status Report* (ed. Kloepper, S.). Common Wadden Sea Secretariat, Wilhelmshaven, Germany, Wadden Sea Quality Status Report.

Bollen, K.A. (2014). *Structural Equations with Latent Variables.* Wiley.

Bouten, W., Baaij, E.W., Shamoun-Baranes, J. & Camphuysen, K.C. (2013). A flexible GPS tracking system for studying bird behaviour at multiple scales. *Journal of Ornithology*, 154, 571–580. Publisher: Springer.

Brinkman, A. & Ens, B. (1998). Integrale Bodemdalingstudie Waddenzee: Vogels. Report.

Buiter, R., Govers, L., Piersma, T. & Team, M. (2016). *Knooppunt Waddenzee.*

Burchard, H. & Bolding, K. (2002). GETM - a General Estuarine Transport Model. Scientific documentation. Technical Report EUR 20253 EN.

Cairns, D.K. (1989). The Regulation of Seabird Colony Size: A Hinterland Model. *The American Naturalist*, 134, 141–146.

Charnov, E.L. (1976). Optimal foraging, the marginal value theorem. *Theoretical population biology*, 9, 129–136.

Compton, T.J., Holthuijsen, S., Koolhaas, A., Dekinga, A., ten Horn, J., Smith, J., Galama, Y., Brugge, M., van der Wal, D., van der Meer, J., van der Veer, H.W. & Piersma, T. (2013). Distinctly variable mudscapes: Distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. *Journal of Sea Research*, 82, 103–116.

De Jong, F., Bakker, J., van Berkel, C., Dahl, K., Dankers, N., Gätje, C., Marencic, H. & Potel, P. (1999). *Wadden Sea Quality Status Report*. No. 9 in Wadden Sea Ecosystem. Wilhelmshaven, Germany.

Dias, M.P., Granadeiro, J.P., Lecoq, M., Santos, C.D. & Palmeirim, J.M. (2006). Distance to high-tide roosts constrains the use of foraging areas by dunlins: Implications for the management of estuarine wetlands. *Biological Conservation*, 131, 446–452.

Dokter, A., van Loon, E., Rappoldt, C., Oosterbeek, K., Baptist, M., Bouten, W. & Ens, B. (2017). Balancing food and density-dependence in the spatial distribution of an interference-prone forager. *Oikos*, 126, 1184–1196. Type: Journal Article.

van den Ende, D., Troost, K., van Asch, M., Brummelhuis, E., Purdon, J. & Zweeden, C.v. (2017). Mosselbanken en oesterbanken op droogvallende platen in de Nederlandse kustwateren in 2017: bestand en arealen. Tech. Rep. 17.022, WMR.

van den Ende, D., Troost, K., van Asch, M., Perdon, J. & van Zweeden, C. (2020). Mosselbanken en oesterbanken op droogvallende platen van de Nederlandse zoute getijdenwateren in 2019 : Bestand en arealen. Tech. rep., Stichting Wageningen Research, Centrum voor Visserijonderzoek (CVO), IJmuiden.

Ens, B. (2006). The conflict between shellfisheries and migratory waterbirds in the Dutch Wadden Sea. In: *Waterbirds around the world* (eds. Boere, G., Galbraith, C. & Stroud, D.). The Stationery Office, Edinburgh, UK, pp. 806–811. Type: Book Section.

Ens, B., Bom, R., Dokter, A., Oosterbeek, K., de Jong, J. & Bouten, W. (2014). Nieuwe ontdekkingen en mogelijkheden in het onderzoek aan Scholeksters dankzij het UvA Bird Tracking Systeem. *Limosa*, 87, 117–128. Type: Journal Article.

Ens, B., Brinkman, A., Dijkman, E., Meesters, E., Kersten, M., Brenninkmeijer, A. & Twisk, F. (2005). Modelling the distribution of waders in the Westerschelde. What is the predictive power of abiotic variables? Report.

Ens, B., Dokter, A., Rappoldt, C. & Oosterbeek, K. (2015). Wat bepaalt de draagkracht van de Waddenzee voor wadvogels: onderzoek naar het verspreidingsgedrag van Scholeksters. Report.

Ens, B., Kersten, M., Wijsman, J.W.M., van der Meer, J., Schekkerman, H., Winden, E. & Rappoldt, C. (2017). Monitoring van het voor vogels oogstbare voedselaanbod in de kombergingen van het Pinkegat en Zoutkamperlaag - rapportage tot en met monitoringjaar 2016. Tech. rep., Nijmegen.

Ens, B., van der Meer, J., Troost, K., van Winden, E., Schekkerman, H. & Rappoldt, K. (2019). Monitoring van het voor vogels oogstbare voedselaanbod in de kombergingen van het Pinkegat en Zoutkamperlaag - rapportage tot en met monitoringjaar 2018. Tech. rep., Sovon Vogelonderzoek Nederland, Nijmegen.

Ens, B., van Winden, E., van Turnhout, C., van Roomen, M., Smit, C. & Jansen, J. (2009). Aantalontwikkeling van wadvogels in de Nederlandse Waddenzee in 1990-2007: verschillen tussen Oost en West. *Limosa*, 82, 100–112. Type: Journal Article.

Ens, B., Wintermans, G. & Smit, C. (1993). Verspreiding van overwinterende wadvogels in de Nederlandse Waddenzee. *Limosa*, 66, 137–144.

Ens, B.J., Eckhardt, R., Kampichler, C., Kleefstra, R., Schekkerman, H., van Wijk, J. & Nienhuis, J. (2021). Aard en omvang verstoring van overtijende wadvogels voor de kwelder bij Westhoek – seizoen 2020 (T0 dynamisch zoneren). Sovon-rapport 2021/30, Sovon Vogelonderzoek Nederland, Nijmegen.

Ens, B.J. & Kats, R.K.H. (2004). Evaluatie van voedselreservering voor eidereenden in de Waddenzee - rapportage in het kader van EVA II deelproject B2. Tech. Rep. 931, Alterra, Wageningen. ISSN: 1566-7197.

Ens, B.J., Krol, J., van der Meer, J., Wijsman, J.W.M., Schekkerman, H. & Rappoldt, C. (2016). Monitoring van het voor vogels oogstbare voedselaanbod in de kombergingen van het Pinkegat en Zoutkamperlaag - rapportage tot en met monitoringjaar 2015. Tech. rep., Nijmegen.

Folmer, E.O., Dekinga, A., Holthuijsen, S., Meer, J.d., Mosk, D., Piersma, T. & Veer, H. (2017). Species Distribution Models of Intertidal Benthos - Tools for Assessing the Impact of Physical and Morphological Drivers on Benthos and Birds in the Wadden Sea. Tech. Rep. 2017-3, NIOZ, Texel.

Folmer, E.O., Drent, J., Troost, K., Büttger, H., Dankers, N., Jansen, J., Van Stralen, M., Millat, G., Herlyn, M. & Philippart, C.J.M. (2014). Large-Scale Spatial Dynamics of Intertidal Mussel (*Mytilus edulis L.*) Bed Coverage in the German and Dutch Wadden Sea. *Ecosystems*, 17, 550–566.

Folmer, E.O., Olff, H. & Piersma, T. (2010). How well do food distributions predict spatial distributions of shorebirds with different degrees of self-organization? *Journal of Animal Ecology*, 79, 747–756.

Folmer, E.O., Olff, H. & Piersma, T. (2012). The spatial distribution of flocking foragers: disentangling the effects of food availability, interference and conspecific attraction by means of spatial autoregressive modeling. *Oikos*, 121, 551–561.

Folmer, E.O., Van Beusekom, J.E.E., Dolch, T., Gräwe, U., Katwijk, M.M., Kolbe, K. & Philippart, C.J.M. (2016). Consensus forecasting of intertidal seagrass habitat in the Wadden Sea. *Journal of Applied Ecology*, 53, 1800–1813.

Fretwell, S.D. (1969). On territorial behavior and other factors influencing habitat distribution in birds: III. Breeding success in a local population of Field Sparrows (Spiza americana Gmel). *Acta Biotheoretica*, 19, 45–52.

van Gils, J.A., De Rooij, S.R., Van Belle, J., van der Meer, J., Dekinga, A., Piersma, T. & Drent, R. (2005). Digestive bottleneck affects foraging decisions in red knots *Calidris canutus.* I. Prey choice. *Journal of Animal Ecology*, 74, 105–119.

van Gils, J.A. & Piersma, T. (1999). Day and nightime movements of radiomarked Red Knots staging in the western Wadden Sea in July-August 1995. *Bulletin-Wader Study Group*, 89, 36–44.

van Gils, J.A., Spaans, B., Dekinga, A. & Piersma, T. (2006). Foraging in a tidally structured environment by red knots (*Calidris canutus*): Ideal, but not free. *Ecology*, 87, 1189–1202.

Goss-Custard, J.D. (1980). Competition for food and interference among waders. *Ardea*, 68, 31–52.

Goss-Custard, J.D. (1996). *The oystercatcher: from individuals to populations.* Oxford University Press, USA.

Granadeiro, J., Santos, C., Dias, M. & Palmeirim, J. (2007). Environmental factors drive habitat partitioning in birds feeding in intertidal flats: implications for conservation. *Hydrobiologia*, 587, 291–302.

Granadeiro, J.P., Andrade, J. & Palmeirim, J.M. (2004). Modelling the distribution of shorebirds in estuarine areas using generalised additive models. *Journal of Sea Research*, 52, 227–240.

Gräwe, U., Flöser, G., Gerkema, T., Duran-Matute, M., Badewien, T.H., Schulz, E. & Burchard, H. (2016). A numerical model for the entire Wadden Sea: Skill assessment and analysis of hydrodynamics. *Journal of Geophysical Research: Oceans*, 121, 5231–5251.

Herman, P., Middelburg, J., Van De Koppel, J. & Heip, C. (1999). Ecology of Estuarine Macrobenthos. In: *Advances in Ecological Research.* Elsevier, vol. 29, pp. 195–240.

Van den Hout, P. (2009). Mortaliteit is het topje van een ijsberg van angst: over slechtvalken en steltlopers in de Waddenzee. *Limosa*, 82, 122–133.

van den Hout, P.J., Spaans, B. & Piersma, T. (2008). Differential mortality of wintering shorebirds on the Banc d'Arguin, Mauritania, due to predation by large falcons. *Ibis*, 150 (Suppl 1), 219–230.

van de Kam, J., Ens, B., Piersma, T. & Zwarts, L. (2004). *Shorebirds: an Illustrated Behavioural Ecology.* KNNV Publishers, Utrecht.

Kampichler, C., Sierdsema, H., Roodbergen, M. & Ens, B. (2013). Ruimtelijke analyses van dichtheden en trends van binnendijks broedende Scholeksters. Report.

Kleefstra, R., Hornman, M., Frikke, J., Guenther, K., Haelterlein, B., Koerber, P., Ludwig, J. & Scheiffarth, G. (2019). Trends of Migratory and Wintering Waterbirds in the Wadden Sea 1987/1988-2016/2017. Tech. rep., Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

Koffijberg, K., Blew, J., Eskildsen, K., Günther, C., Koks, B., Laursen, K., Rasmussen, L., Potel, P. & Sudbeck, P. (2003). High tide roosts in the Wadden Sea: A review of bird distribution, protection regimes and potential sources of anthropogenic disturbance. A Report of the Wadden Sea Plan Project 34. Report.

Koffijberg, K., Frikke, J., Hälterlein, B., Laursen, K., Reichert, G. & Soldaat, L. (2017). Breeding birds. In: *Wadden Sea Quality Status Report 2017* (eds. Kloepper, S. & al., e.). Common Wadden Sea Secretariat, Wilhelmshaven, Germany, pp. 1–19. Section: Downloaded 16.01.2018. qsr.waddenseaworldheritage.org/reports/breeding-birds Type: Book Section.

van der Kolk, H.J., Allen, A.M., Ens, B.J., Oosterbeek, K., Jongejans, E. & van de Pol, M. (2020). Spatiotemporal variation in disturbance impacts derived from simultaneous tracking of aircraft and shorebirds. *Journal of Applied Ecology*, 57, 2406–2418. Type: Journal Article.

Kraan, C., van Gils, J.A., Spaans, B., Dekinga, A., Bijleveld, A., van Roomen, M., Kleefstra, R. & Piersma, T. (2009). Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *Journal of Animal Ecology*, 78, 1259–1268.

Leopold, M., Smit, C., Goedhart, P., Roomen, M., Winden, A. & Turnhout, C. (2004a). Langjarige trends in aantallen wadvogels, in relatie tot de kokkelvisserij en het gevoerde beleid in deze. Eindverslag EVA II (Evaluatie Schelpdiervisserij tweede fase) Deelproject C2. Tech. rep., Alterra, Wageningen.

Leopold, M.F., Smit, C.J., Goedhart, P.W., Van Roomen, M.W.J., van Winden, A.J. & Van Turnhout, C. (2004b). Langjarige trends in aantallen wadvogels, in relatie tot kokkelvisserij en het gevoerde beleid in deze. Tech. Rep. Alterra-rapport 954, Alterra, Wageningen.

Lotze, H.K. (2005). Radical changes in the Wadden Sea fauna and flora over the last 2,000 years. *Helgoland Marine Research*, 59, 71–83.

Lotze, H.K., Reise, K., Worm, B., van Beusekom, J., Busch, M., Ehlers, A., Heinrich, D., Hoffmann, R.C., Holm, P., Jensen, C., Knottnerus, O.S., Langhanki, N., Prummel, W., Vollmer, M. & Wolff, W.J. (2005). Human transformations of the Wadden Sea ecosystem through time: a synthesis. *Helgoland marine research.* Publisher: Springer-Verlag.

Meer, J.V.D. & Ens, B.J. (1997). Models of Interference and Their Consequences for the Spatial Distribution of Ideal and Free Predators. *The Journal of Animal Ecology*, 66, 846.

Nebel, S., Piersma, T., van Gils, J., Dekinga, A. & Spaans, B. (2000). Length of stopover, fuel storage and a sex-bias in the occurrence of red knots *Calidris c. canutus* and *C-c. islandica* in the Wadden Sea during southward migration. *Ardea*, 88, 165–176.

Piersma, T., van Aelst, R., Kurk, K., Berkhoudt, H. & Maas, L. (1998). A new pressure sensory mechanism for prey detection in birds: the use of principles of seabed dynamics? *Proceedings of the Royal Society B*, 265, 1377–1383.

van de Pol, M., Atkinson, P., Blew, J., Crowe, O., Delany, S., Duriez, O., Ens, B., Hälterlein, B., Hötker, H., Laursen, K., Oosterbeek, K., Petersen, Æ., Thorup, O., Tjørve, K., Triplet, P. & Yésou, P. (2014). A global assessment of the conservation status of the nominate subspecies of Eurasian Oystercatcher Haematopus ostralegus ostralegus. *International Wader Studies*, 20, 47–61. Type: Journal Article.

van de Pol, M., Ens, B., Heg, D., Brouwer, L., Krol, J., Maier, M., Exo, K., Oosterbeek, K., Lok, T., Eising, C. & Koffijberg, K. (2010). Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *Journal of Applied Ecology*, 47, 720–730. Type: Journal Article.

Polwijk, F., Kleefstra, R., van Winden, E. & Ens, B.J. (2018). Monitoring van verstoringsbronnen en verstoringen als onderdeel van hoogwatertellingen in de Waddenzee. *Limosa*, 91, 131–143.

Rappoldt, C., Ens, B. & Schekkerman, H. (2019). Wadvogel habitat model Wadmap. Technische documentatie. Tech. Rep. 30, EcoCurves, Haren.

Rappoldt, C., Kersten, M. & Smit, C. (1985). Errors in large scale shorebird counts. *Ardea*, 73, 13–24. Type: Journal Article.

Reise, K. (2005). Coast of change: habitat loss and transformations in the Wadden Sea. *Helgoland Marine Research*, 59, 9–21.

Reneerkens, J., Piersma, T. & Spaans, B. (2005). De waddenzee als kruispunt van vogeltrekwegen. Literatuurstudie naar de kansen en bedreigingen van wadvogels in internationaal perspectief. Tech. rep., NIOZ, Texel.

van Roomen, M., Laursen, K., van Turnhout, C., van Winden, E., Blew, J., Eskildsen, K., Guenther, K., Haelterlein, B., Kleefstra, R., Potel, P., Schrader, S., Luerssen, G. & Ens, B.J. (2012). Signals from the Wadden sea: Population declines dominate among waterbirds depending on intertidal mudflats. *Ocean & Coastal Management*, 68, 79–88. WOS:000311472700007.

Santiago-Quesada, F., Masero, J.A., Albano, N. & Sánchez-Guzmán, J.M. (2014). Roost location and landscape attributes influencing habitat selection of migratory waterbirds in rice fields. *Agriculture, Ecosystems & Environment*, 188, 97–102.

Soldaat, L., Visser, H., van Roomen, M. & van Strien, A. (2007). Smoothing and trend detection in waterbird monitoring data using Structural Time-Series Analysis and the Kalman filter. *Journal for Ornithology*, DOI 10.1007/s10336-007-0176-7. Type: Journal Article.

Stephens, D.W. & Krebs, J.R. (1986). *Foraging Theory.* Princeton University Press, Princeton N.J.

Stillman, R.A. & Goss-Custard, J.D. (2010). Individual-based ecology of coastal birds. *Biological Reviews*, 85, 413–434.

Troost, K., van Asch, M., Brummelhuis, E., van den Ende, D., van Es, Y., Perdon, K., van der Pool, J., van Zweeden, C. & van Zwol, J. (2021). Schelpdierbestanden in de Nederlandse kustzone, Waddenzee en zoute deltawateren in 2020. Report, Centrum voor Visserijonderzoek (CVO).

van der Tuuk, B., Ens, B., Meijles, E., Sijtsma, F., Heslinga, J. & van der Zee, E.M. (2019). Monitoring vaarrecreatie en natuur Waddenzee Samenvatting vaarseizoen 2018. Tech. rep., Programma naar een Rijke Waddenzee.

Underhill, L. & Prys-Jones, R. (1994). Index numbers for waterbird populations. I. Review and methodology. *Journal of Applied Ecology*, 31, 463–480. Type: Journal Article.

Van Roomen, M., Nagy, S., Citegetse, G. & Schekkerman, H. (2018). East Atlantic Flyway Assessment 2017: the status of coastal waterbird populations and their sites. Report, CWSS / Wetlands International / Birdlife International.

Van Roomen, M., Van Turnhout, C., Blew, J., Koffijberg, K., Nagy, S., Citegetse, G. & Foppen, R. (2017). East Atlantic Flyway. In: *Wadden Sea Quality Status Report 2017* (ed. Kloepper, S.). Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

Visser, H. (2004). Estimation and detection of flexible trends. *Atmospheric Environment*, 38, 4135–4145. Type: Journal Article.

Watts, B.D., Smith, F.M., Hines, C., Duval, L., Hamilton, D.J., Keyes, T., Paquet, J., Pirie-Dominix, L., Rausch, J., Truitt, B., Winn, B. & Woodard, P. (2021). The costs of using night roosts for migrating whimbrels.

Wolff, W.J. (1983). *Ecology of the Wadden Sea.* A.A. Balkema, Rotterdam. Appendix to report 9, Landscape & vegetation maps. Includes bibliographies.

Yates, M.G., Goss-Custard, J.D., McGrorty, S., Lakhani, K.H., Dit Durell, S.E.A.L.V., Clarke, R.T., Rispin, W.E., Moy, I., Yates, T., Plant, R.A. & Frost, A.J. (1993). Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *Journal of Applied Ecology*, 30, 599–614.

Zwarts, L. (1988). De bodemfauna van de Fries - Groningse Waddenkust. Tech. Rep. 294, R.IJ.P., Lelystad.

Zwarts, L., Ens, B., Goss-Custard, J.D., Hulscher, J.B. & Durell, S. E. A. le V dit (1996a). Causes of variation in prey profitability and its consequences for the intake rate of the oystercatcher Haematopus ostralegus. *Ardea*, 84A, 229–268.

Zwarts, L., Ens, B.J., Goss-Custard, J.D., Hulscher, J.B. & Kersten, M. (1996b). Why oystercatchers *Haematopus ostralegus* cannot meet their daily energy requirements in a single low water period. *ARDEA*, 84, 269–290.

Zwarts, L. & Wanink, J.H. (1993). How the food-supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body-weight, biomass, burying depth and behavior of tidal-flat invertebrates. *Netherlands Journal of Sea Research*, 31, 441–476.

A Benthos

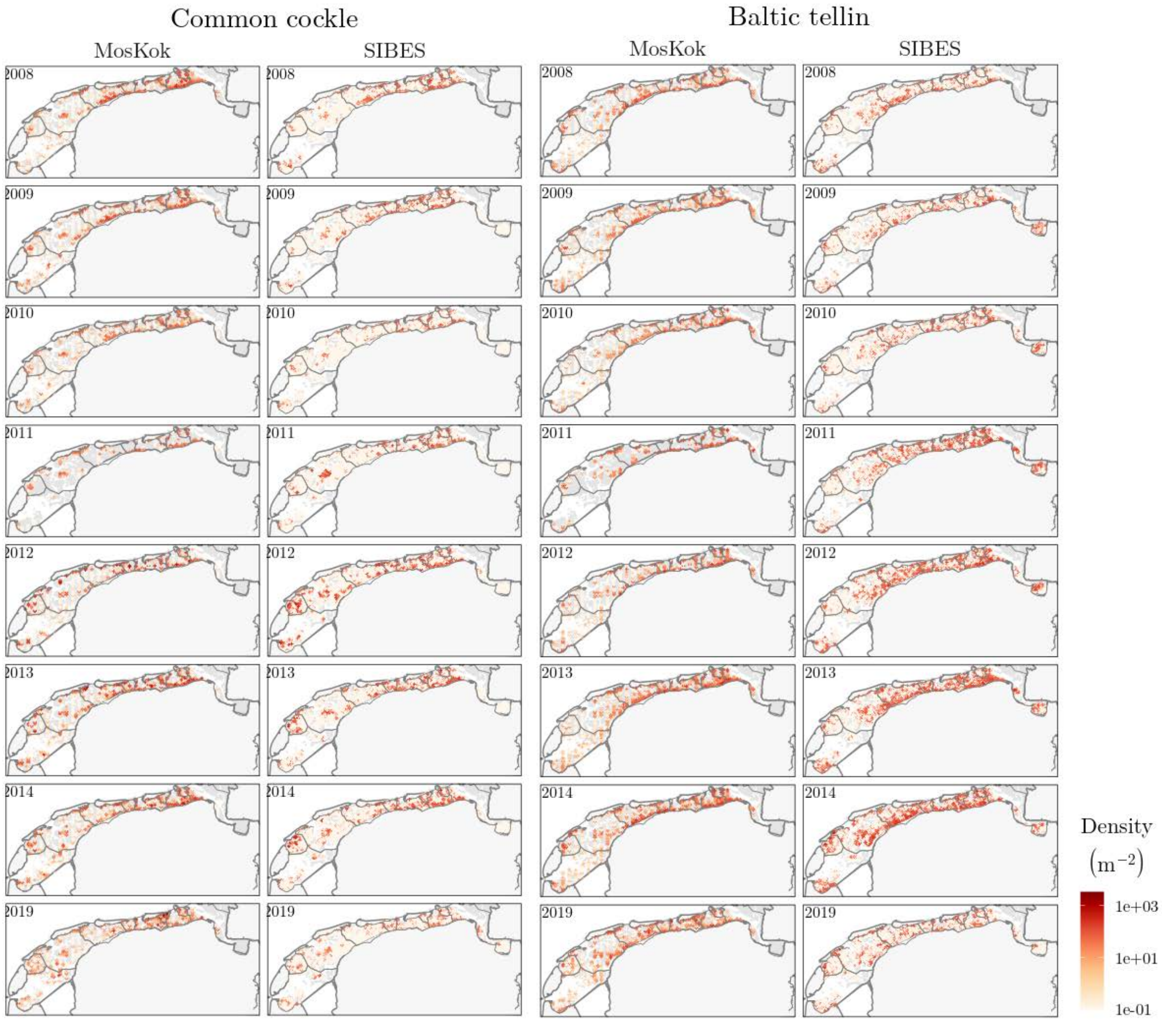


Figure 31: Maps with the densities of common cockles and Baltic tellins in the MosKok and SIBES programs.

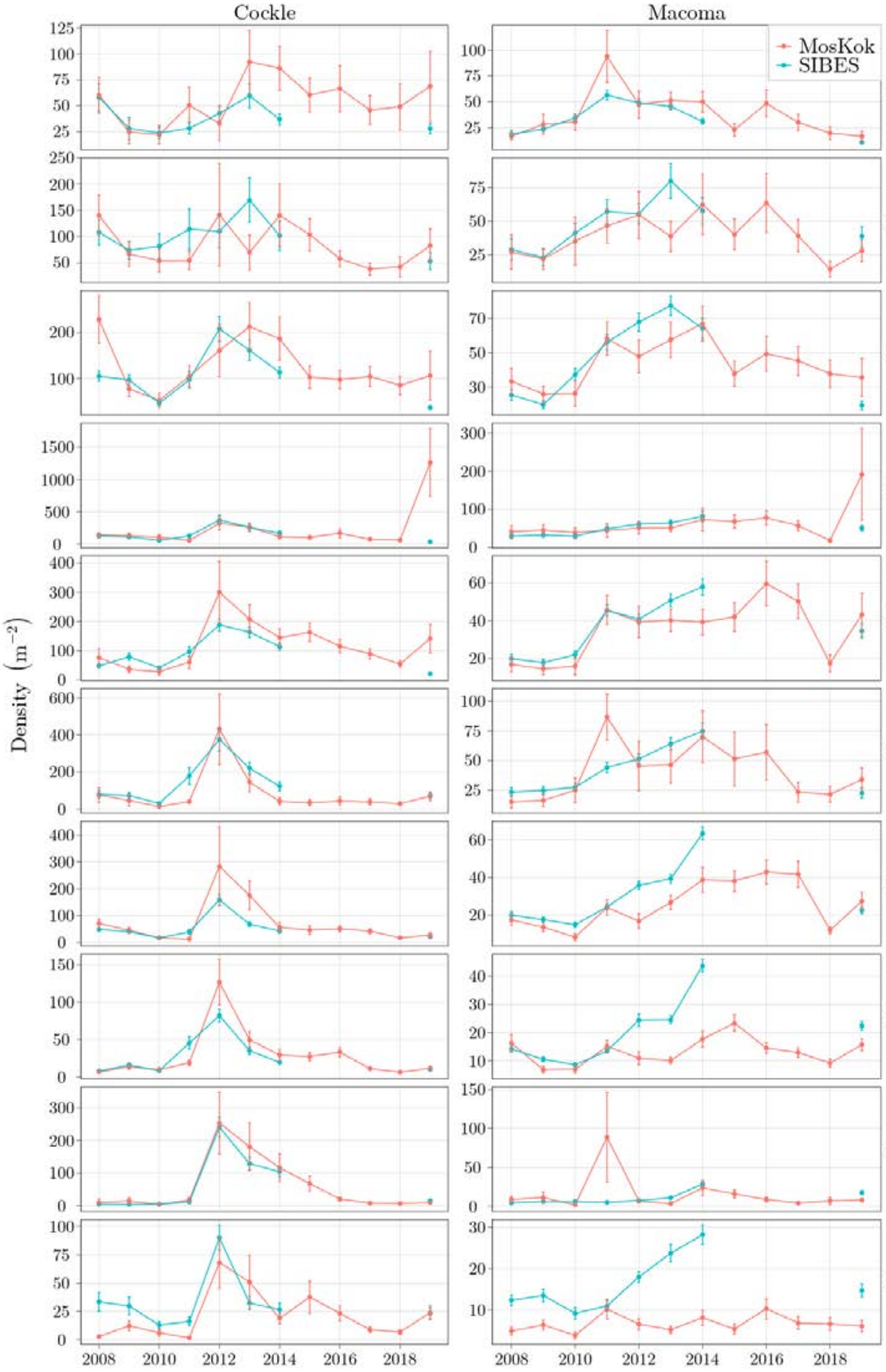


Figure 32: Density estimates (mean ± standard error) of common cockles and Baltic tellins in the SIBES and MosKok surveys by tidal basin.

B Data and SEM

B.1 Data and modelling results

B.1.1 Oystercatcher

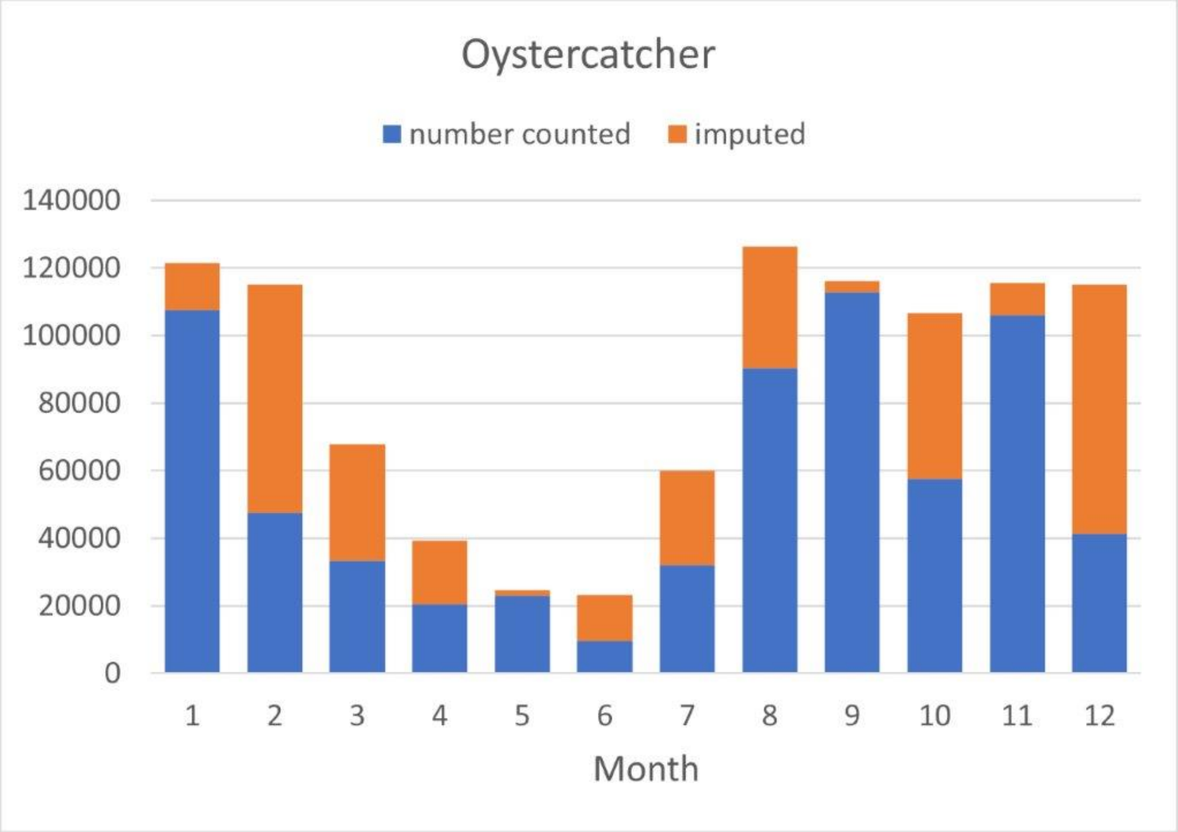


Figure 33: Oystercatcher - seasonal pattern in the number of birds in the Dutch Wadden Sea based on counts and imputation. In the stacked bars, dark blue refers to numbers actually counted and orange to numbers imputed. Data apply to 2015-2020. Copyright: Netwerk Ecologische Monitoring (Sovon, RWS, CBS).

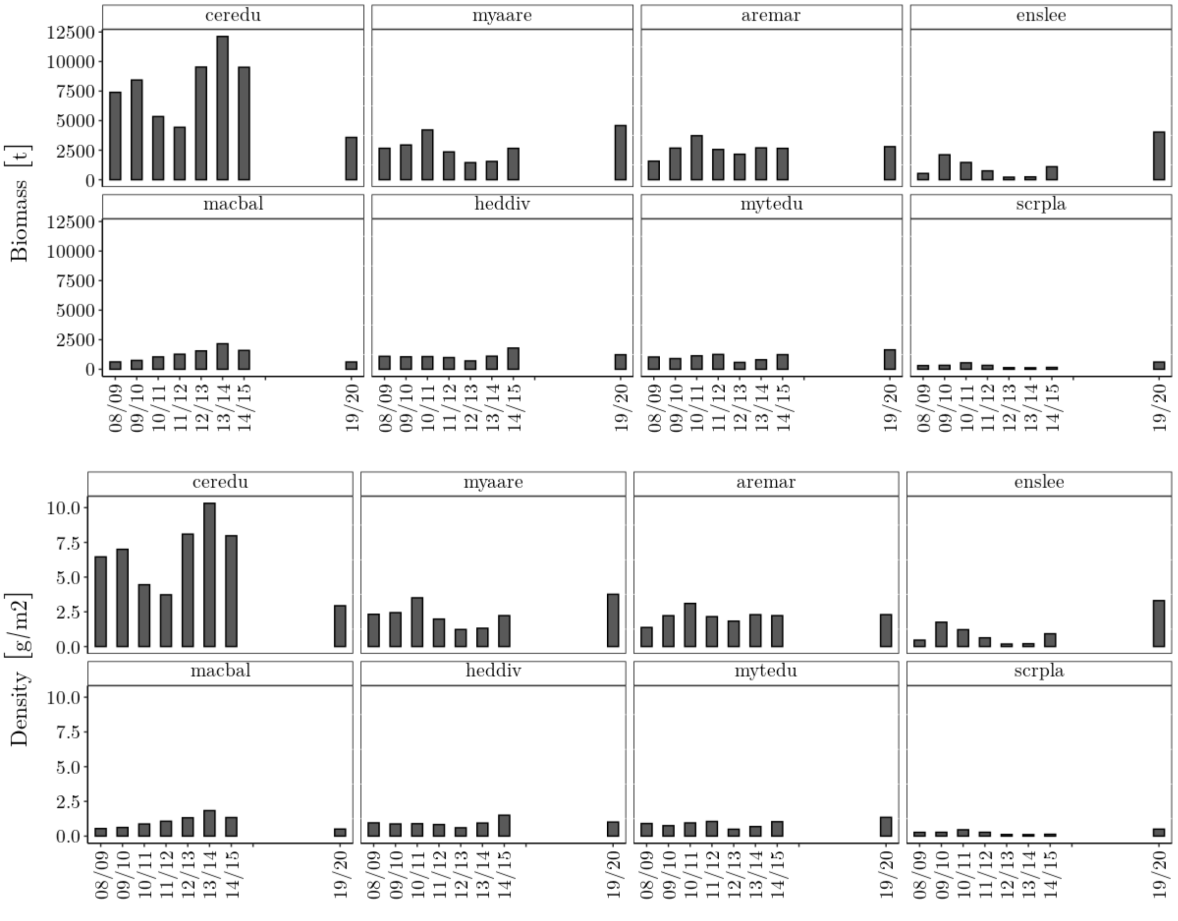
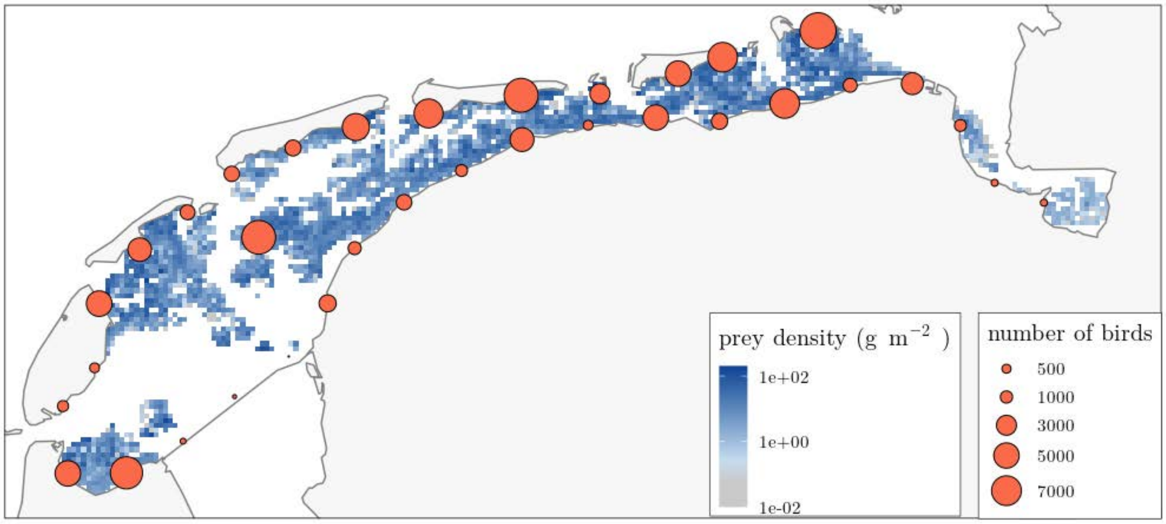


Figure 34: Total biomass (t) and density (g m^{-2}) of Oystercatcher prey for the period 08/09 - 14/15 and 19/20.

Oystercatcher



Prey density per species and roost quality

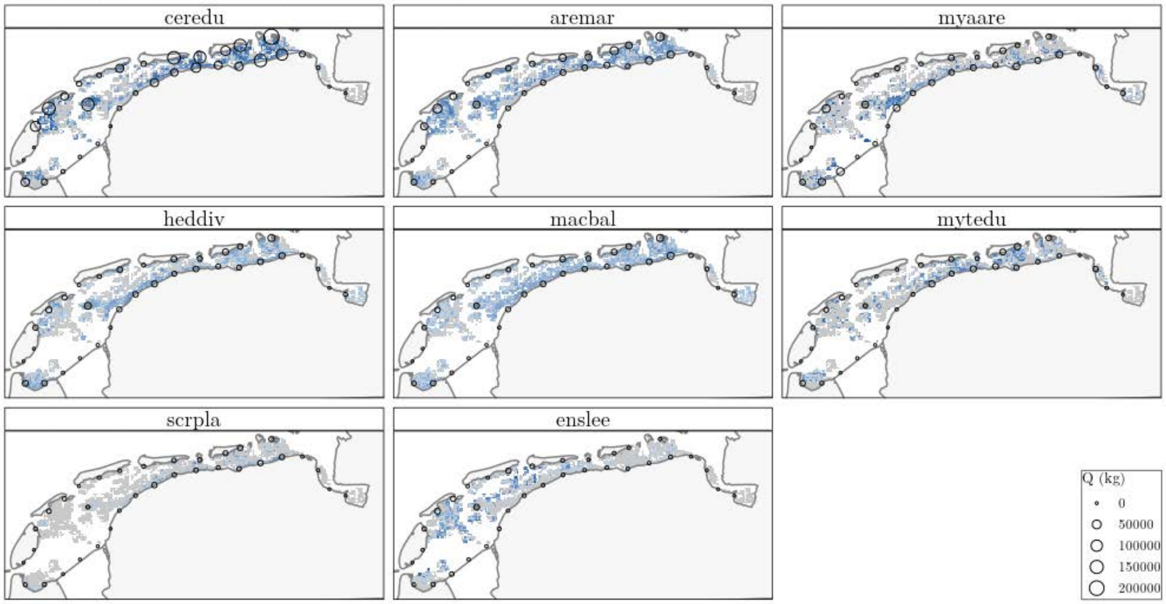


Figure 35: Average number of Oystercatchers per virtual roost (top panel, red dots) and the distribution of prey. The intensity of the colour represents the average prey density (g m^{-2}) over the period 08/09 - 14/15 and 19/20; in the upper panel it is the average of the summed prey densities and in the lower panels it is the average per benthos species. The size of the dots in the lower panels represents the weighed biomass at the virtual roost, i.e. P_{js} (eqn.1).

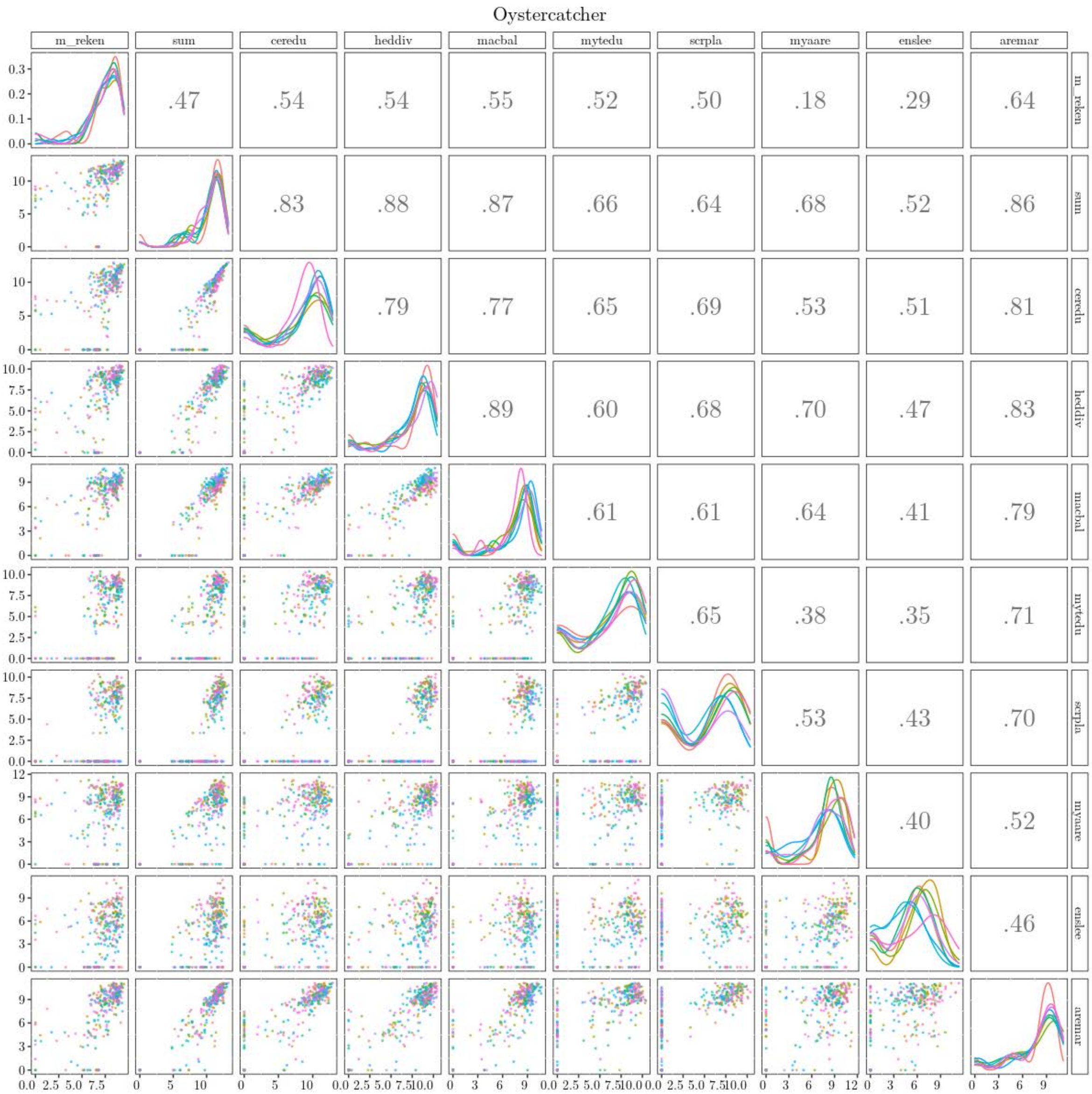


Figure 36: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for Oystercatcher. *m_reken* is the log-transformed number individuals and the prey names represent the log-transformed P_{js} (eqn.1). The different colours represent the different years.

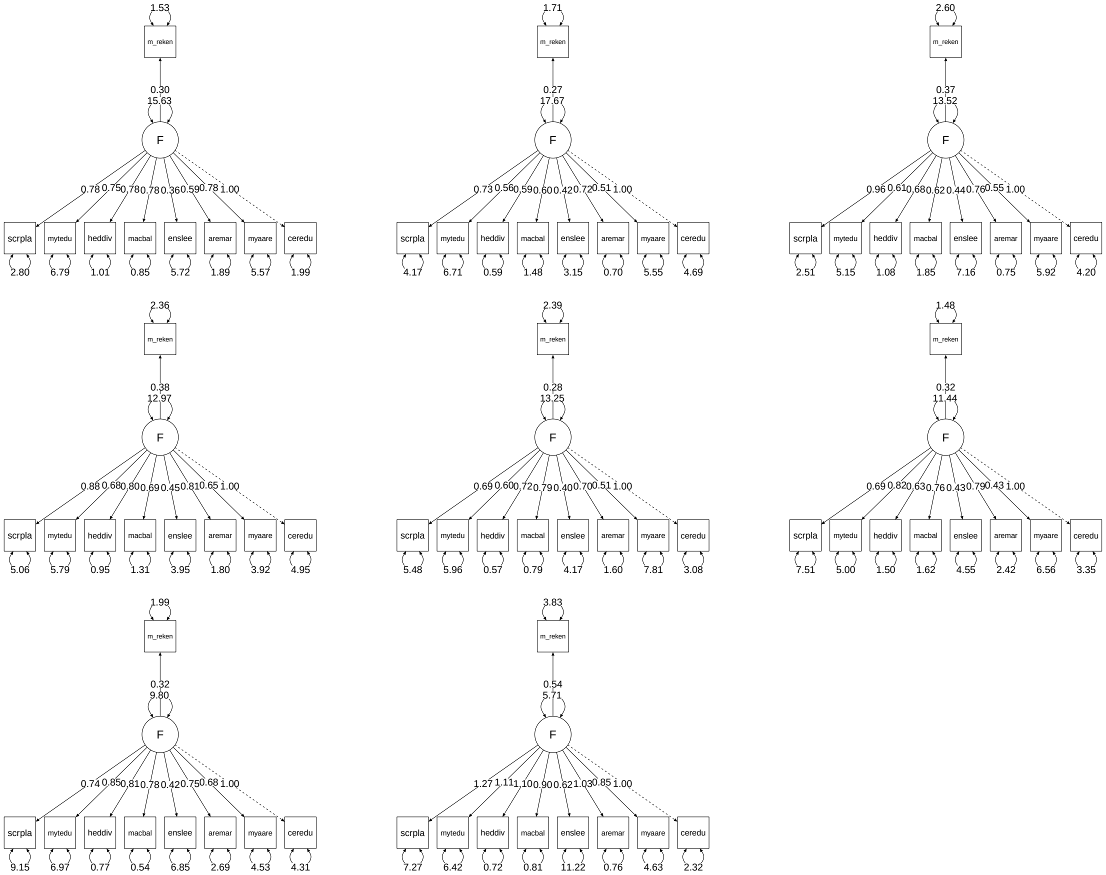


Figure 37: Structural equation model of the number of Oystercatchers per virtual roost as a function of the latent variable F which is measured by Q_{js} (eqn.1) for the period 08/09 - 14/15 and 19/20. Each period is modeled as a group; they are ordered from top left (08/09) to bottom right (19/20).

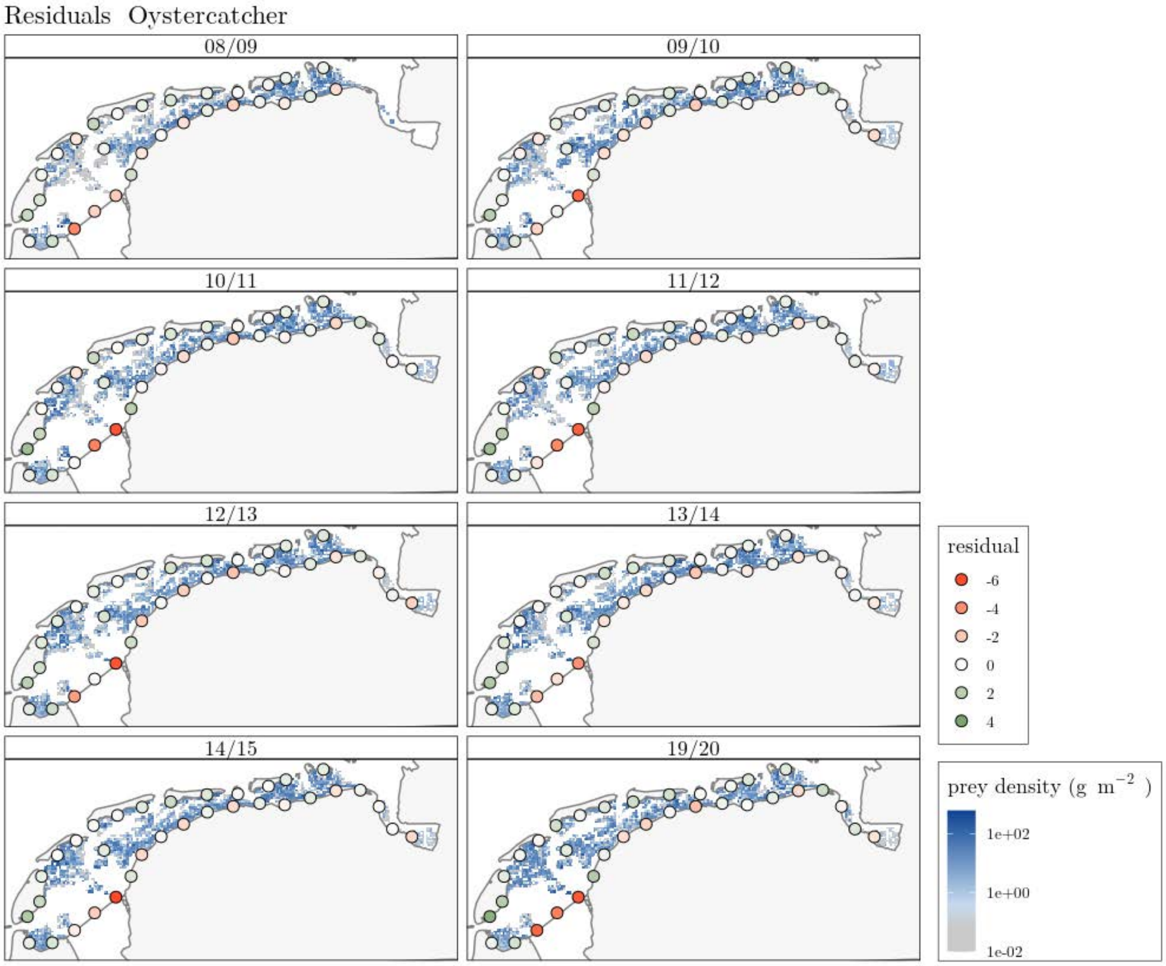


Figure 38: Residuals between the observed and implied number of Oystercatchers at the virtual roosts.

B.1.2 Red Knot - period 1

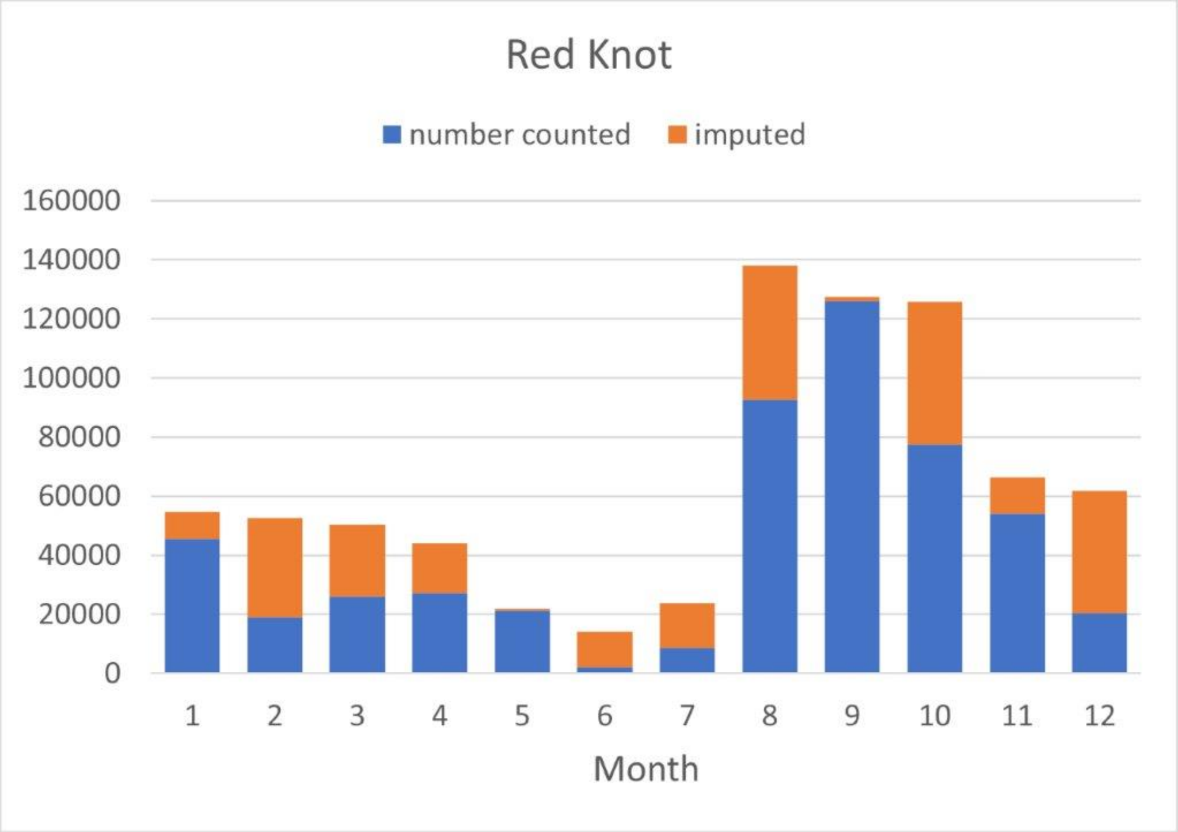


Figure 39: Red knot - seasonal pattern in the number of birds in the Dutch Wadden Sea. See figure 33 for details.

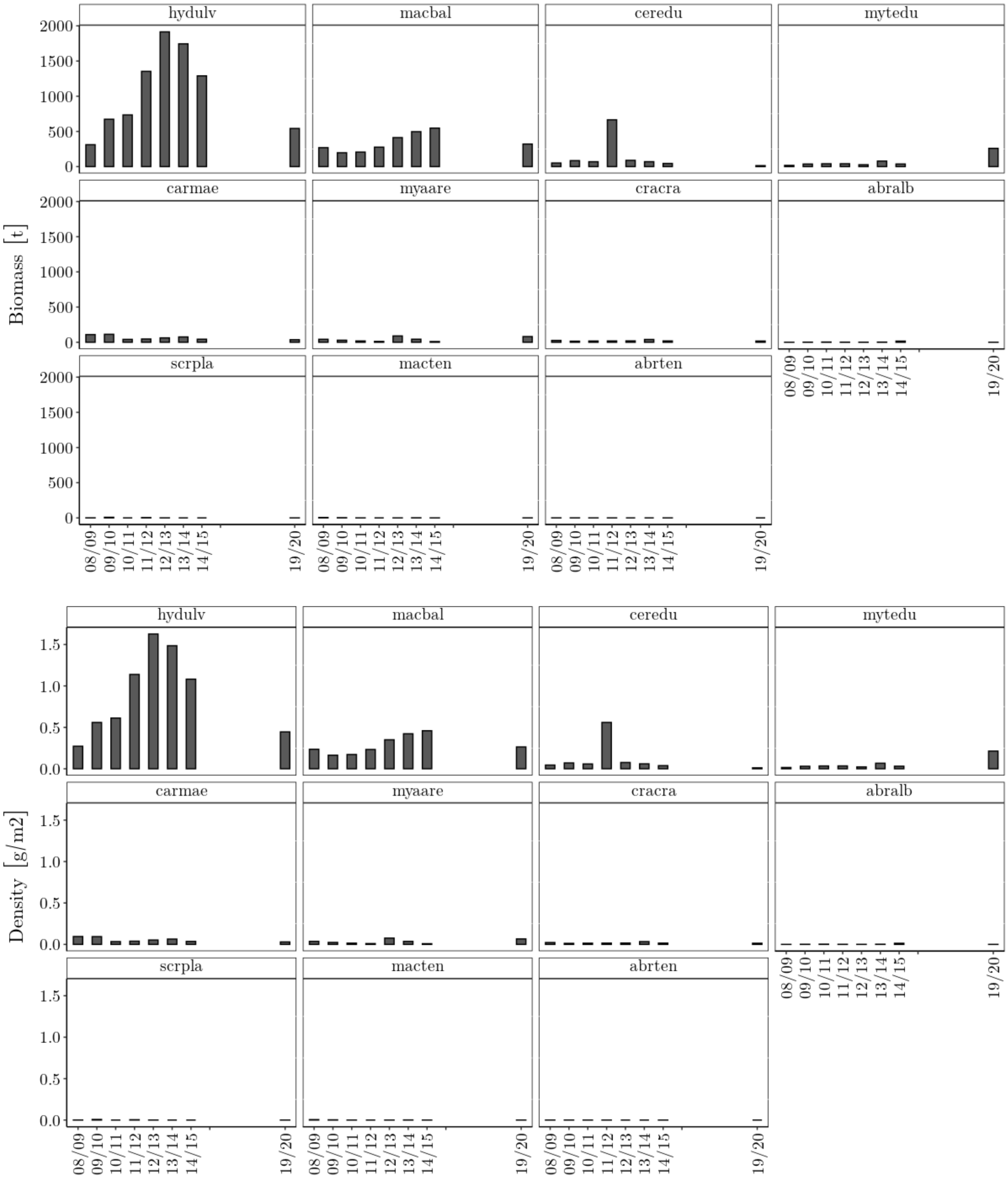


Figure 40: Total biomass (t) and density (g m^{-2}) of Red Knot prey for the period 08/09 - 14/15 and 19/20.

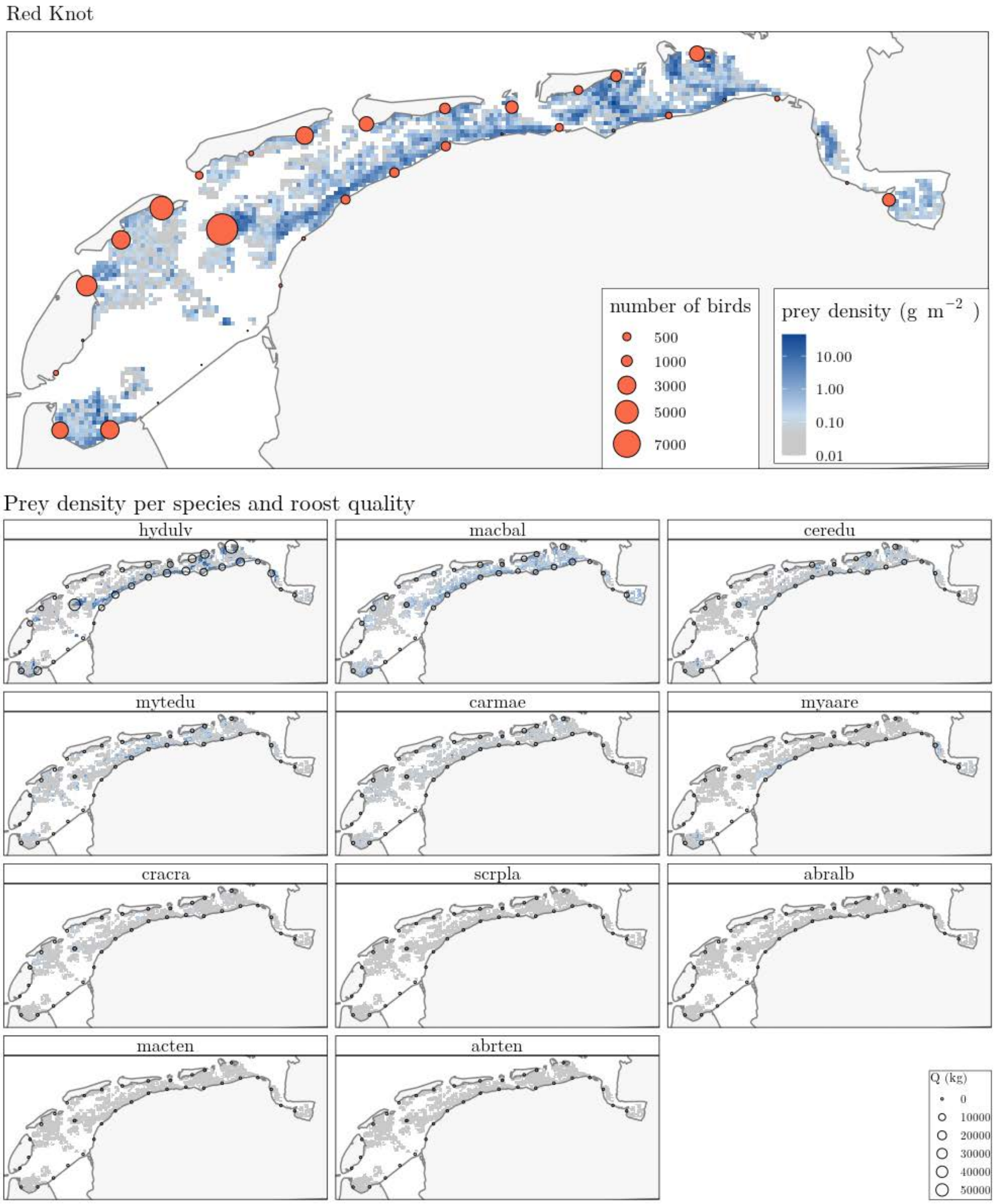


Figure 41: Average number of Red Knots per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

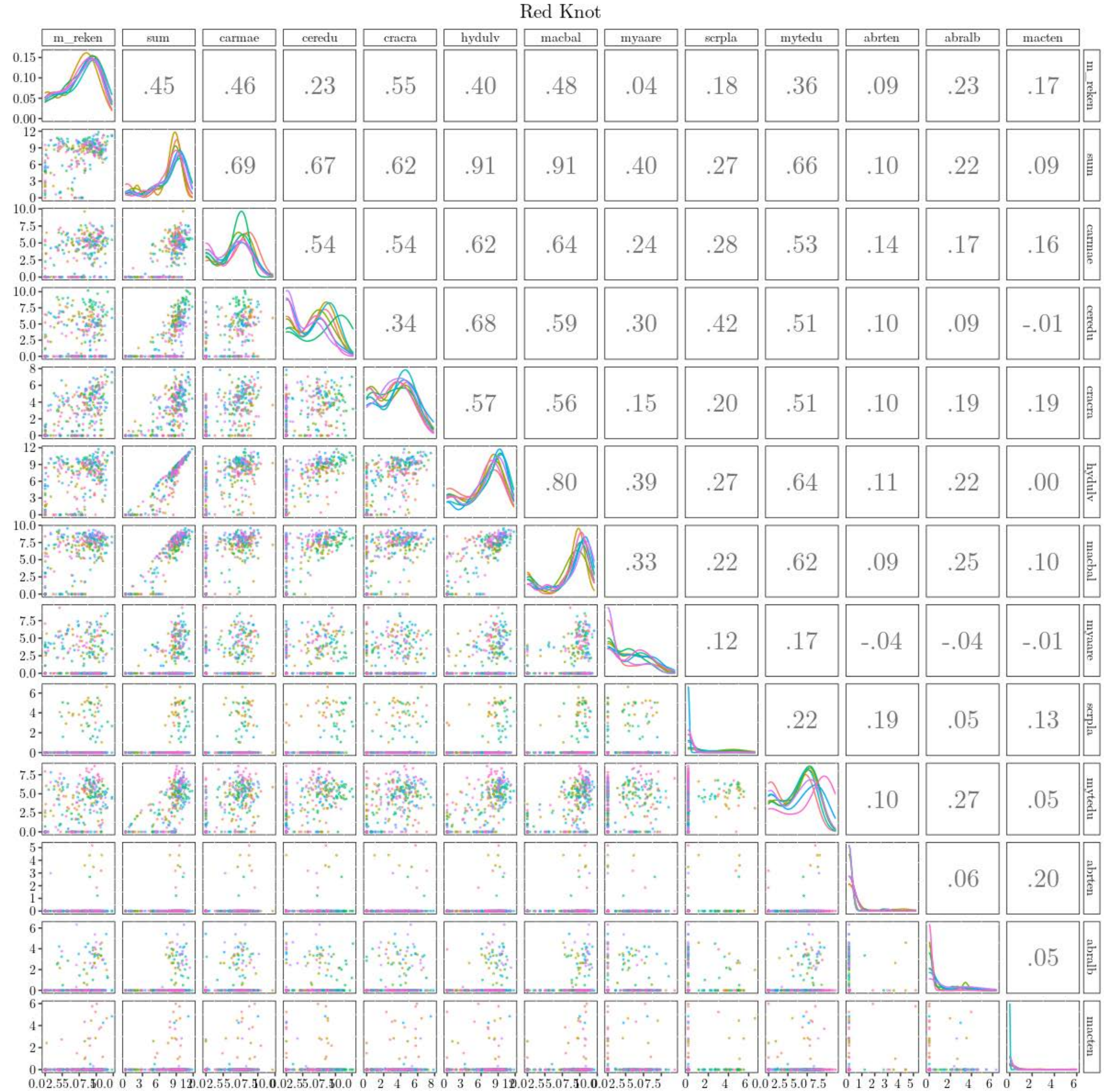


Figure 42: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for Red Knot. See the caption of Figure 36 for further details.

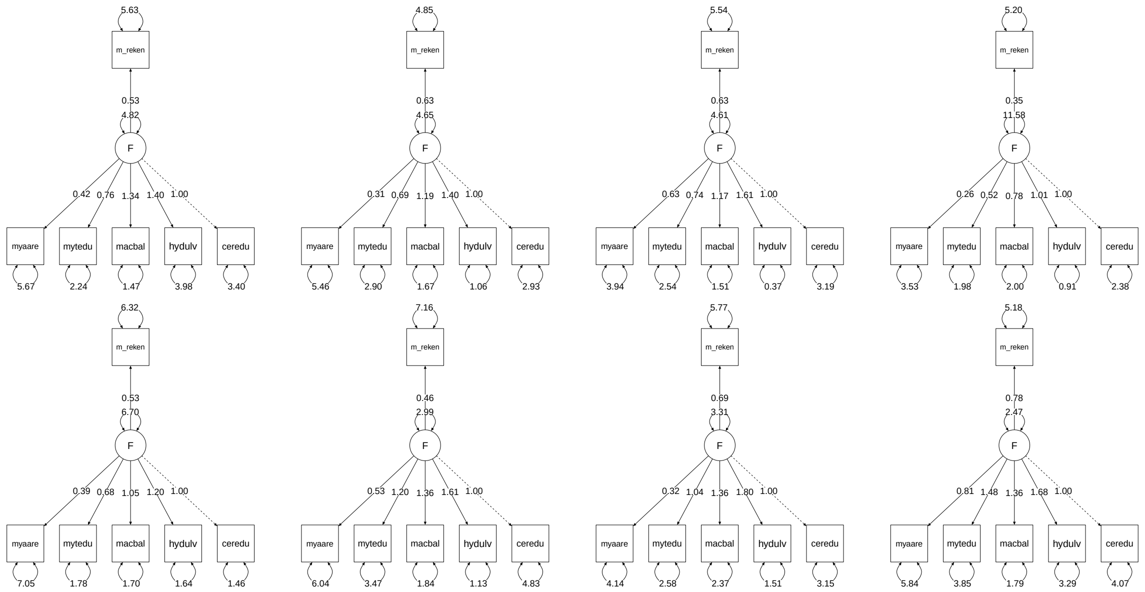


Figure 43: Structural equation model of the number of Red Knots during period 1. See the caption of Figure 37 for further information.

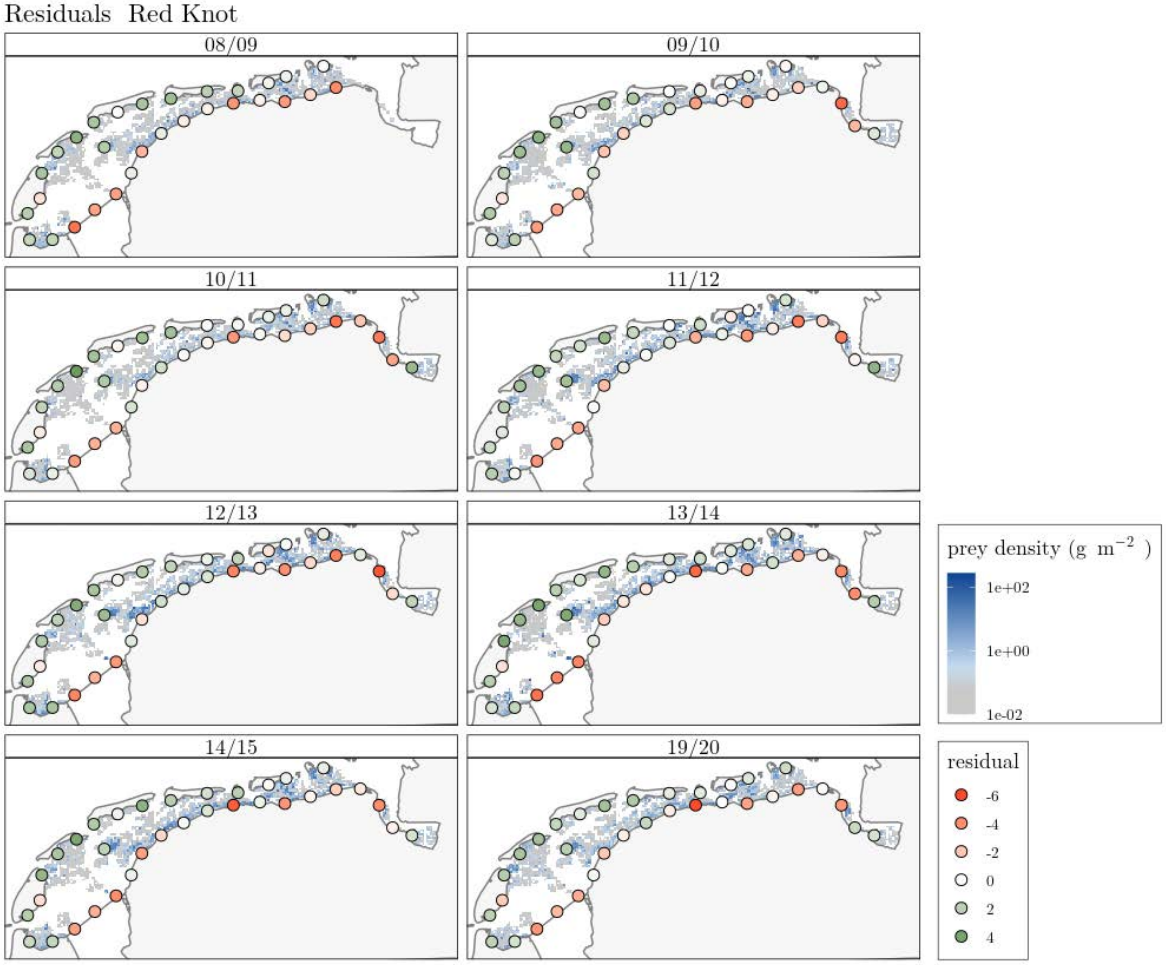


Figure 44: Residuals between the observed and implied number of Red knots during period 1 at the virtual roosts.

B.1.3 Red Knot - period 2

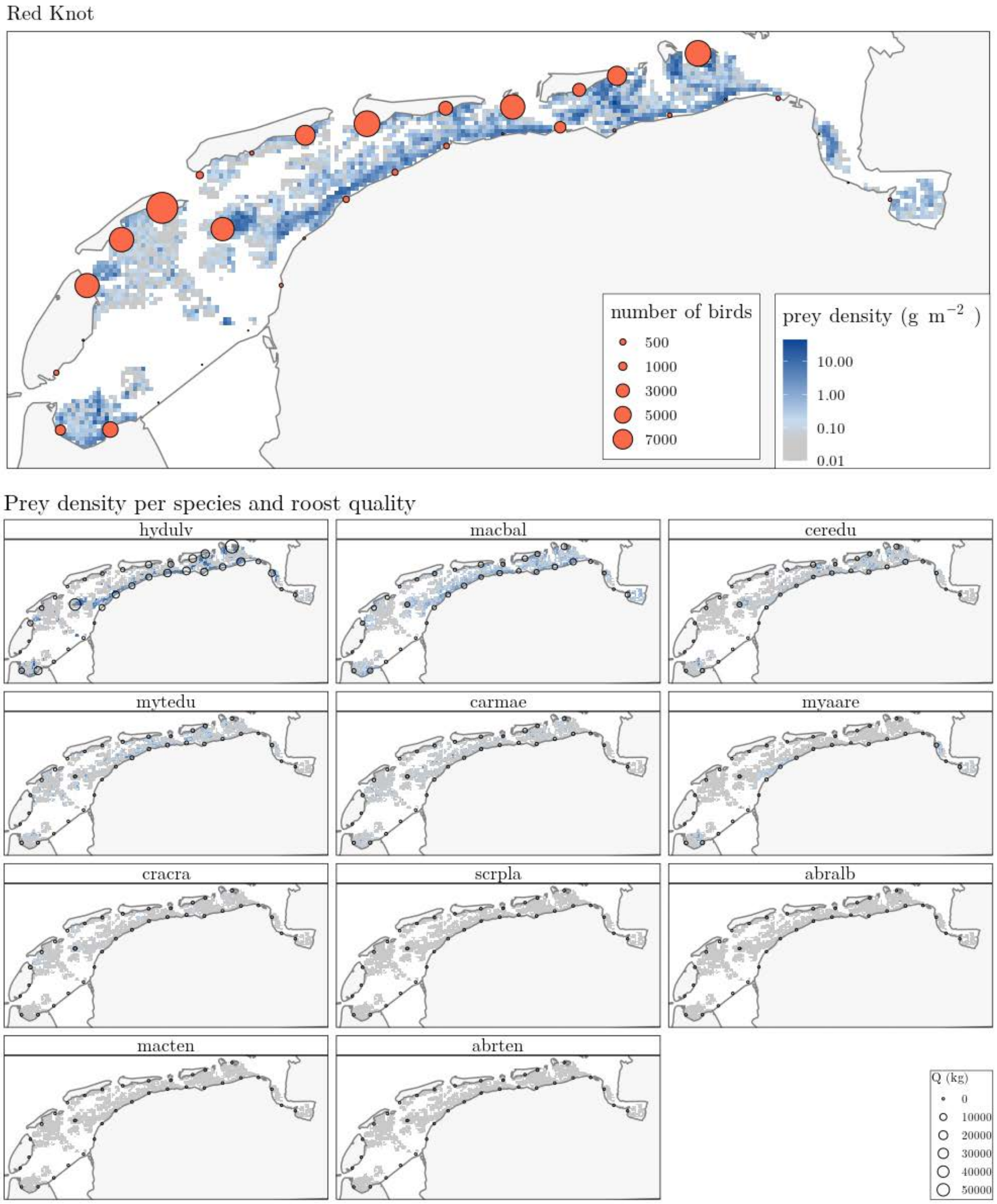


Figure 45: Average number of Red Knots per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

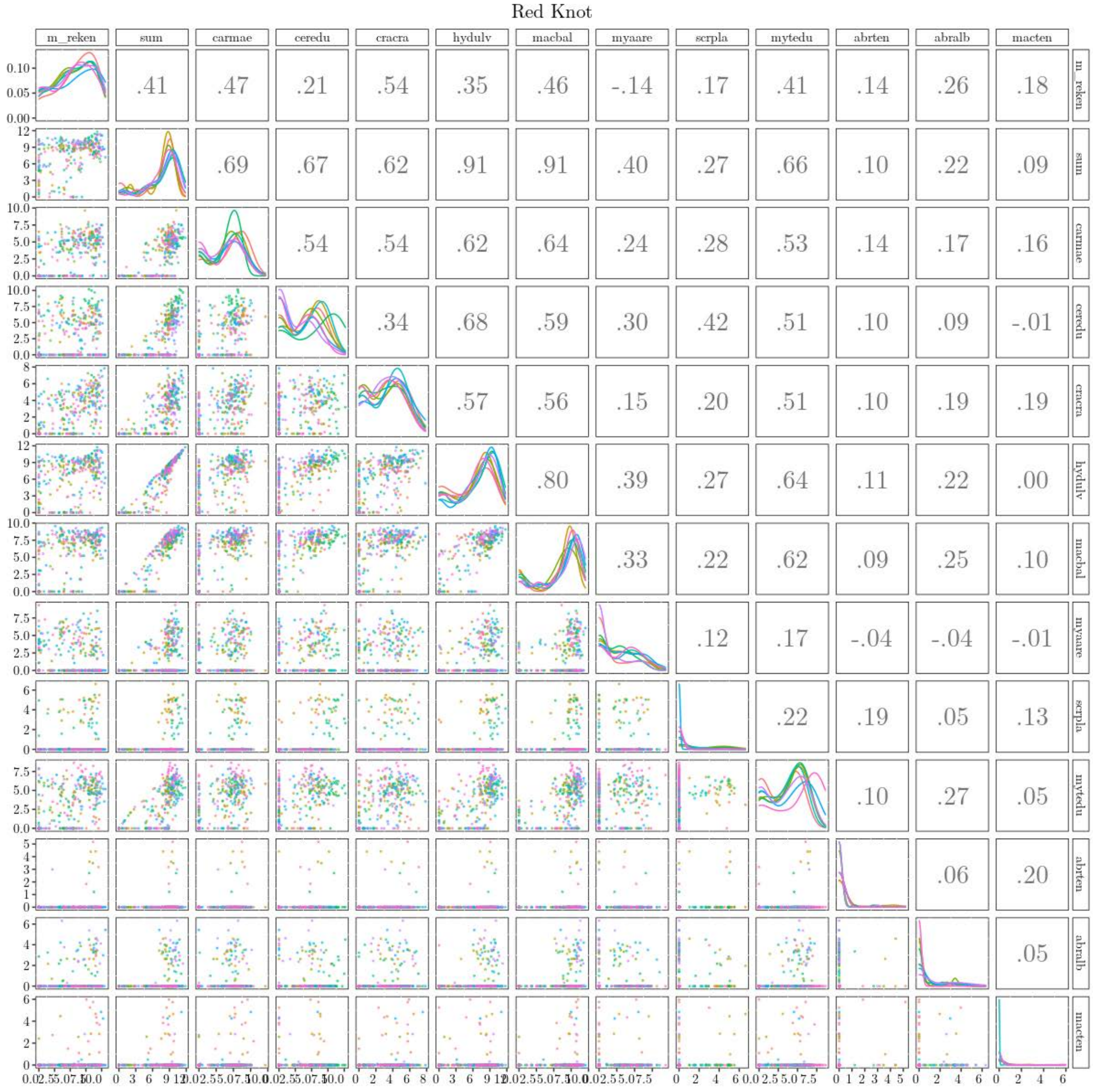


Figure 46: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Red Knot. See the caption of Figure 36 for further details.

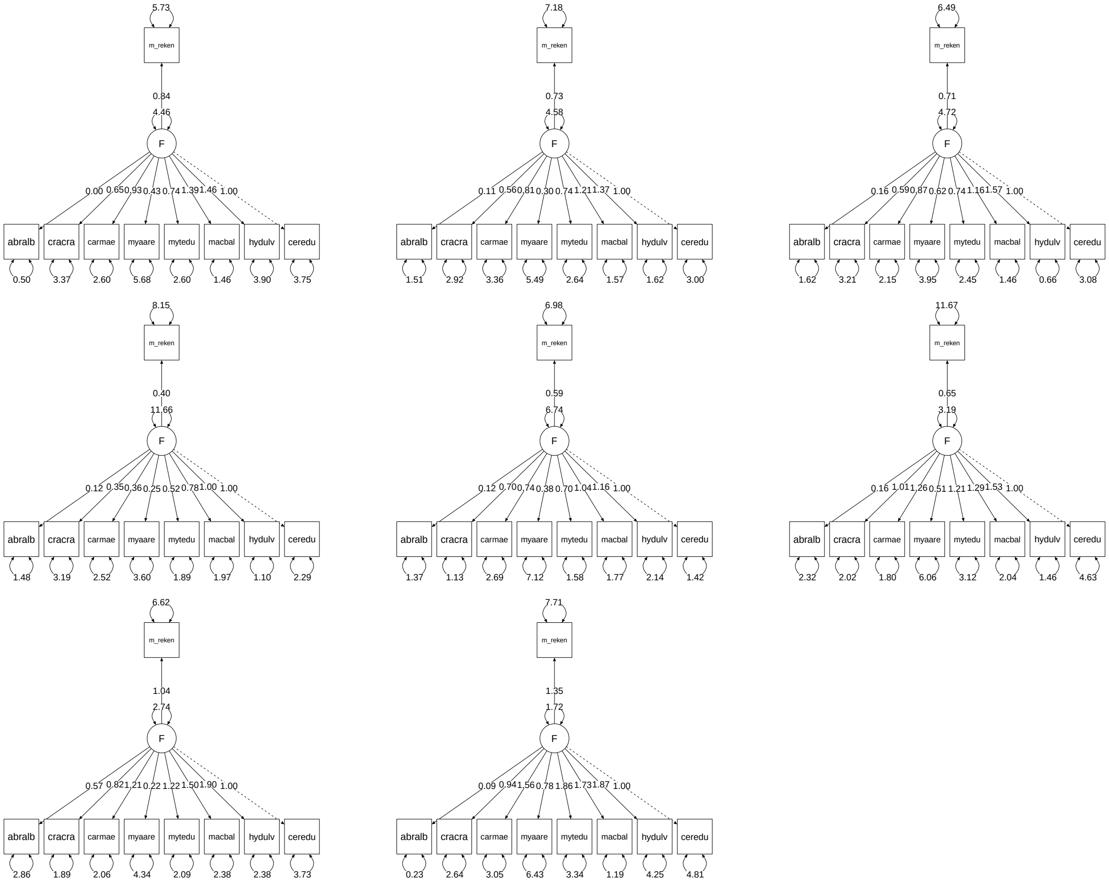


Figure 47: Structural equation model of the number of Red Knots during period 2. See the caption of Figure 37 for further information.

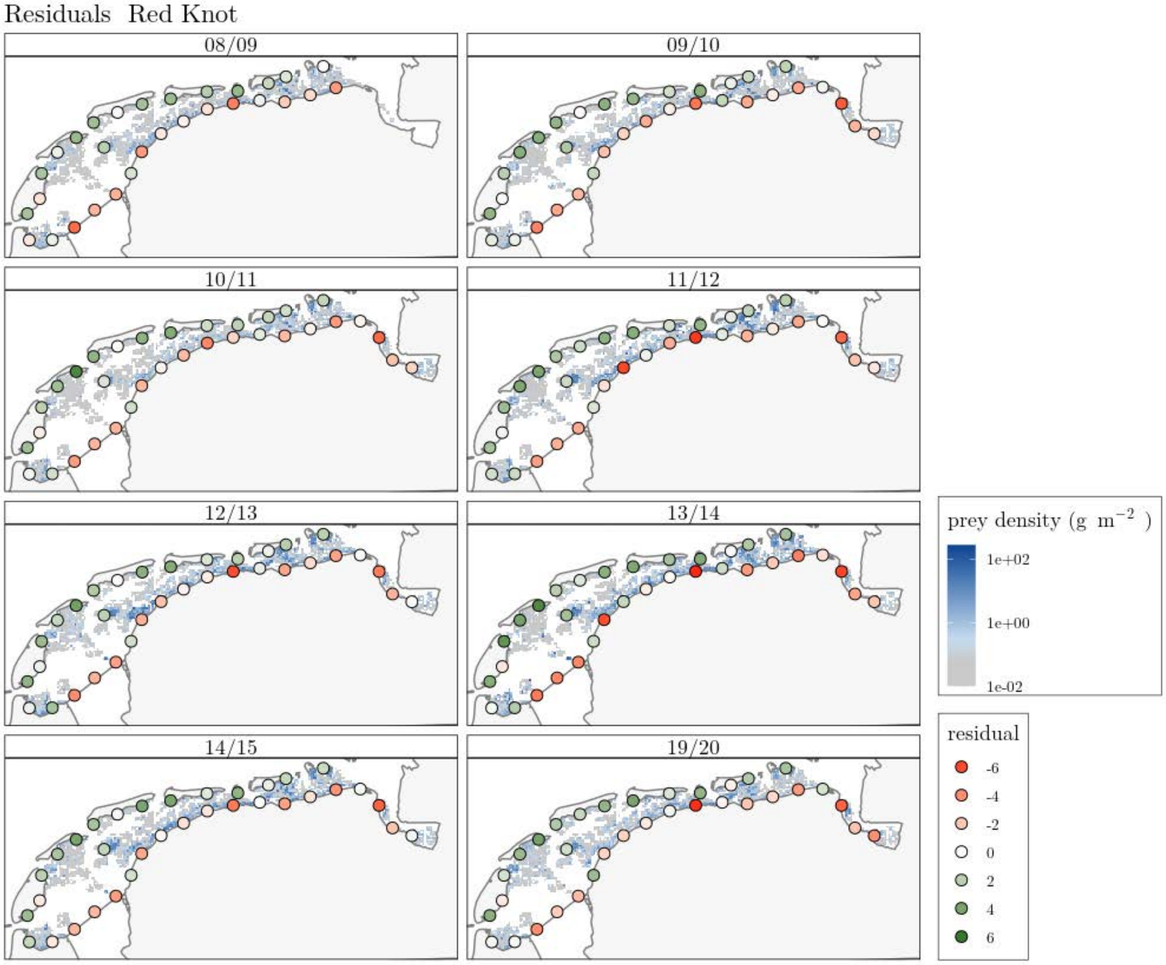


Figure 48: Residuals between the observed and implied number of Red knots during period 2 at the virtual roosts.

B.1.4 Curlew

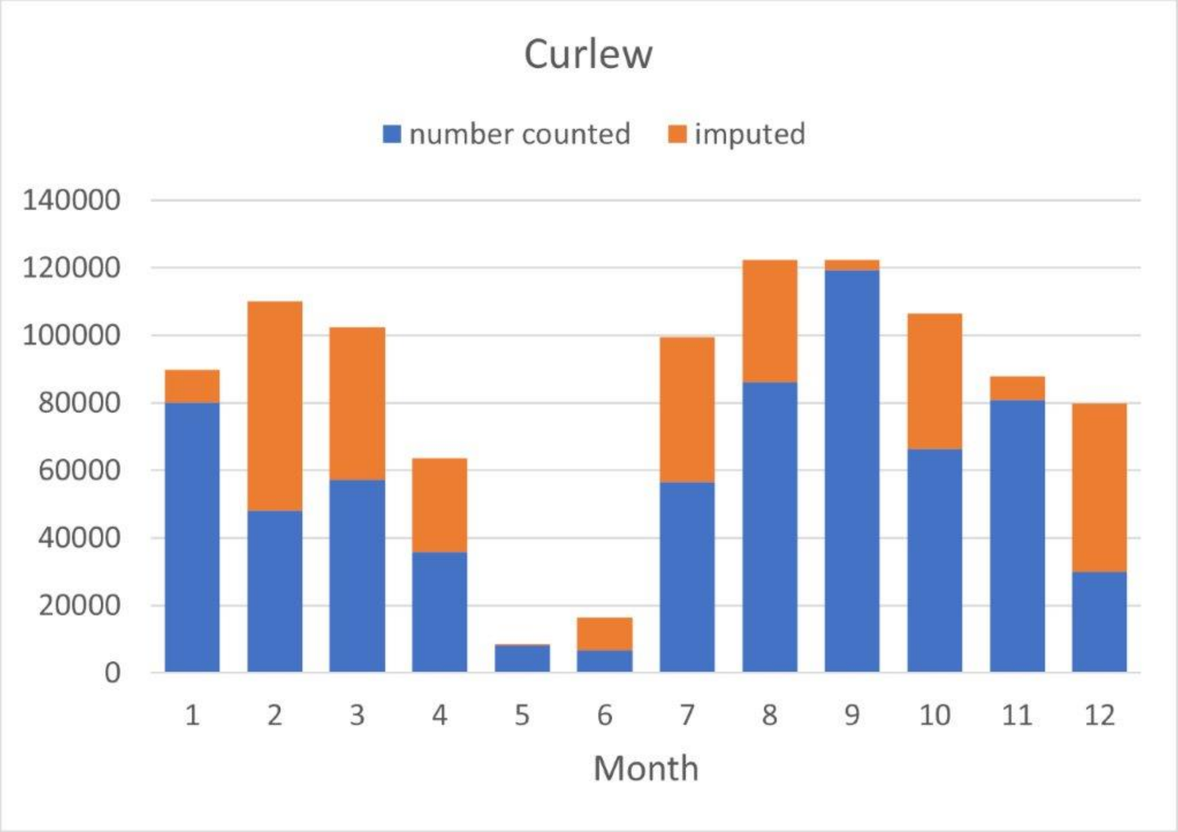


Figure 49: Curlew - seasonal pattern in the number of birds in the Dutch Wadden Sea. See figure 33 for details.

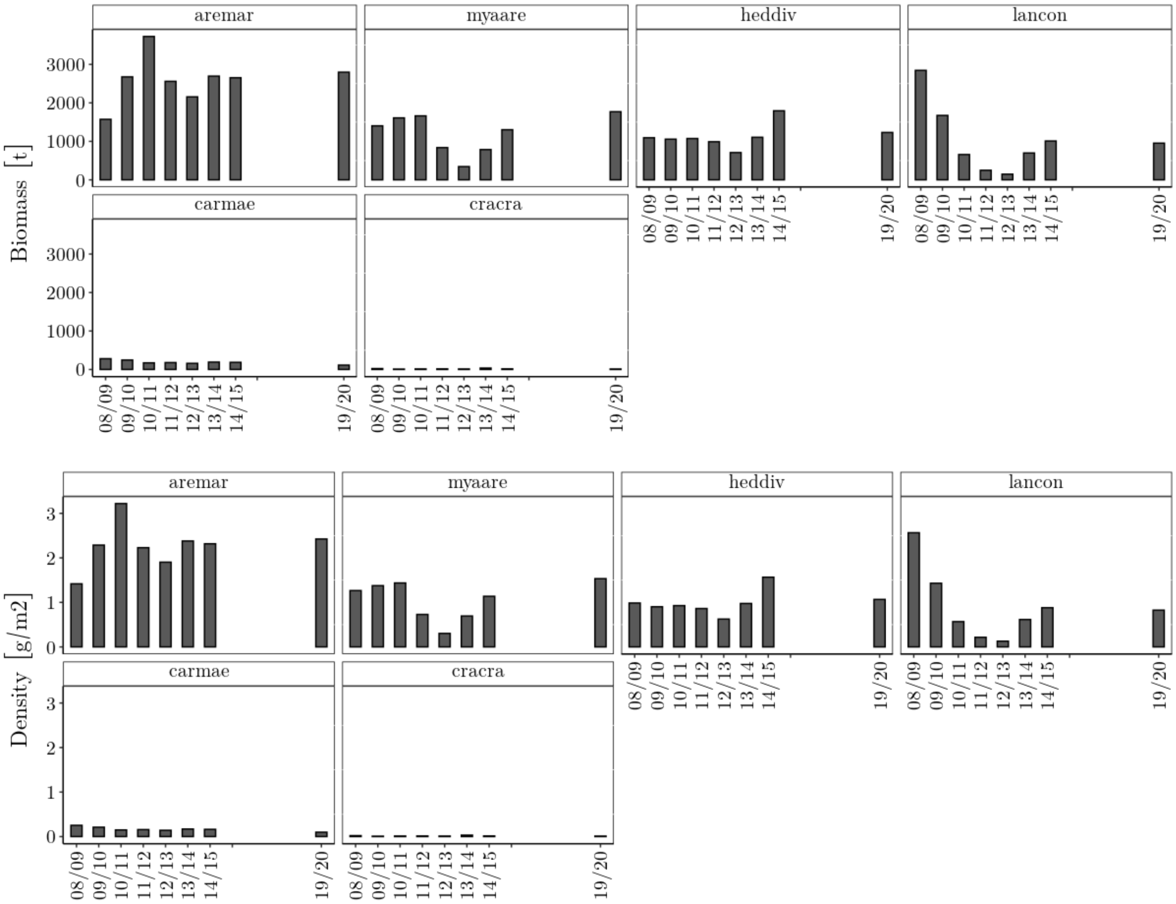


Figure 50: Total biomass (t) and density (g m^{-2}) of Curlew prey for the period 08/09 - 14/15 and 19/20.

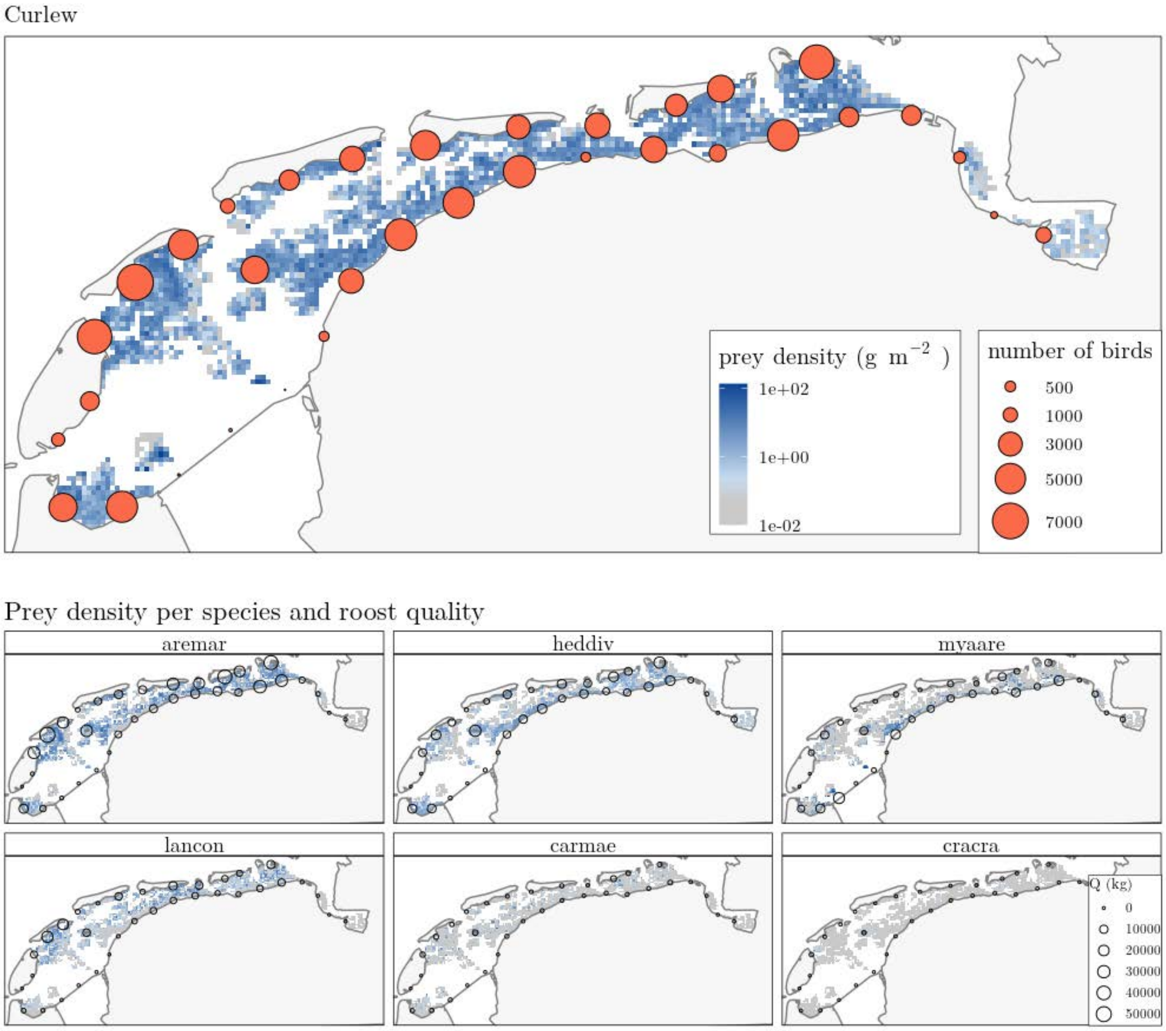


Figure 51: Average number of Curlews per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

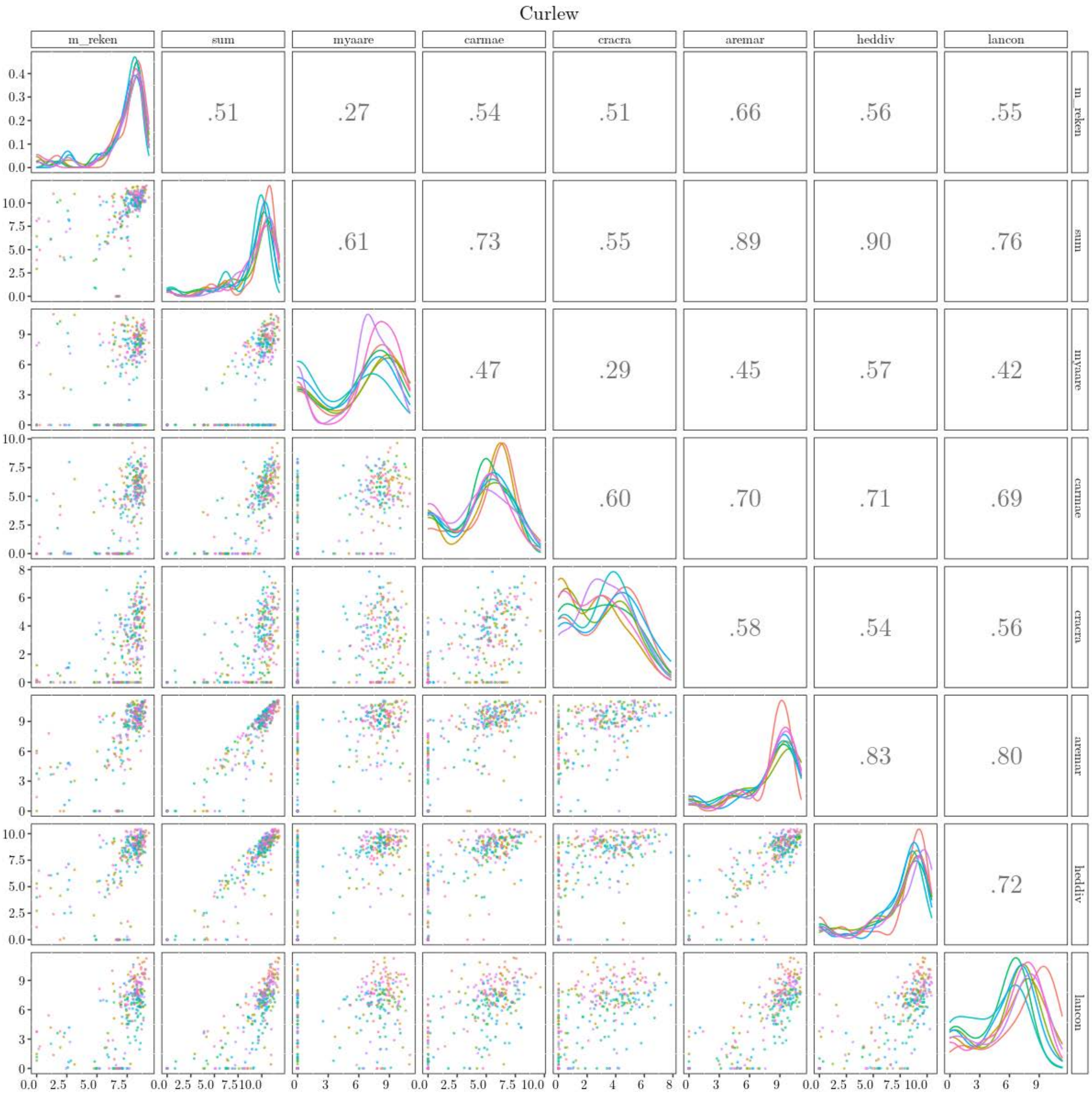


Figure 52: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Curlew. See the caption of Figure 36 for further details.

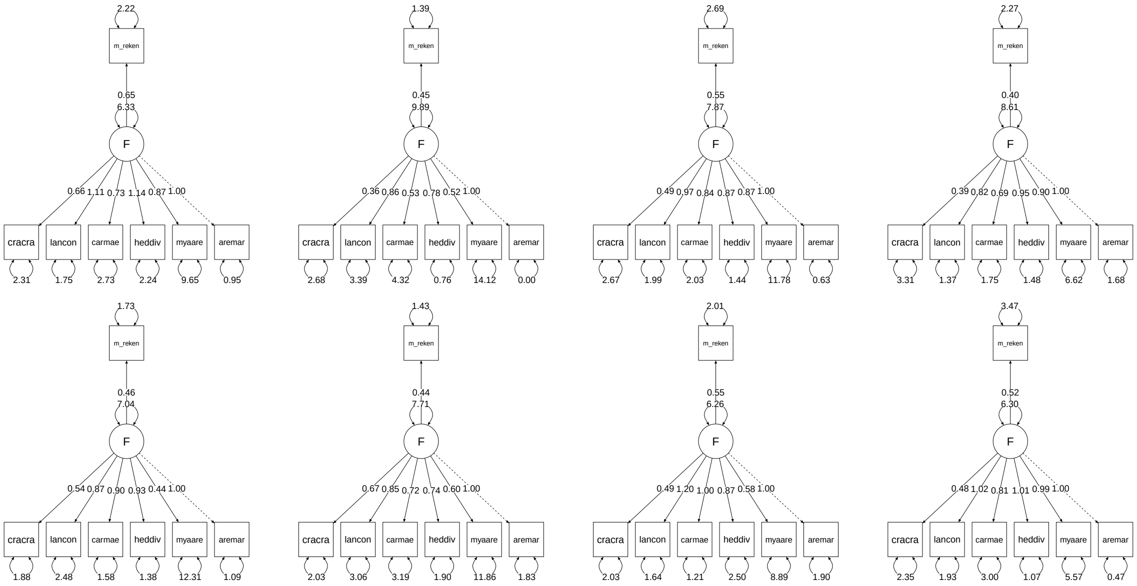


Figure 53: Structural equation model of the number of Curlews during period 2. See the caption of Figure 37 for further information.

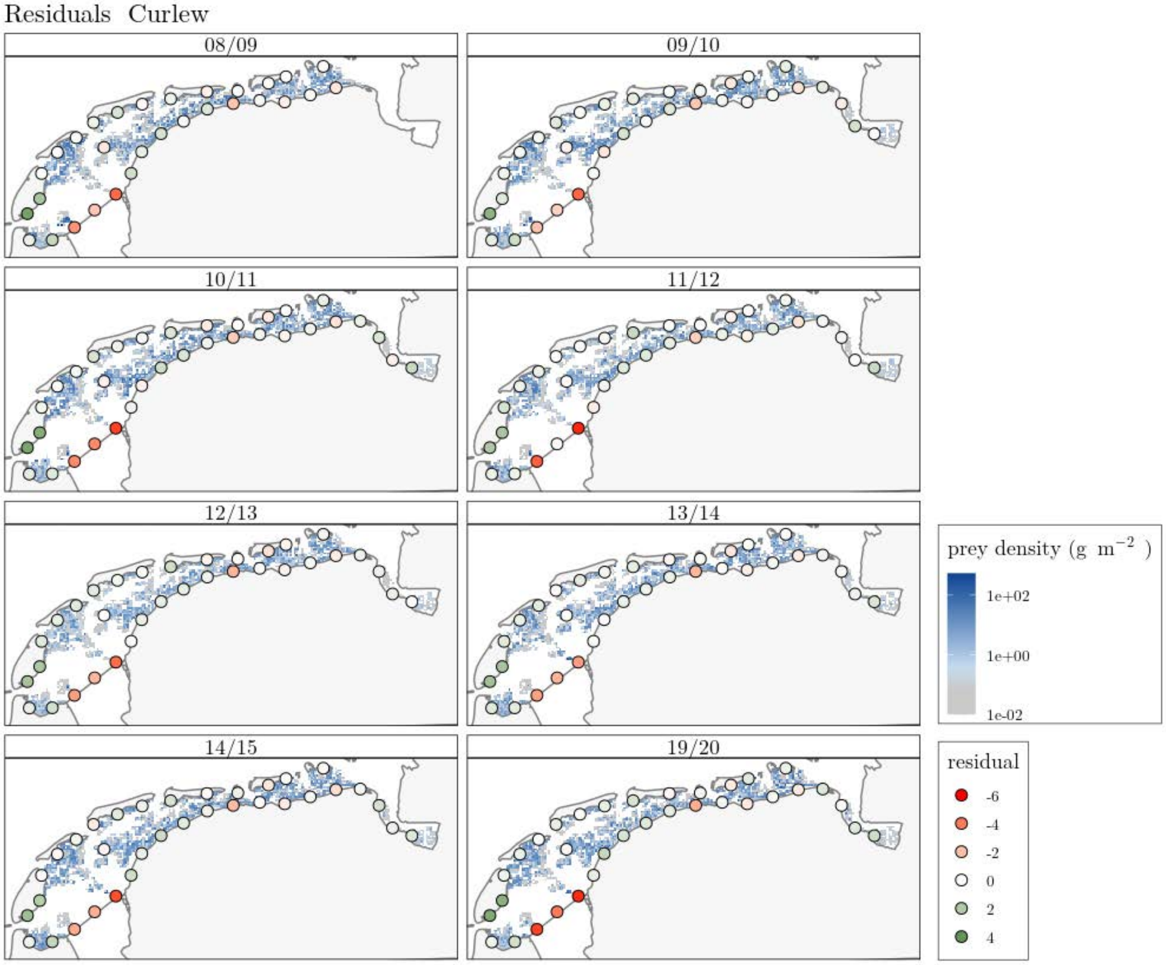


Figure 54: Residuals between the observed and implied number of Curlews at the virtual roosts.

B.1.5 Dunlin

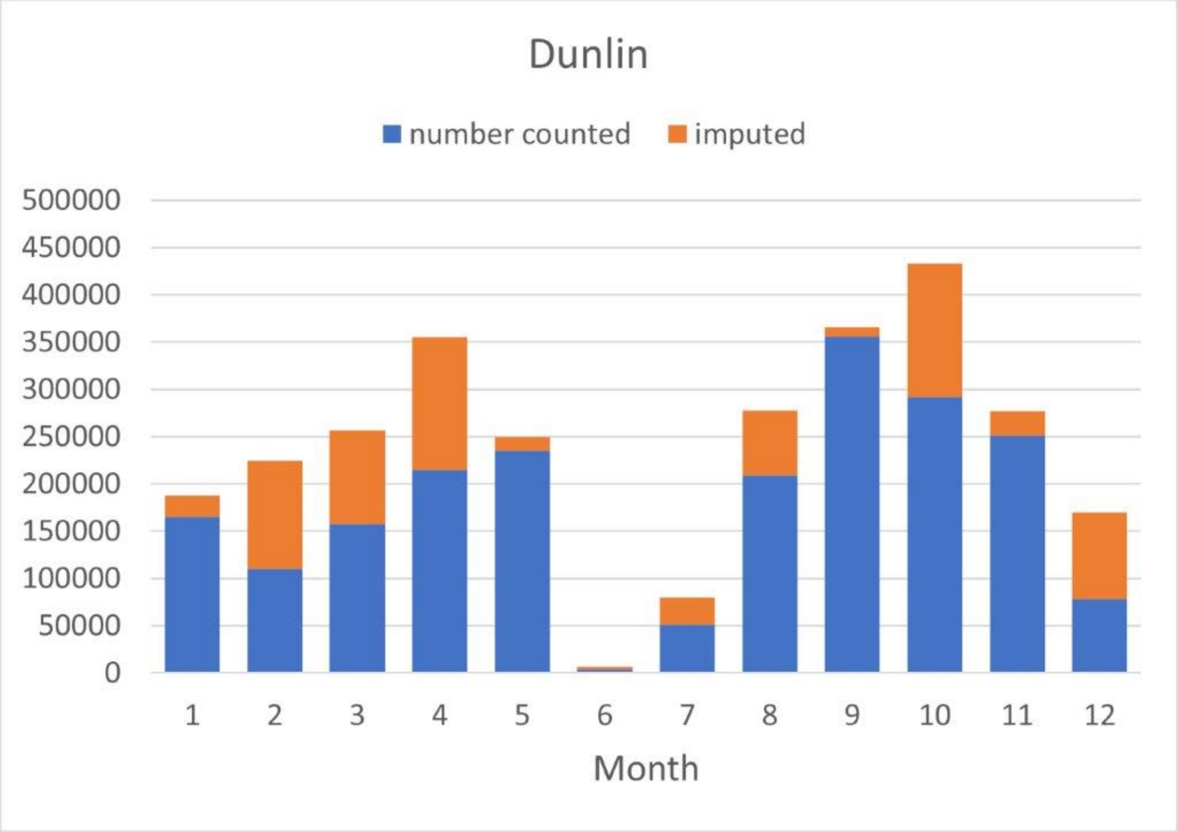


Figure 55: Dunlin - seasonal pattern in the number of birds in the Dutch Wadden Sea. See figure 33 for details.

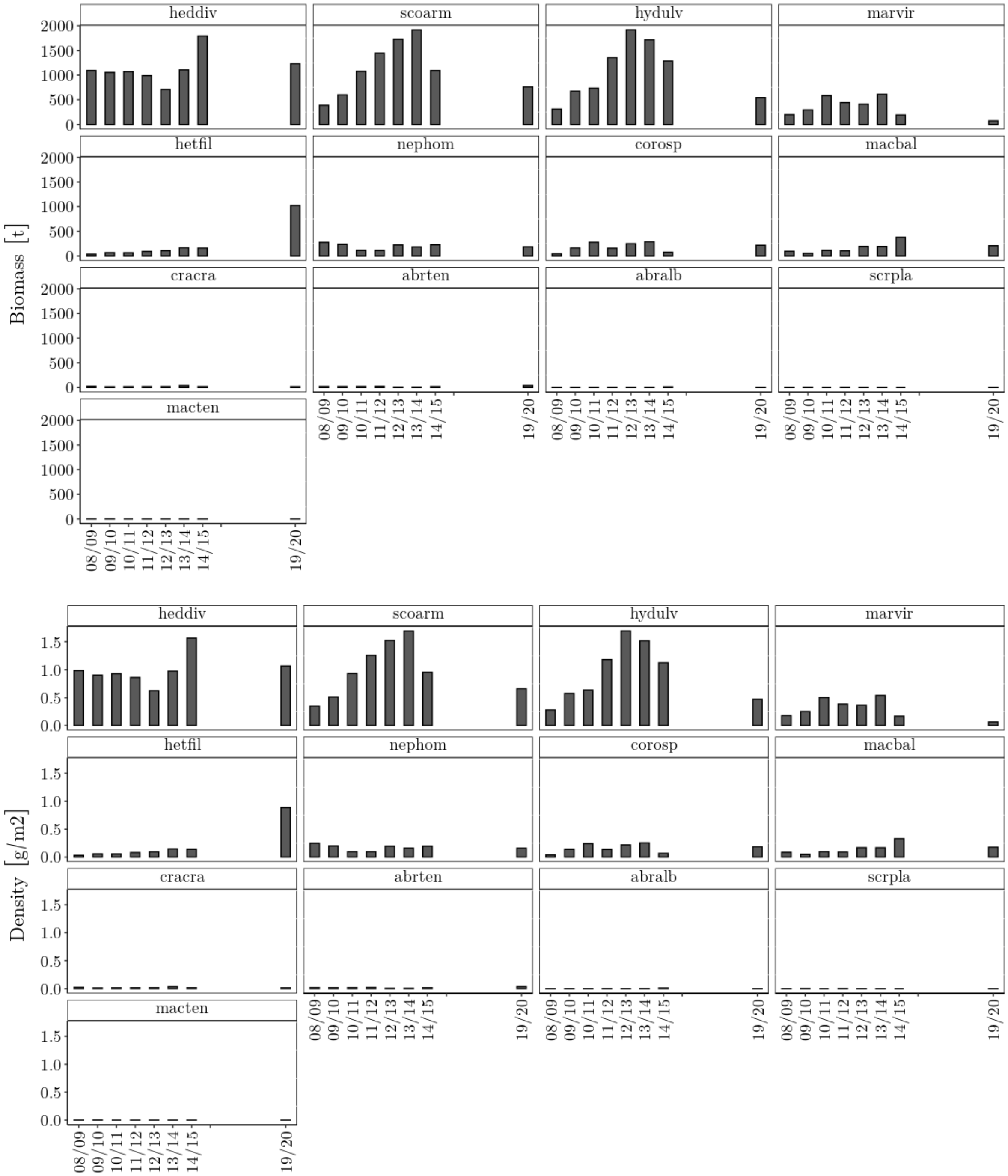


Figure 56: Total biomass (t) and density (g m^{-2}) of Dunlin prey for the period 08/09 - 14/15 and 19/20.

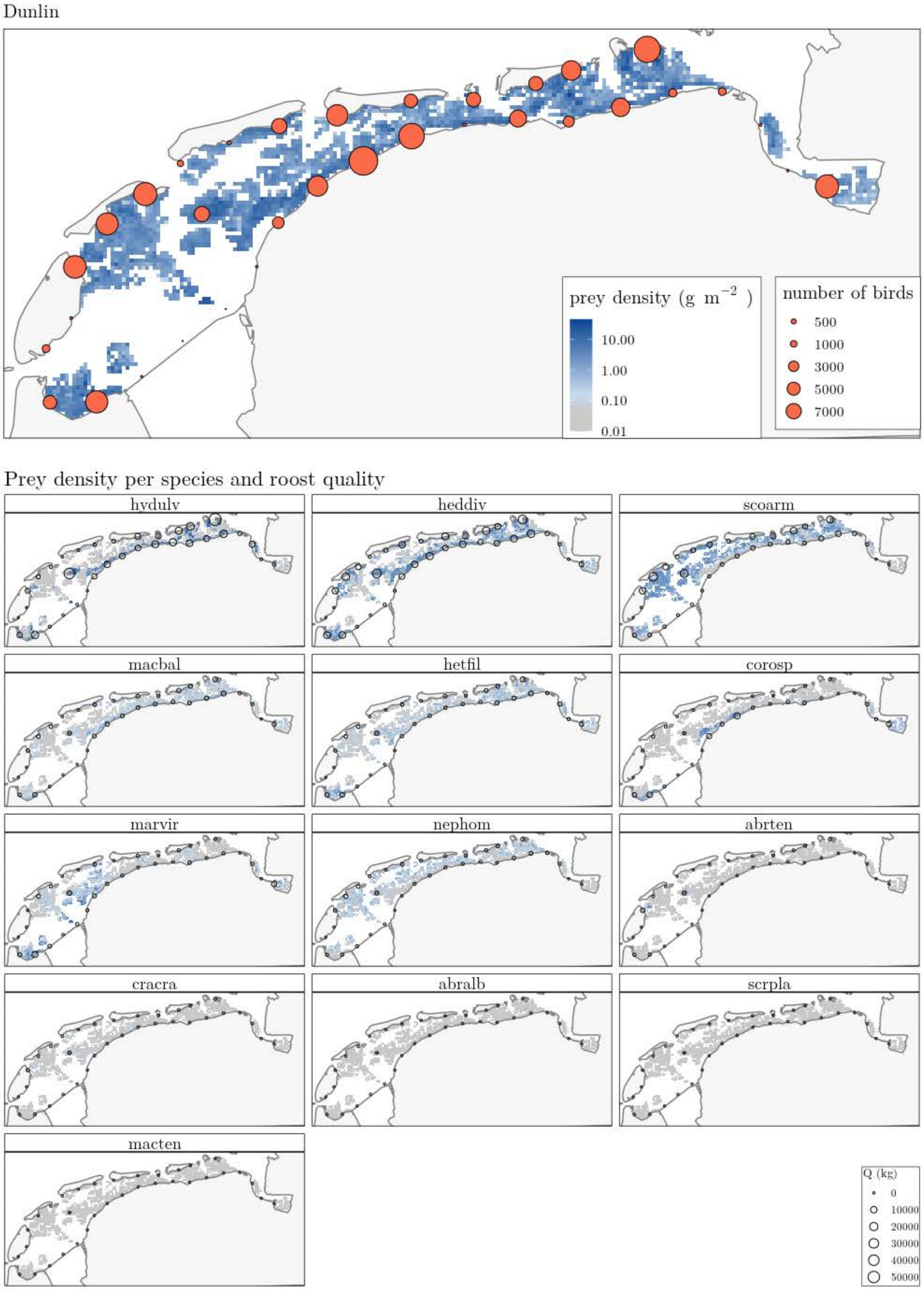


Figure 57: Average number of Dunlins per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

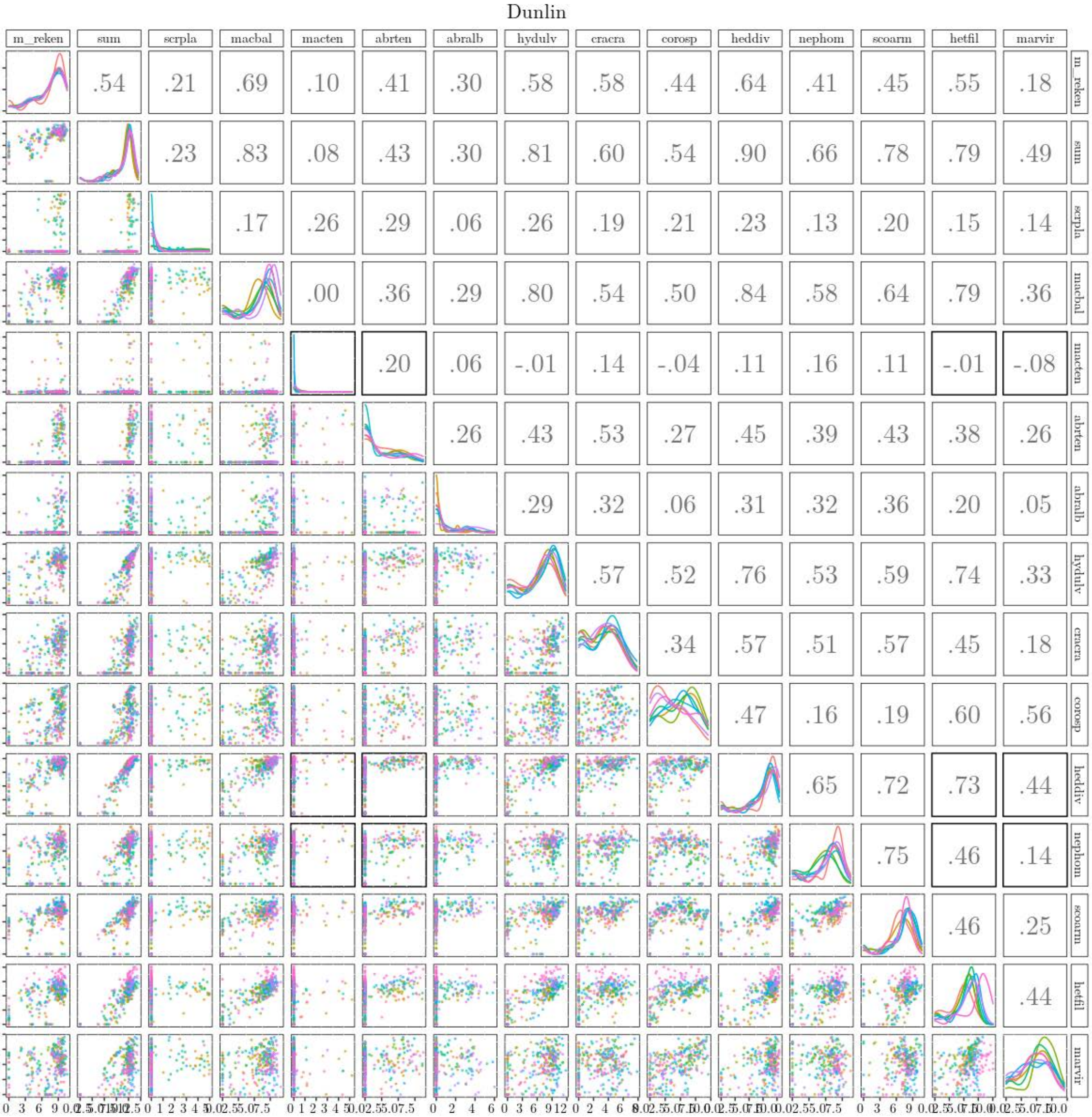


Figure 58: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Dunlin. See the caption of Figure 36 for further details.

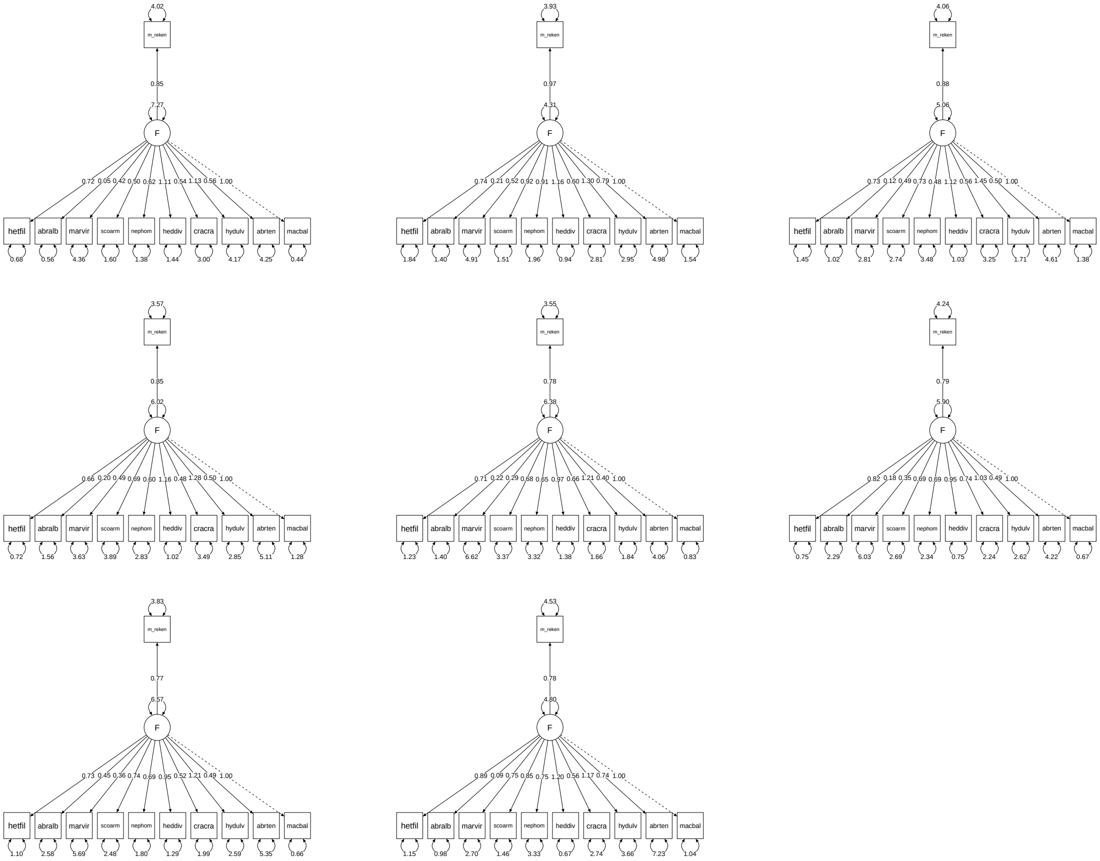


Figure 59: Structural equation model of the number of Dunlin. See the caption of Figure 37 for further information.

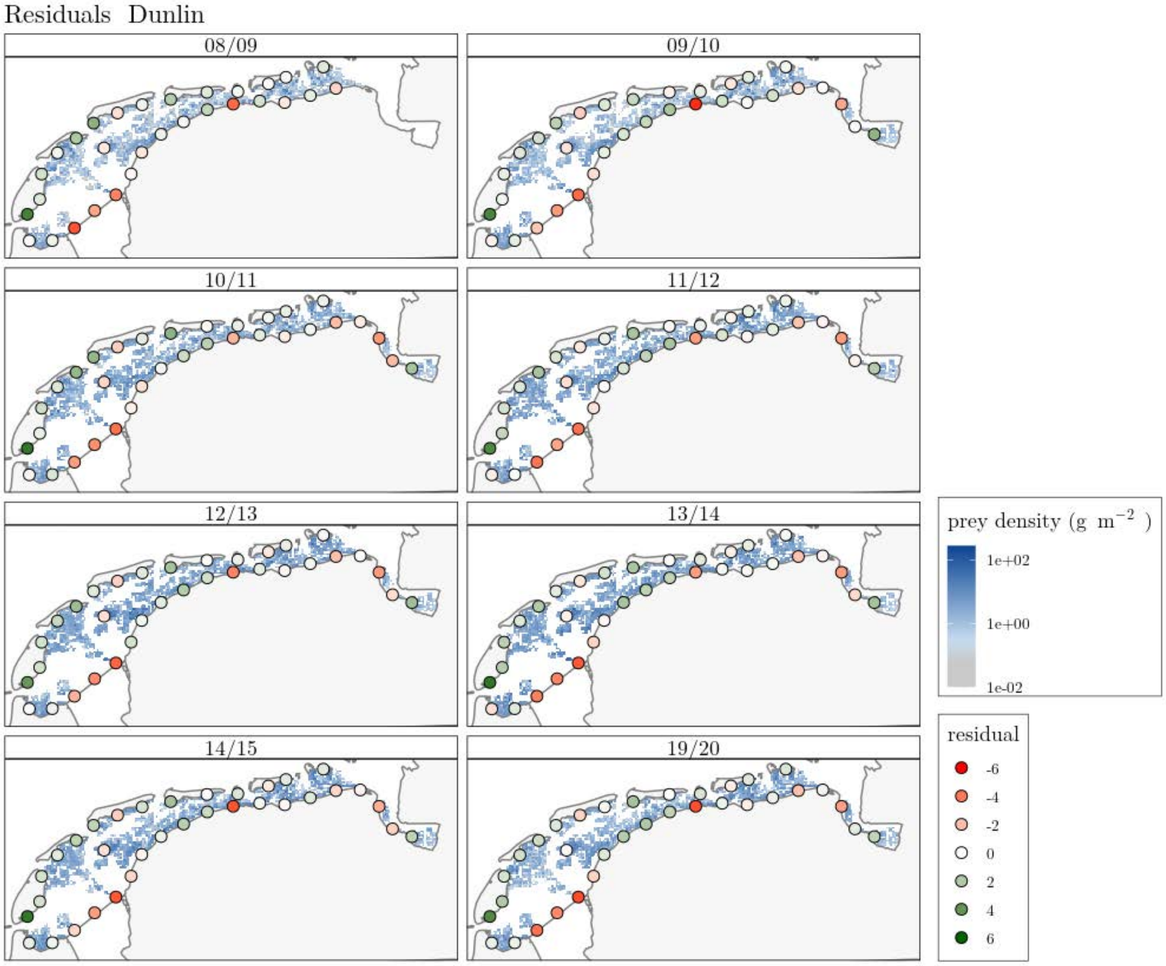


Figure 60: Residuals between the observed and implied number of Dunlins at the virtual roosts.

B.1.6 Grey Plover

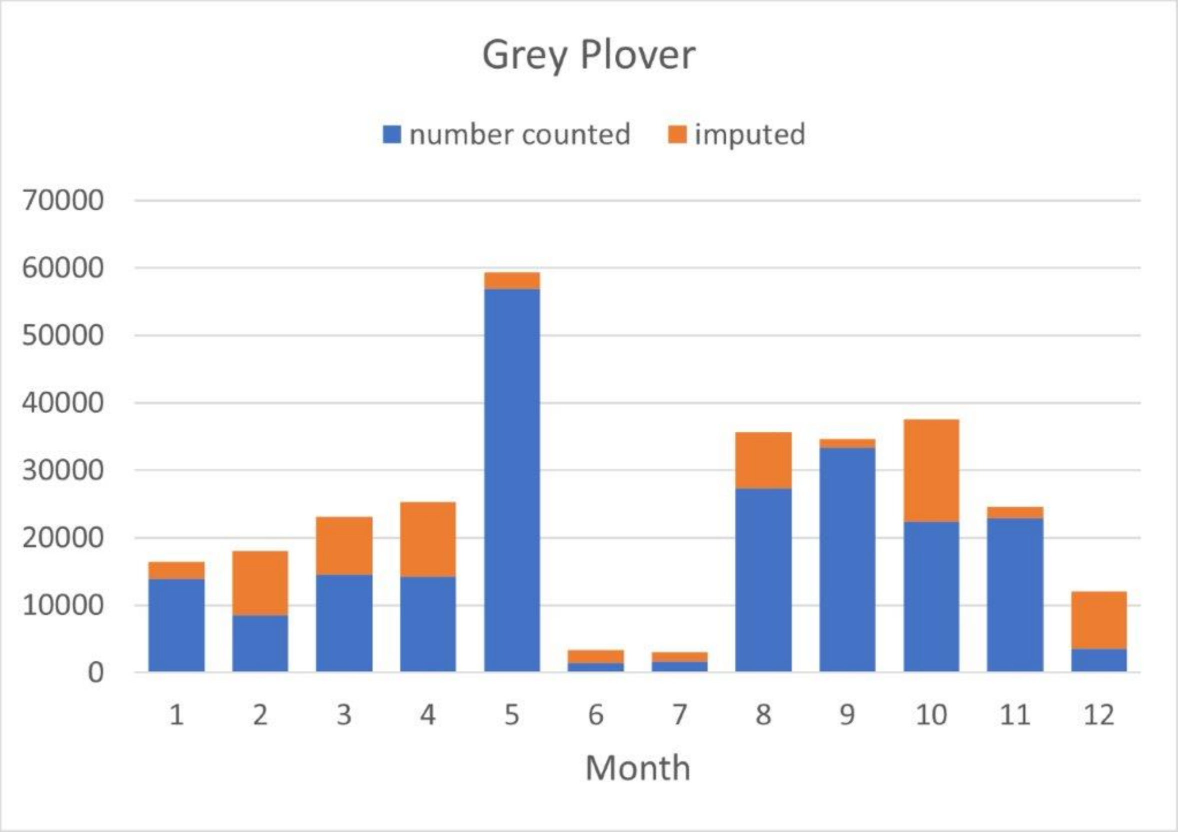


Figure 61: Grey plover - seasonal pattern in the number of birds in the Dutch Wadden Sea. See figure 33 for details.

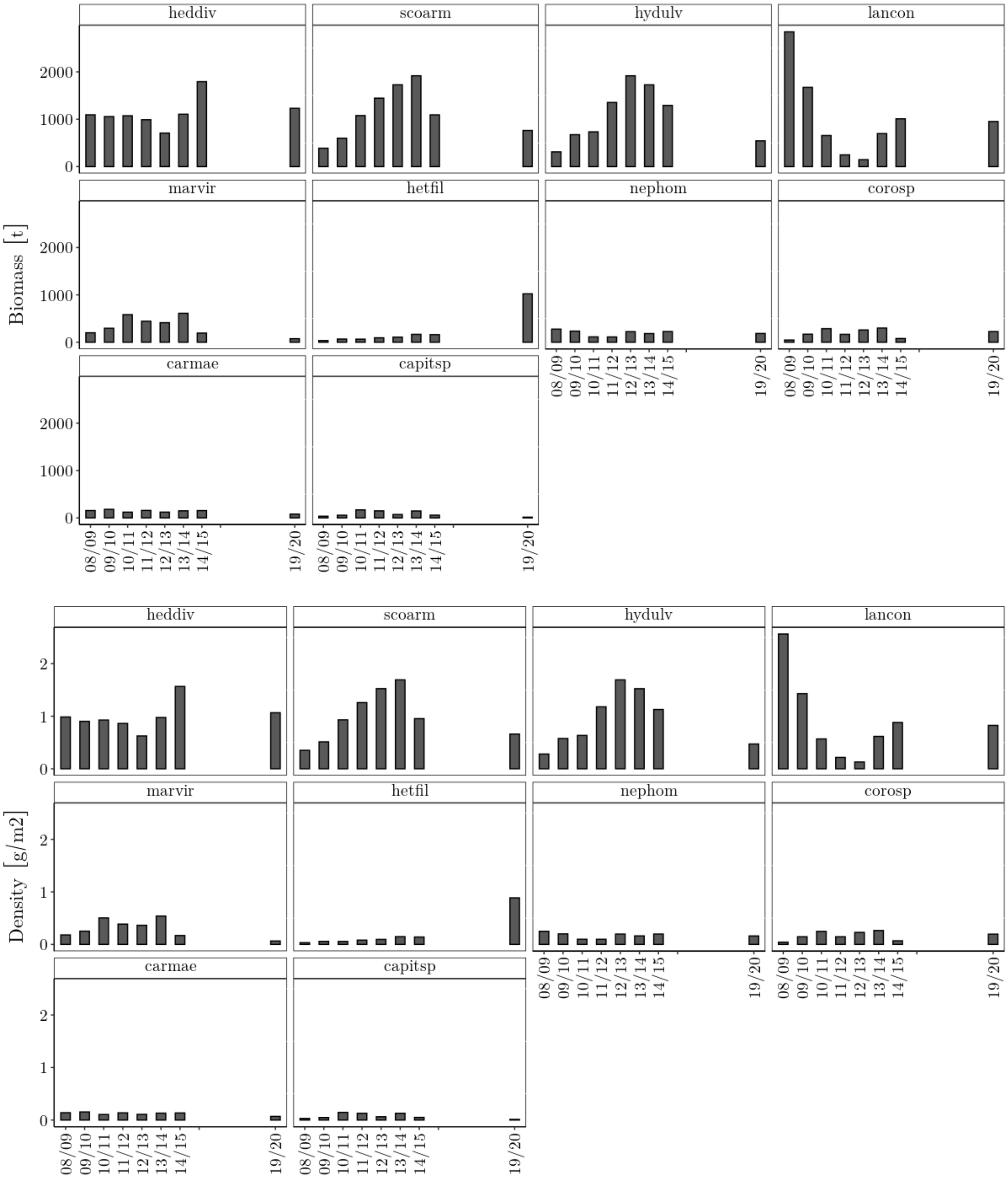


Figure 62: Total biomass (t) and density (g m^{-2}) of Grey Plover prey for the period 08/09 - 14/15 and 19/20.

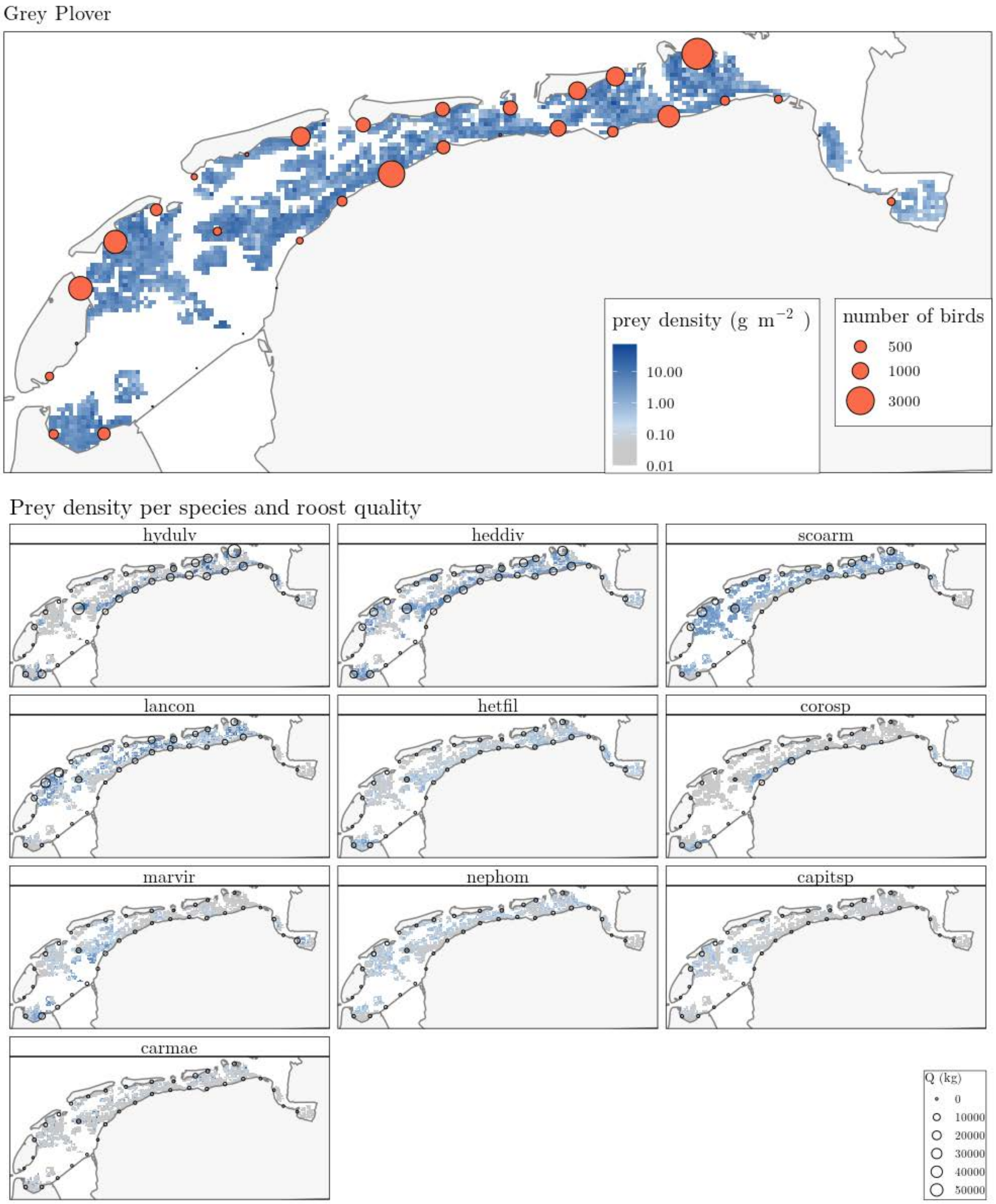


Figure 63: Average number of Grey Plovers per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

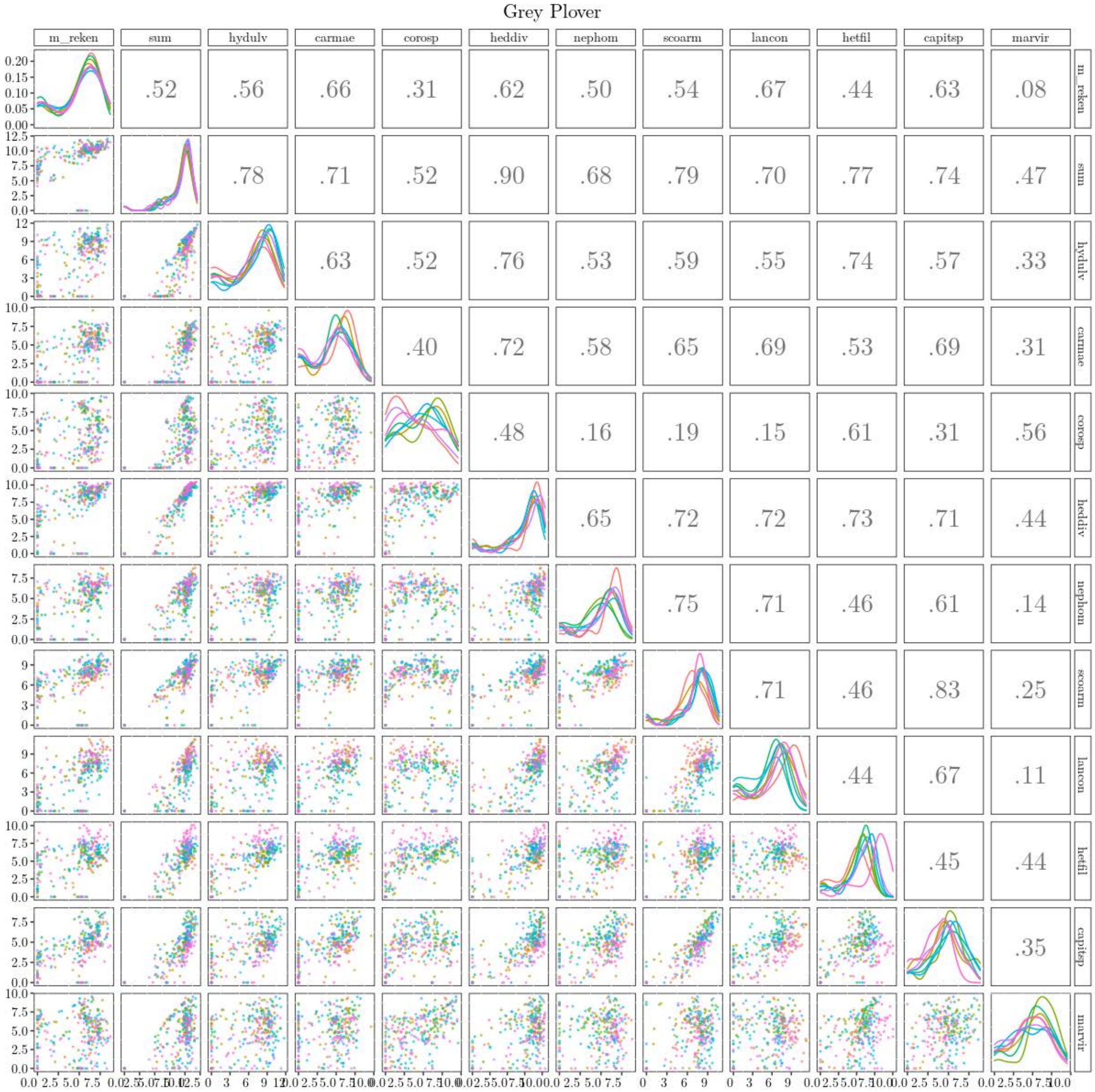


Figure 64: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Grey Plover. See the caption of Figure 36 for further details.

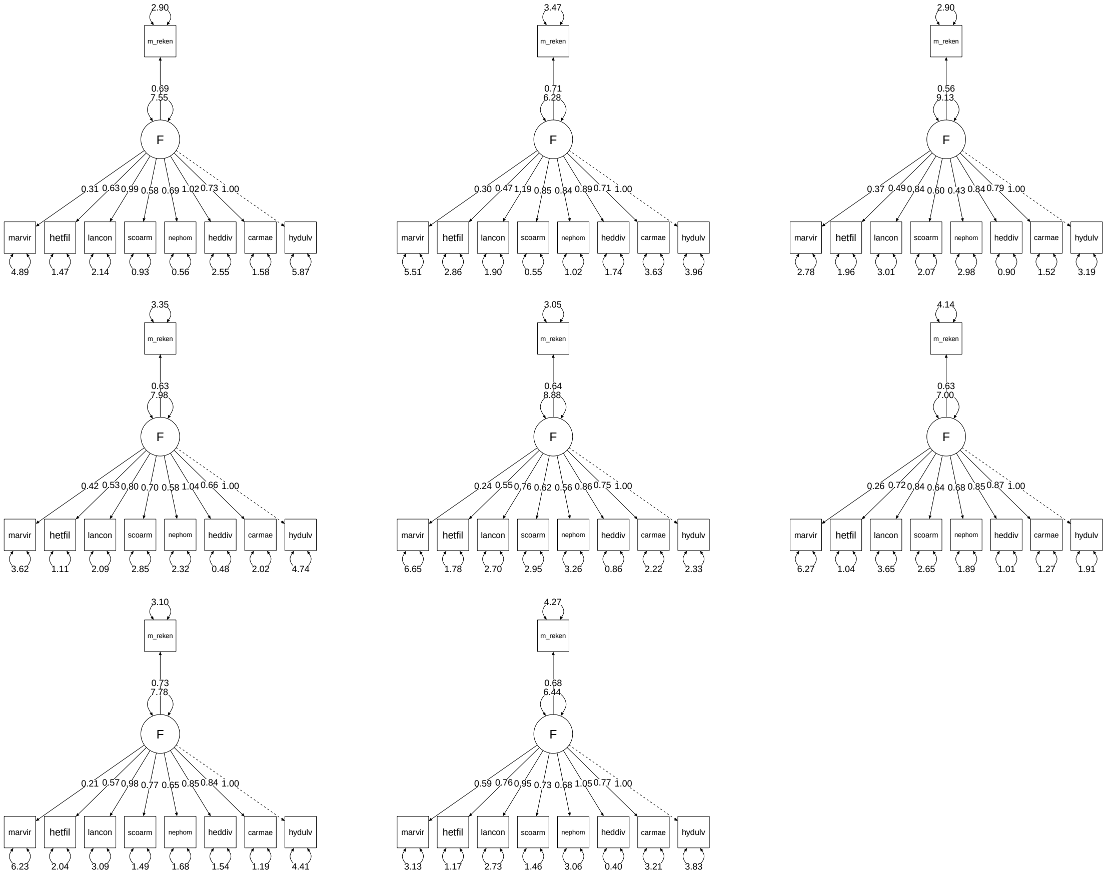


Figure 65: Structural equation model of the number of Grey Plovers. See the caption of Figure 37 for further information.

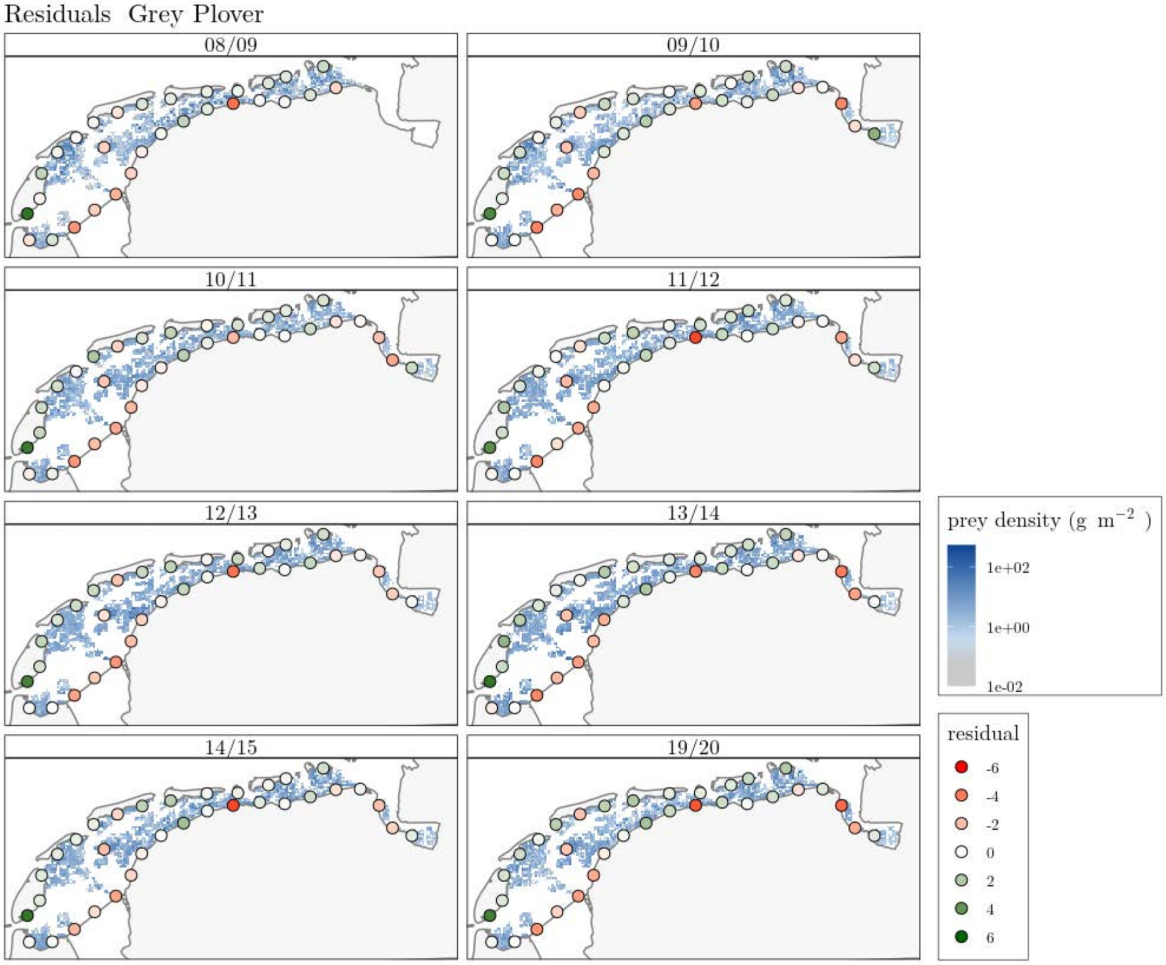


Figure 66: Residuals between the observed and implied number of Grey Plovers at the virtual roosts.

B.1.7 Bar-tailed Godwit - period 1

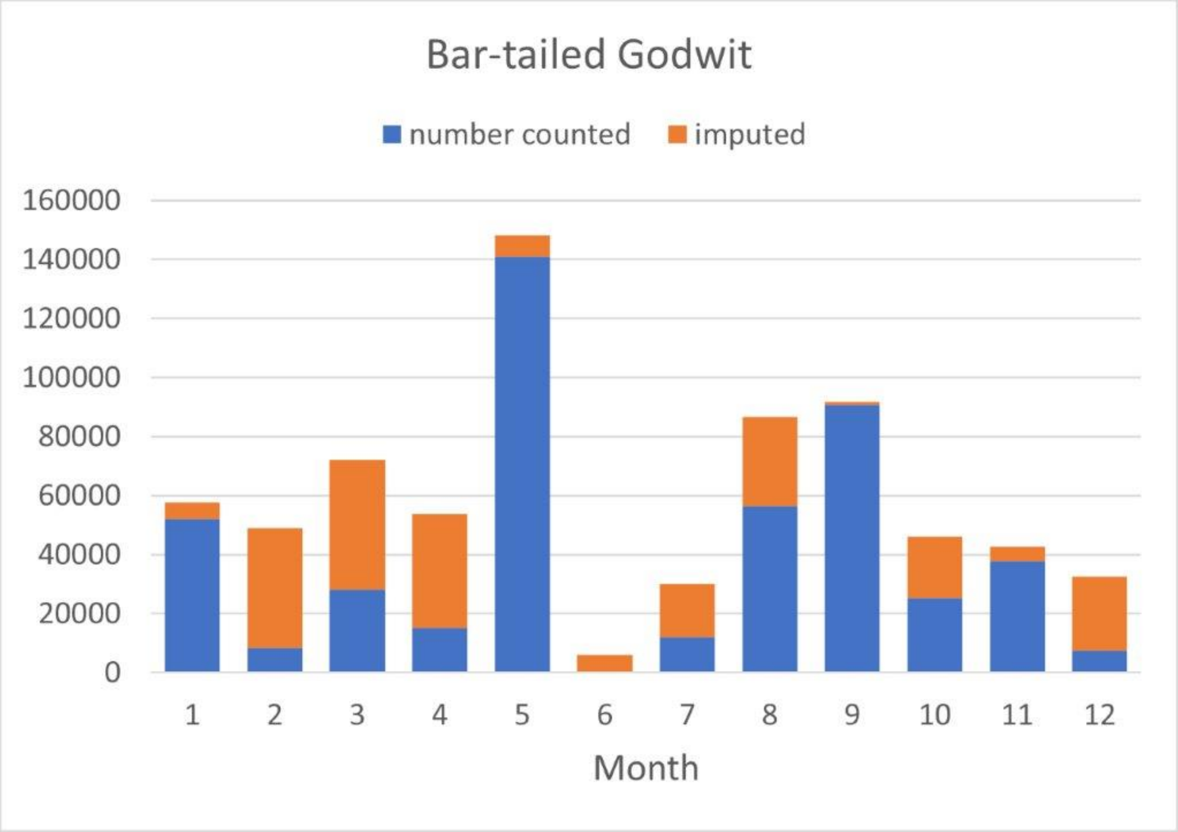


Figure 67: Bar-tailed Godwit - seasonal pattern in the number of birds in the Dutch Wadden Sea. See figure 33 for details.

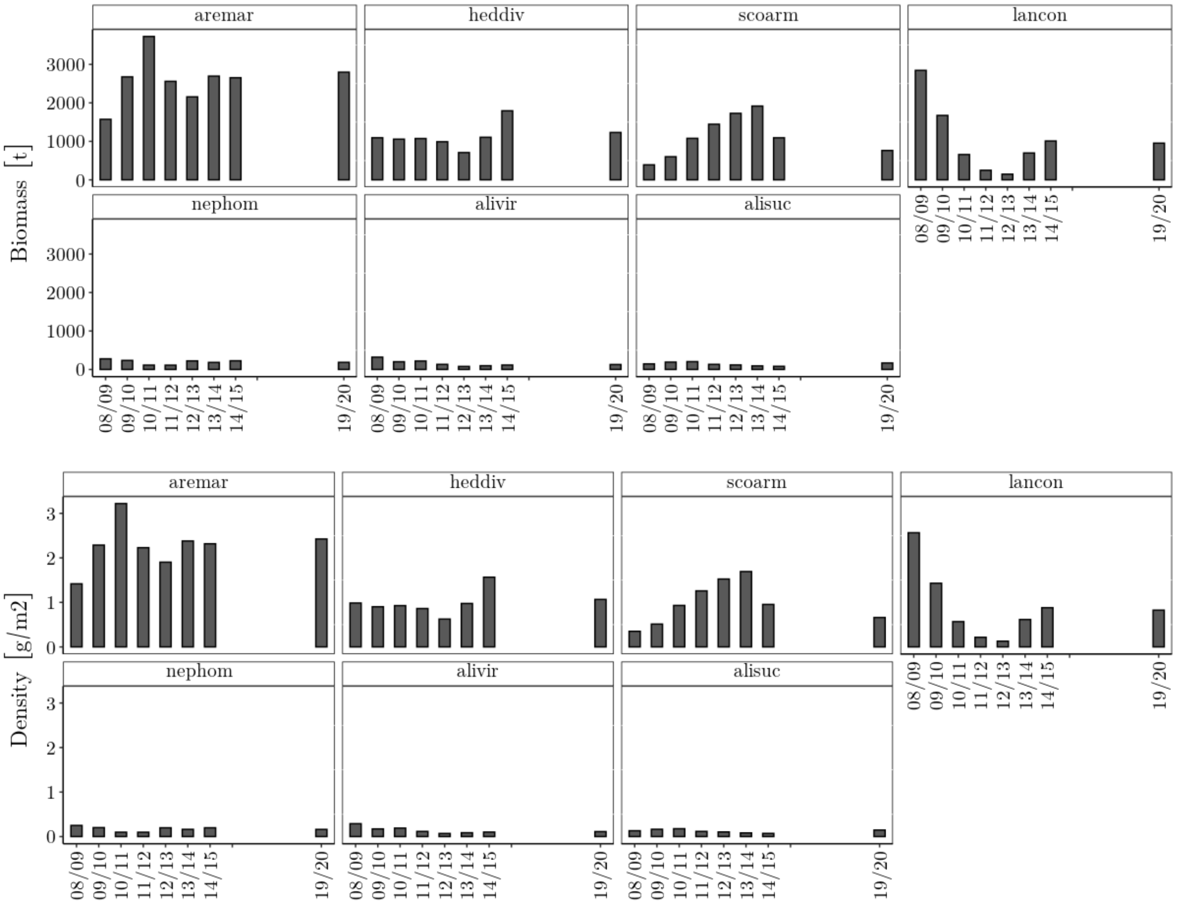
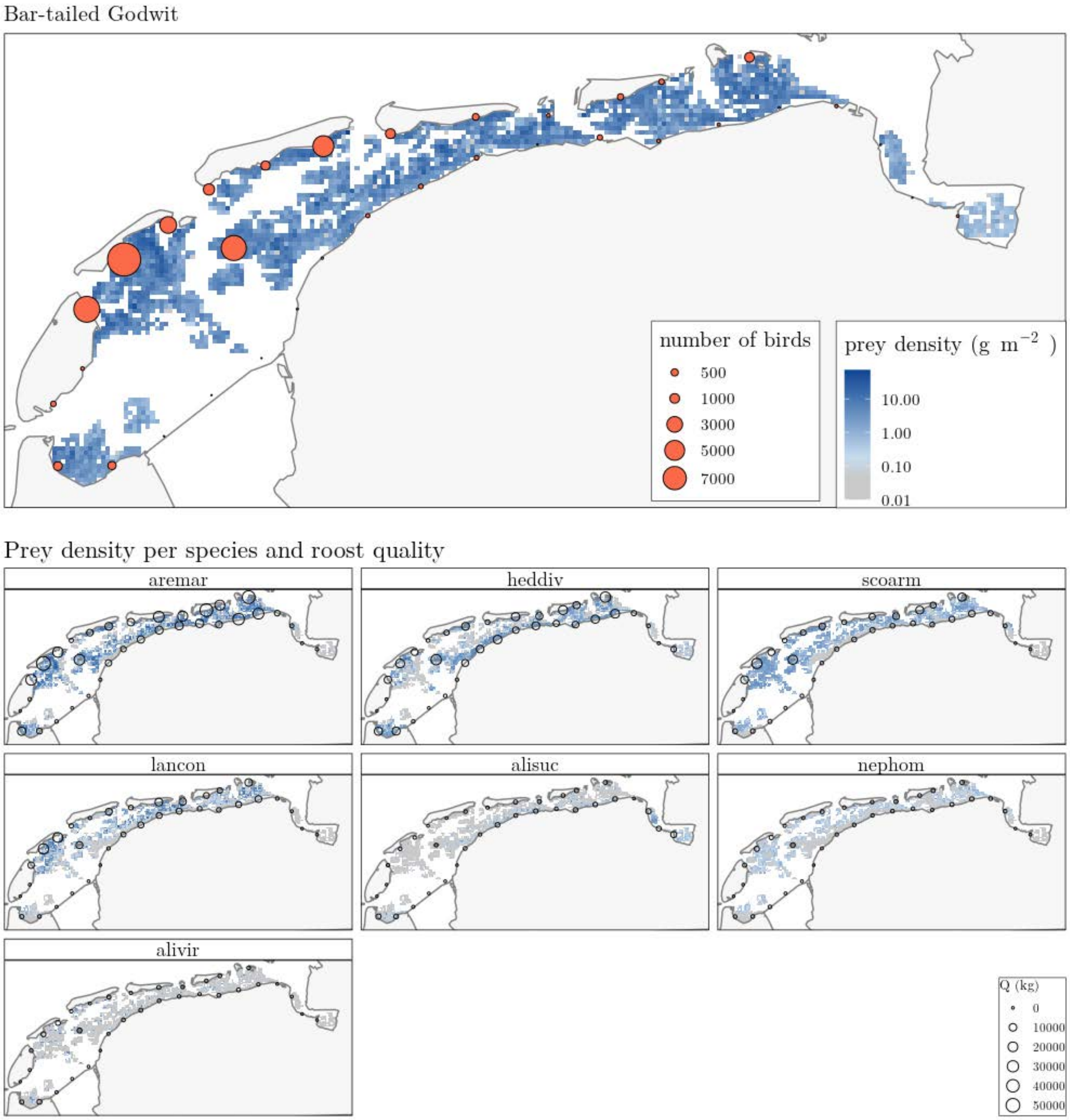


Figure 68: Total biomass (t) and density (g m^{-2}) of Bar-tailed Godwit prey for the period 08/09 - 14/15 and 19/20..


Bar-tailed Godwit

Prey density per species and roost quality

Figure 69: Average number of Grey Plovers per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

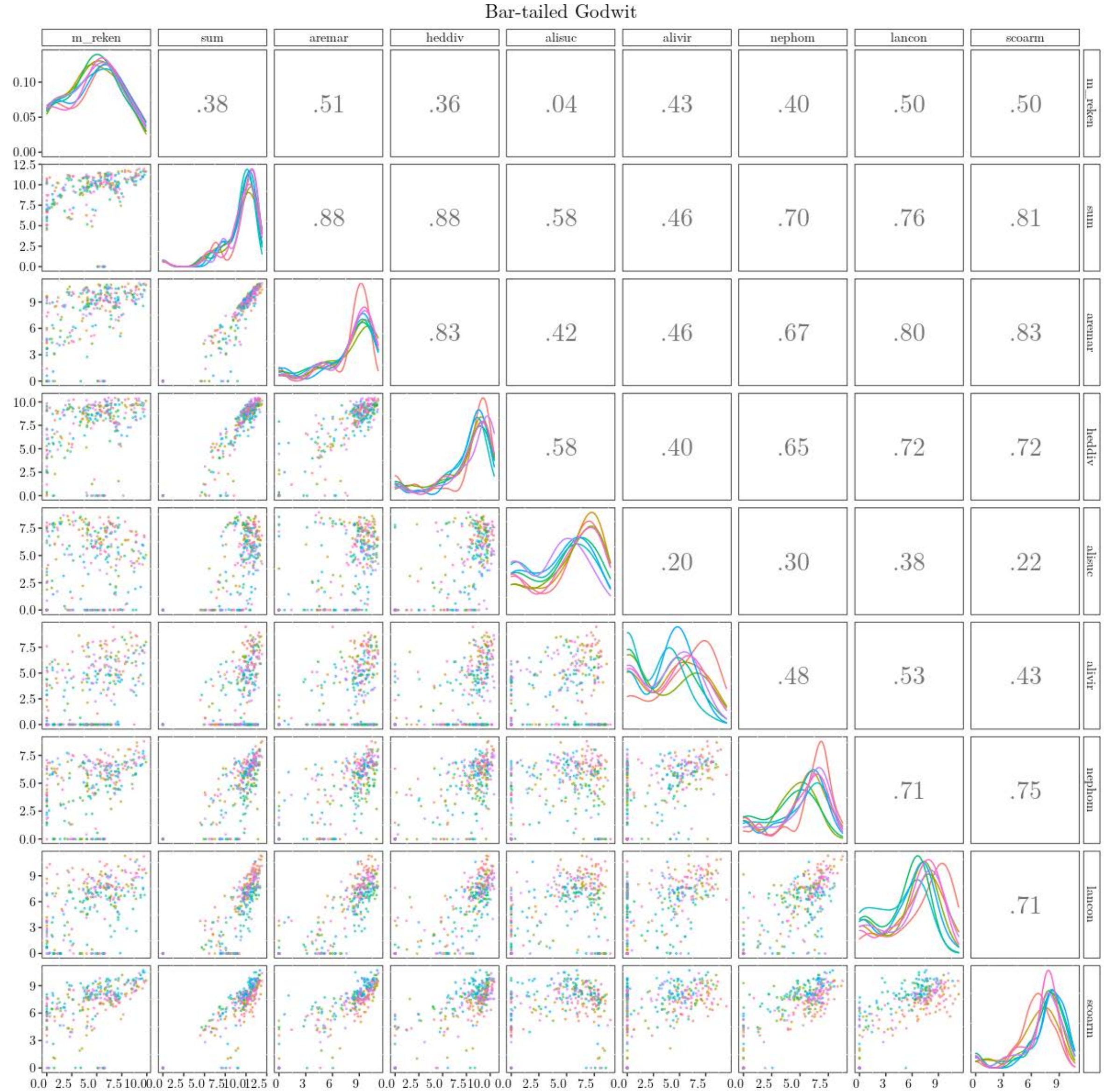


Figure 70: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Grey Plover. See the caption of Figure 36 for further details.

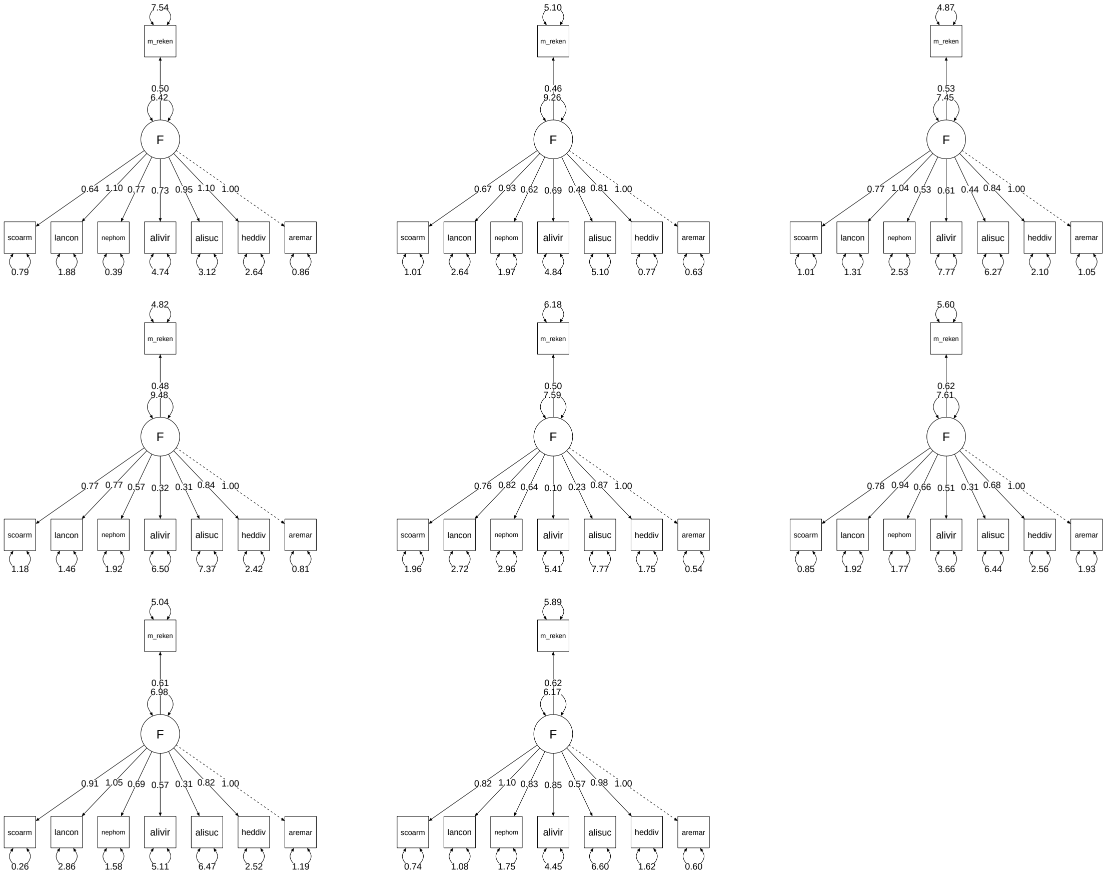


Figure 71: Structural equation model of the number of Bar-tailed Godwits during period 1. See the caption of Figure 37 for further information.

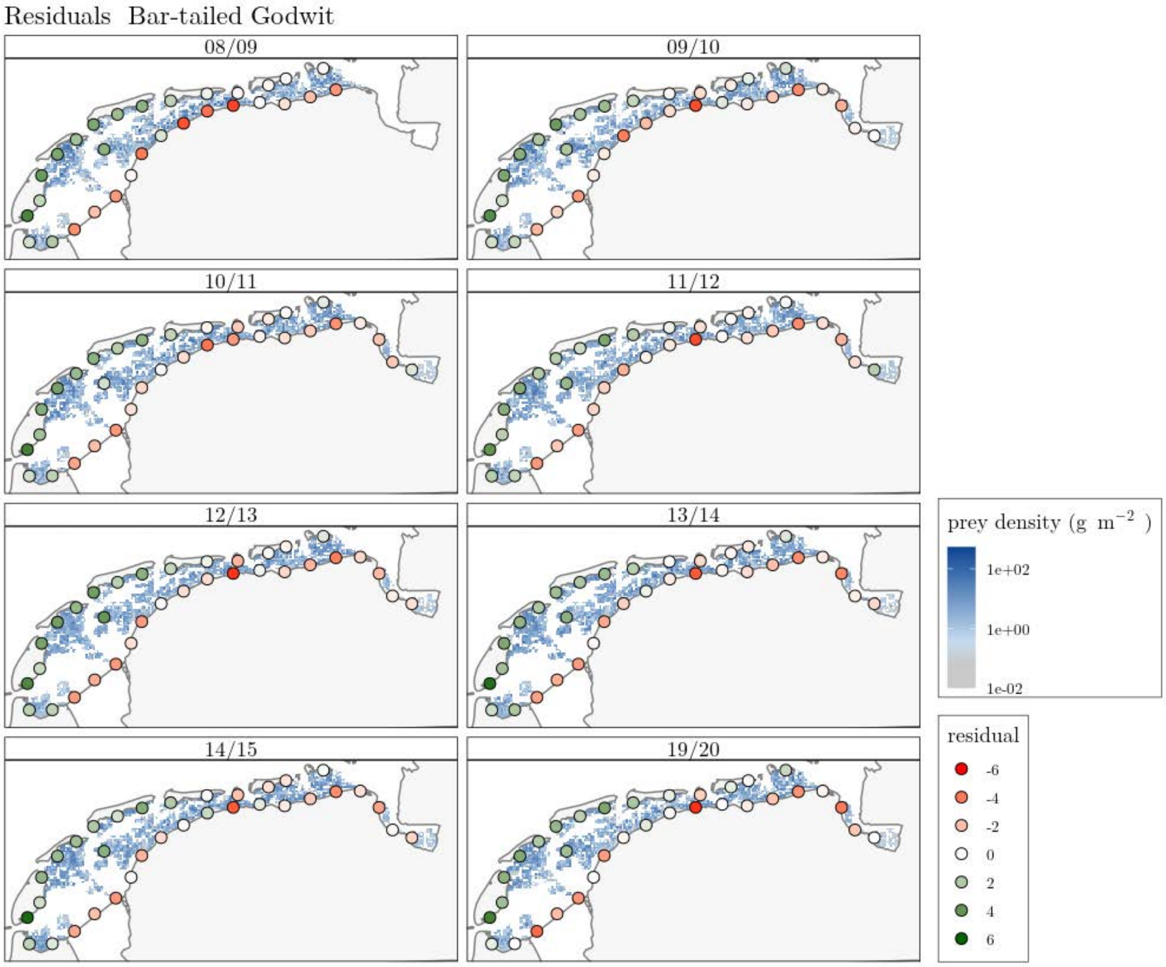


Figure 72: Residuals between the observed and implied number of Bar-tailed Godwits during period 1 at the virtual roosts.

B.1.8 Bar-tailed Godwit - period 2

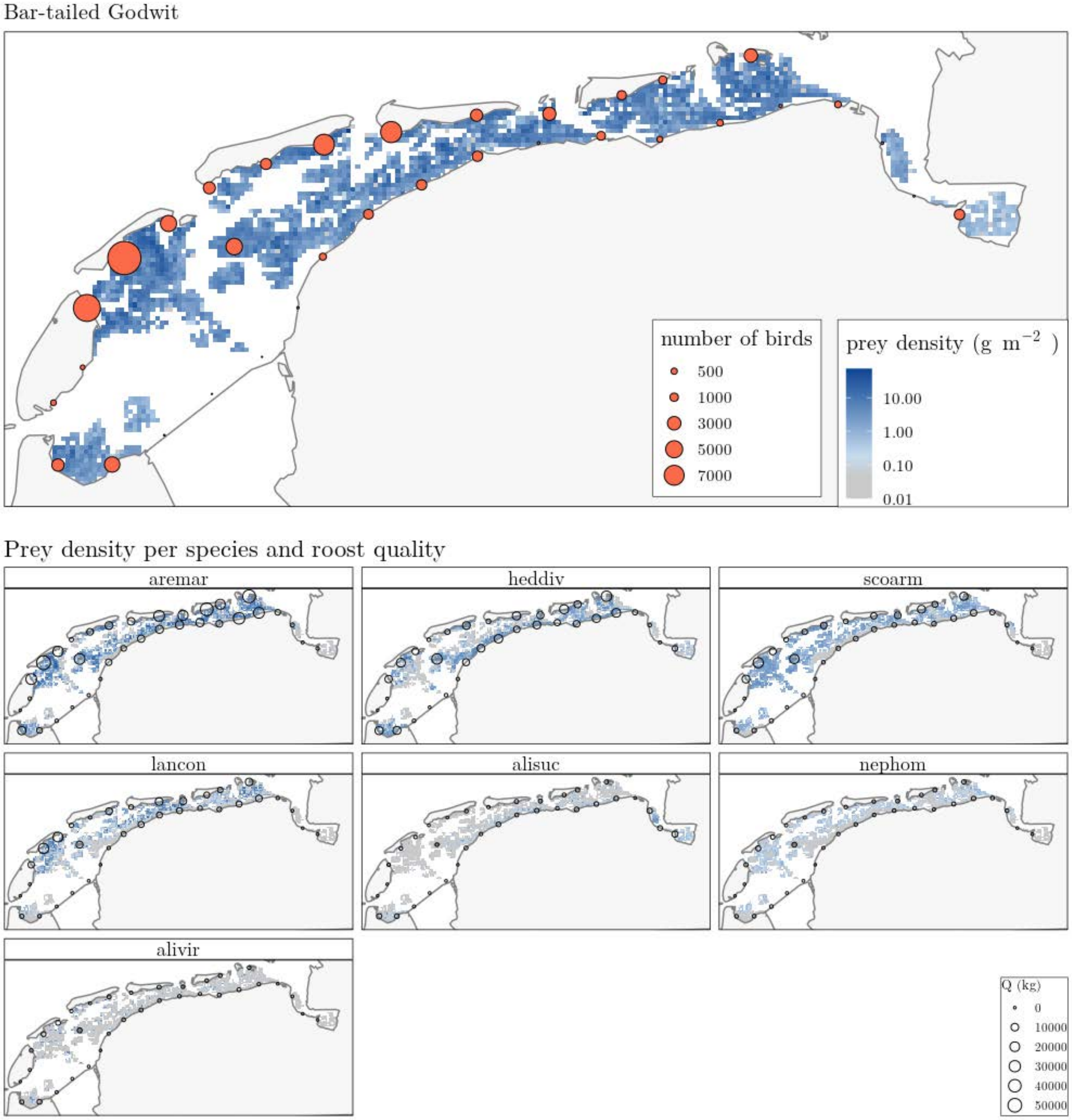


Figure 73: Average number of Grey Plovers per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

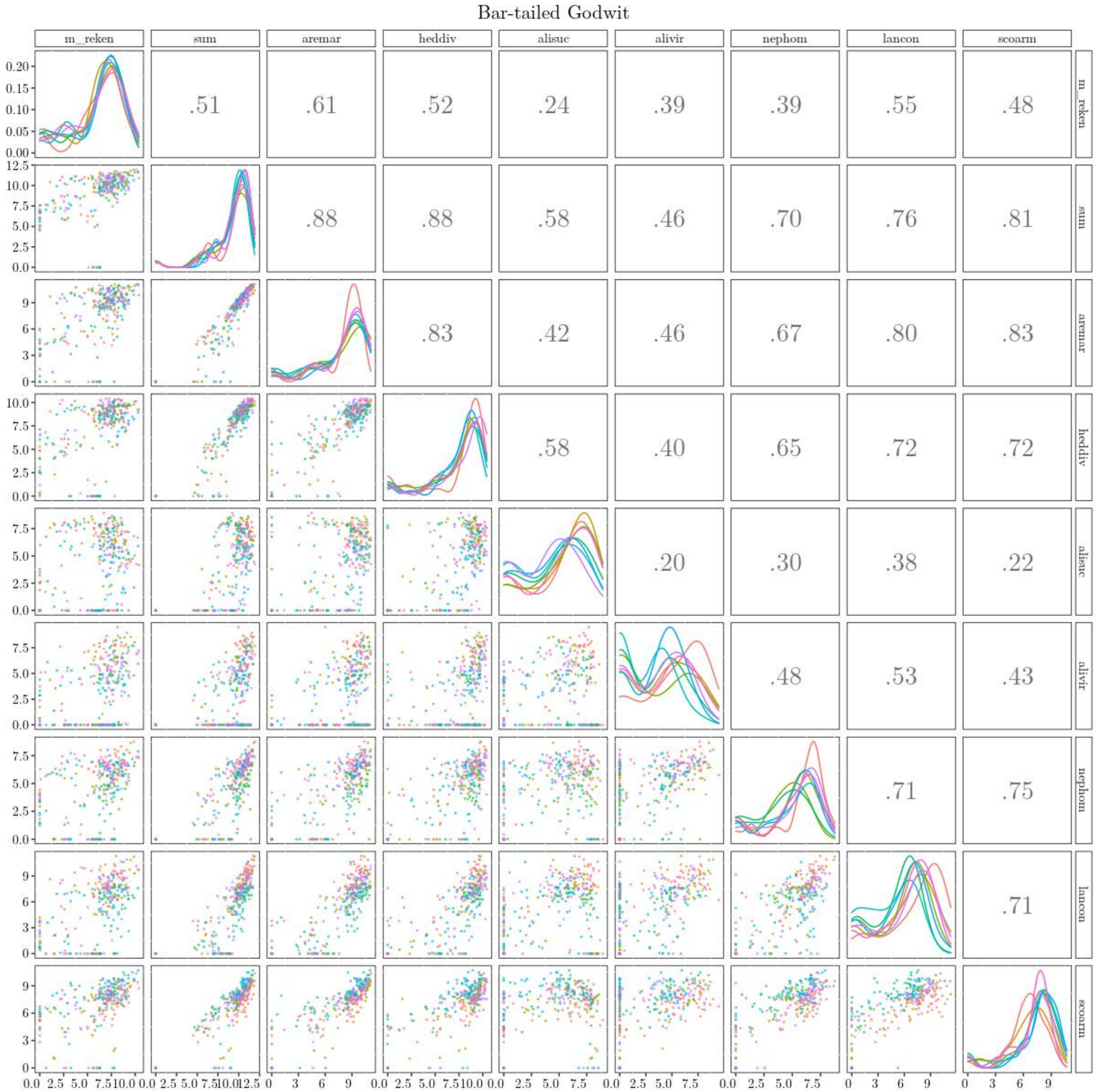


Figure 74: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Grey Plover. See the caption of Figure 36 for further details.

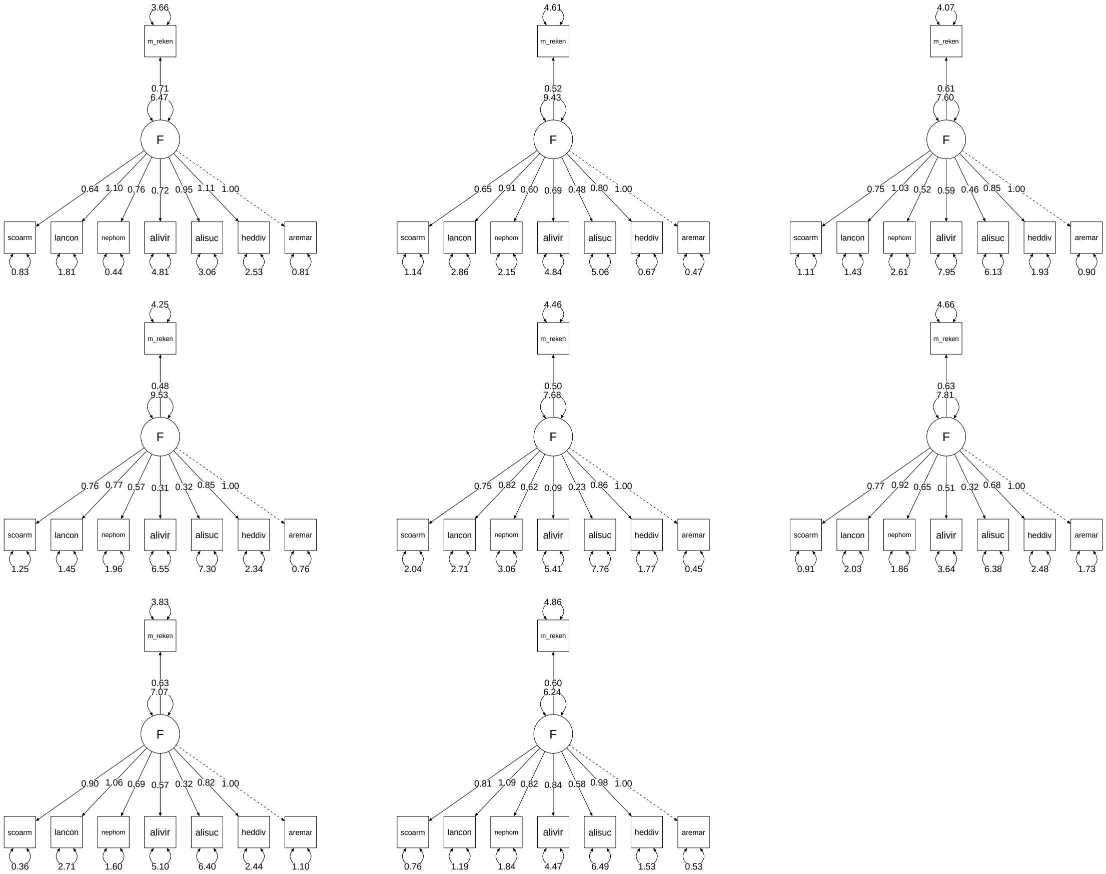


Figure 75: Structural equation model of the number of Bar-tailed Godwits during period 2. See the caption of Figure 37 for further information.

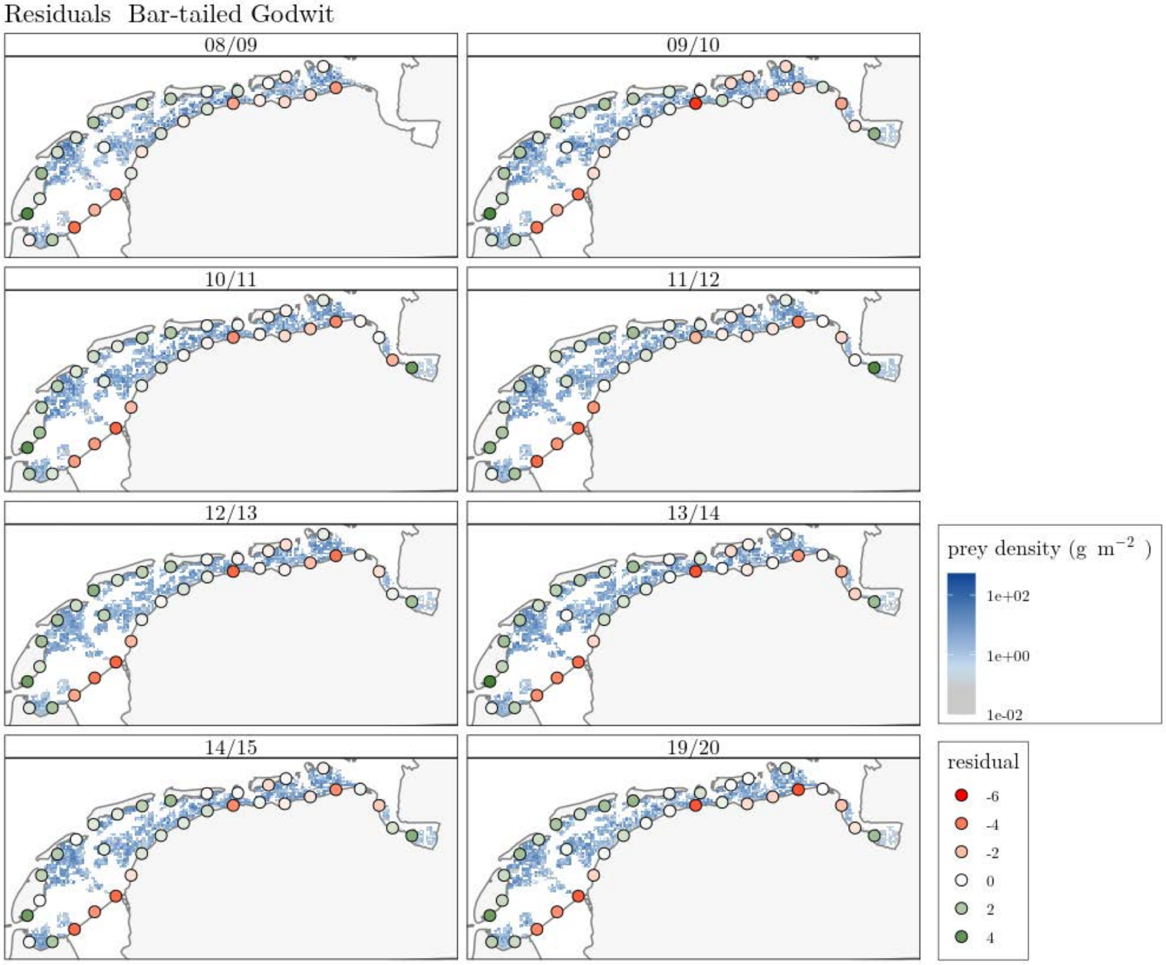


Figure 76: Residuals between the observed and implied number of Bar-tailed Godwits during period 2 at the virtual roosts.

B.1.9 Turnstone

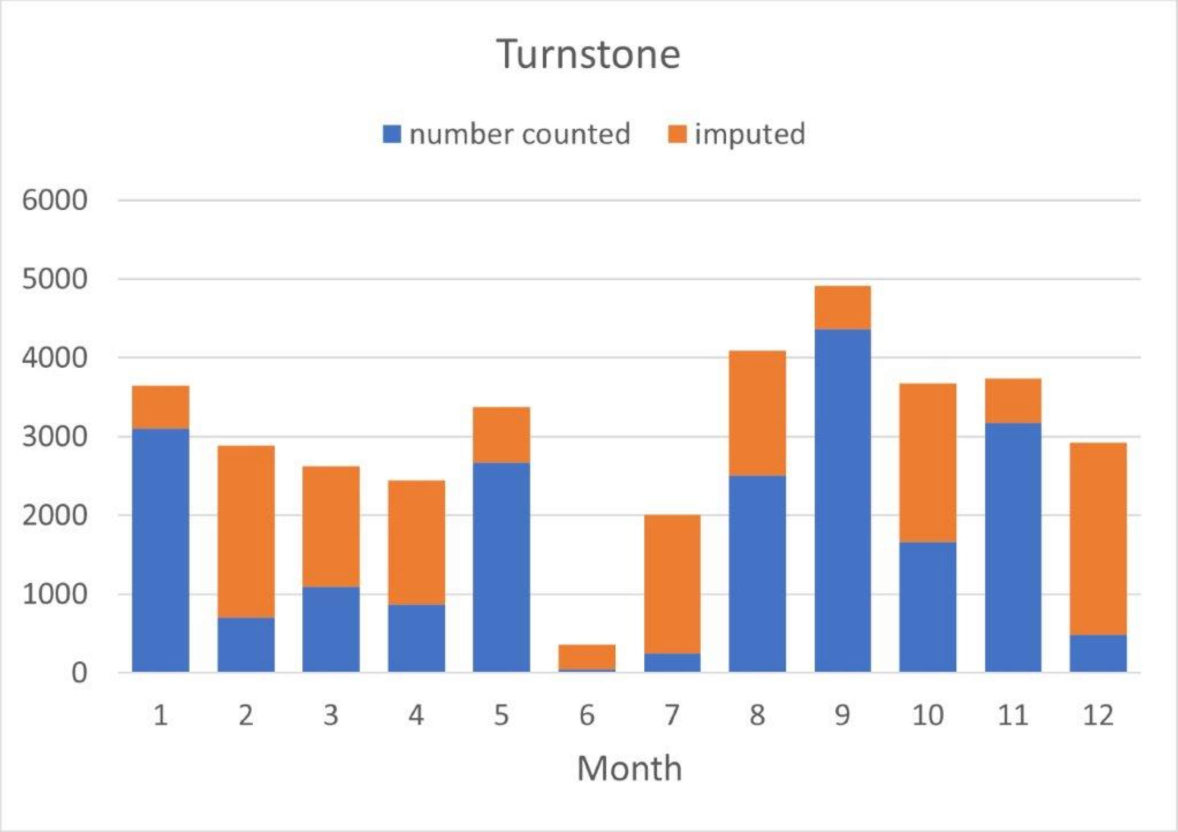


Figure 77: Turnstone - seasonal pattern in the number of birds in the Dutch Wadden Sea. See figure 33 for details.

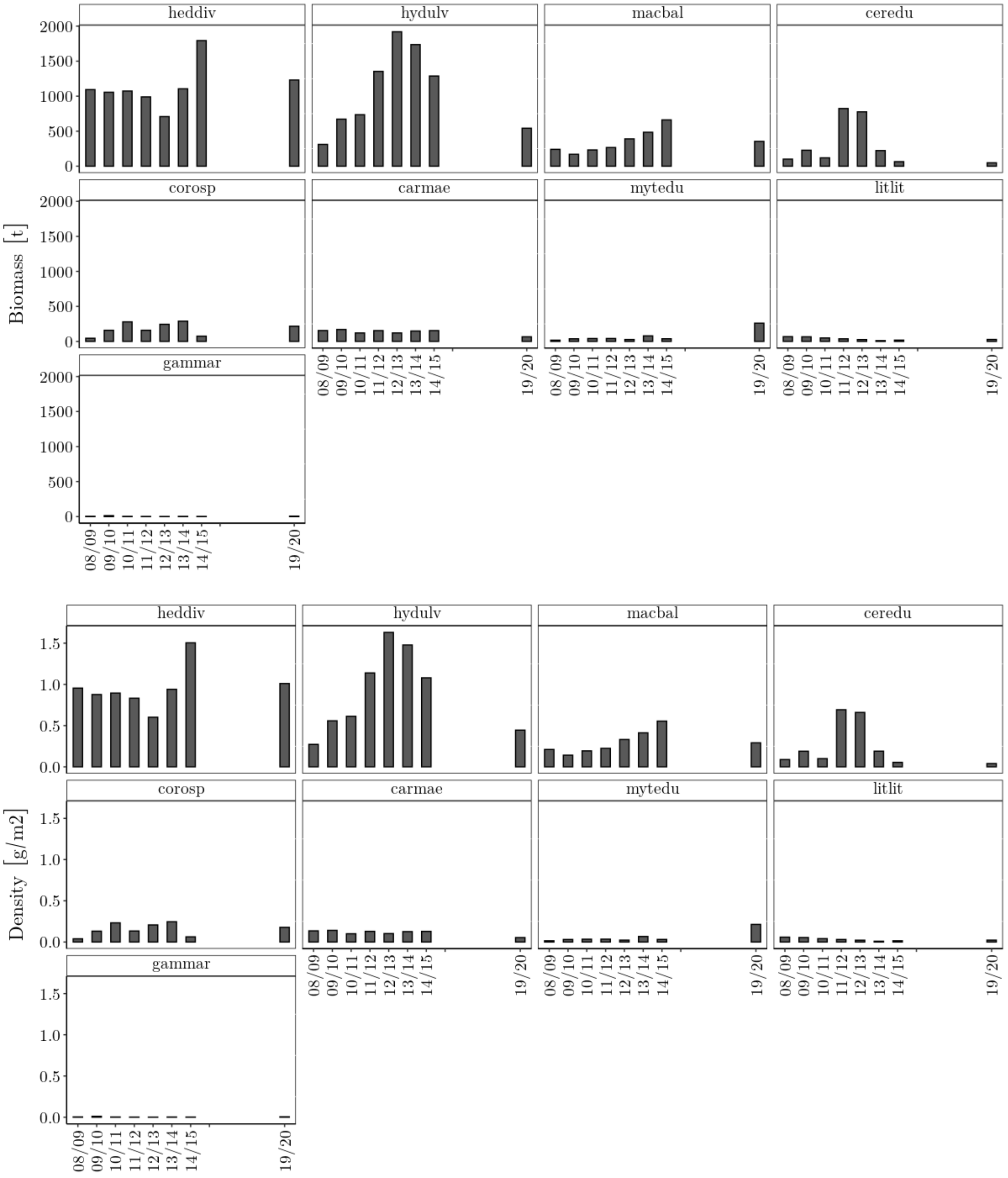


Figure 78: Total biomass (t) and density (g m^{-2}) of Turnstone prey for the period 08/09 - 14/15 and 19/20.

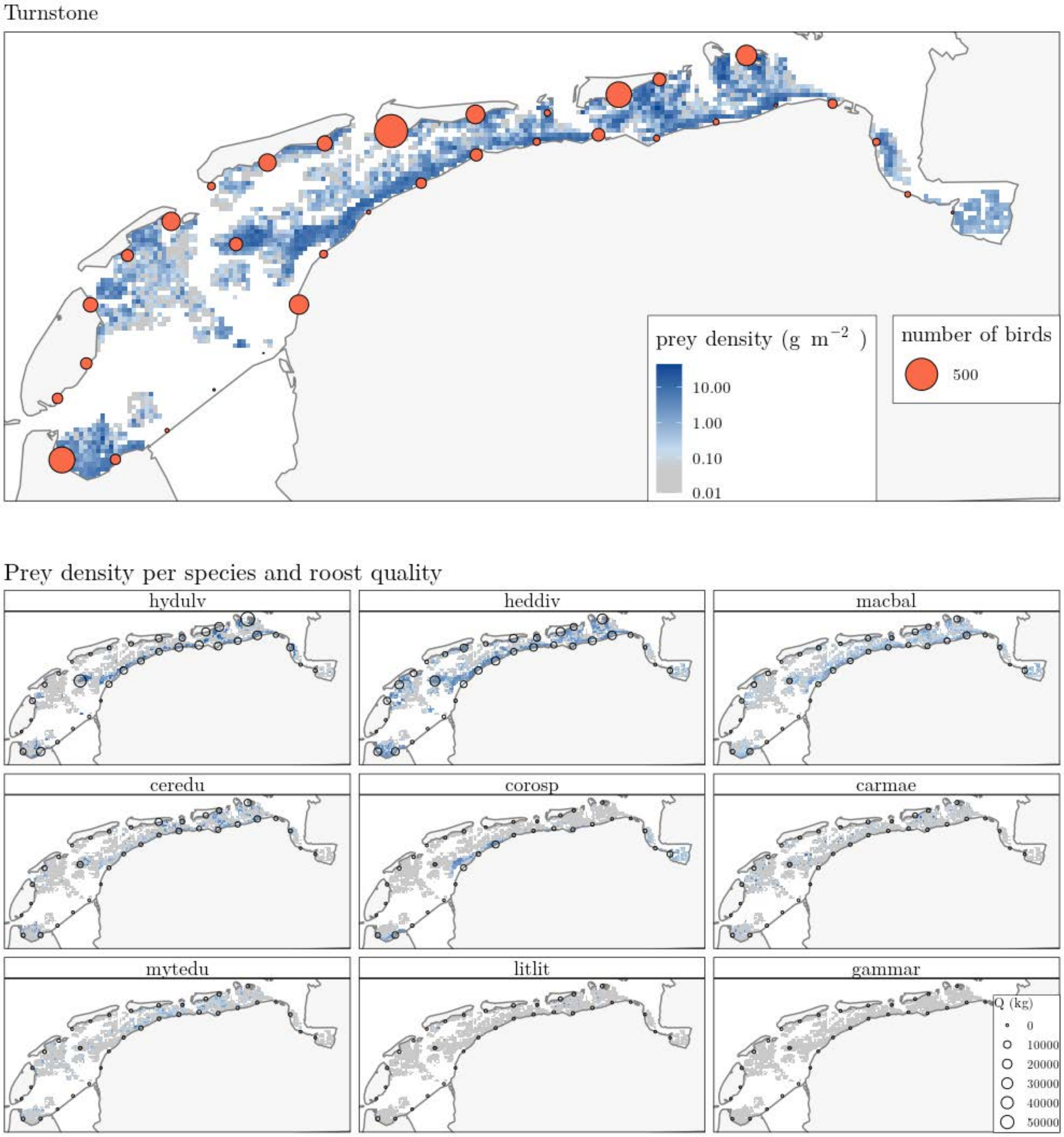


Figure 79: Average number of Turnstones per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

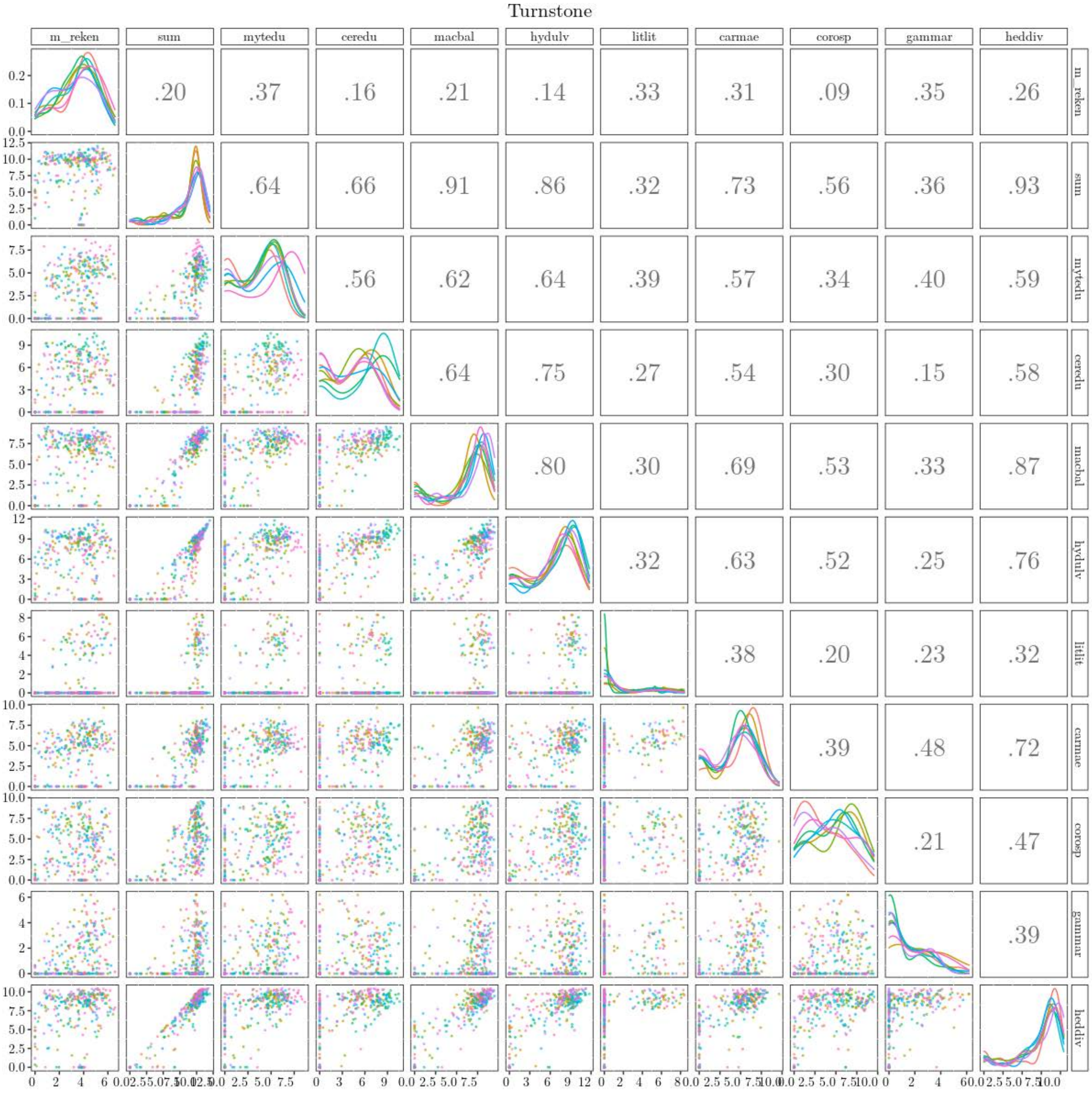


Figure 80: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Turnstone. See the caption of Figure 36 for further details.

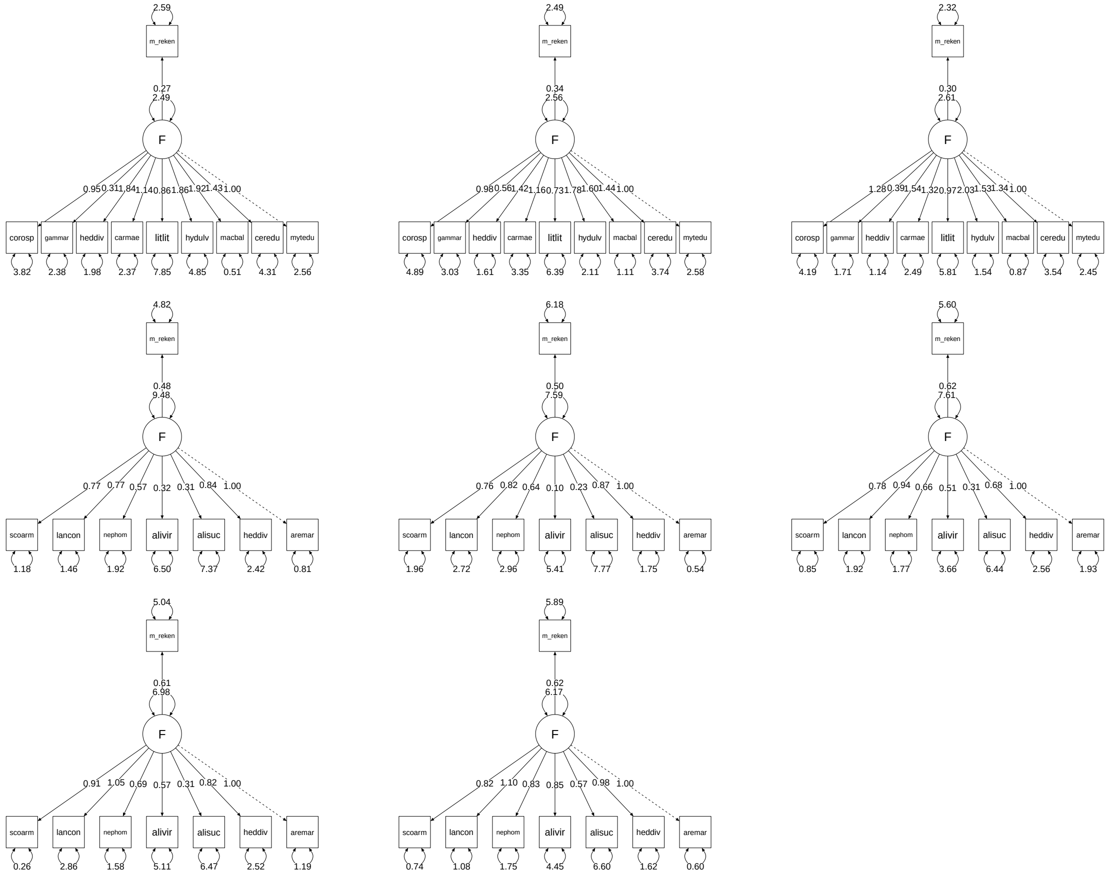


Figure 81: Structural equation model of the number of Turnstones. See the caption of Figure 37 for further information.

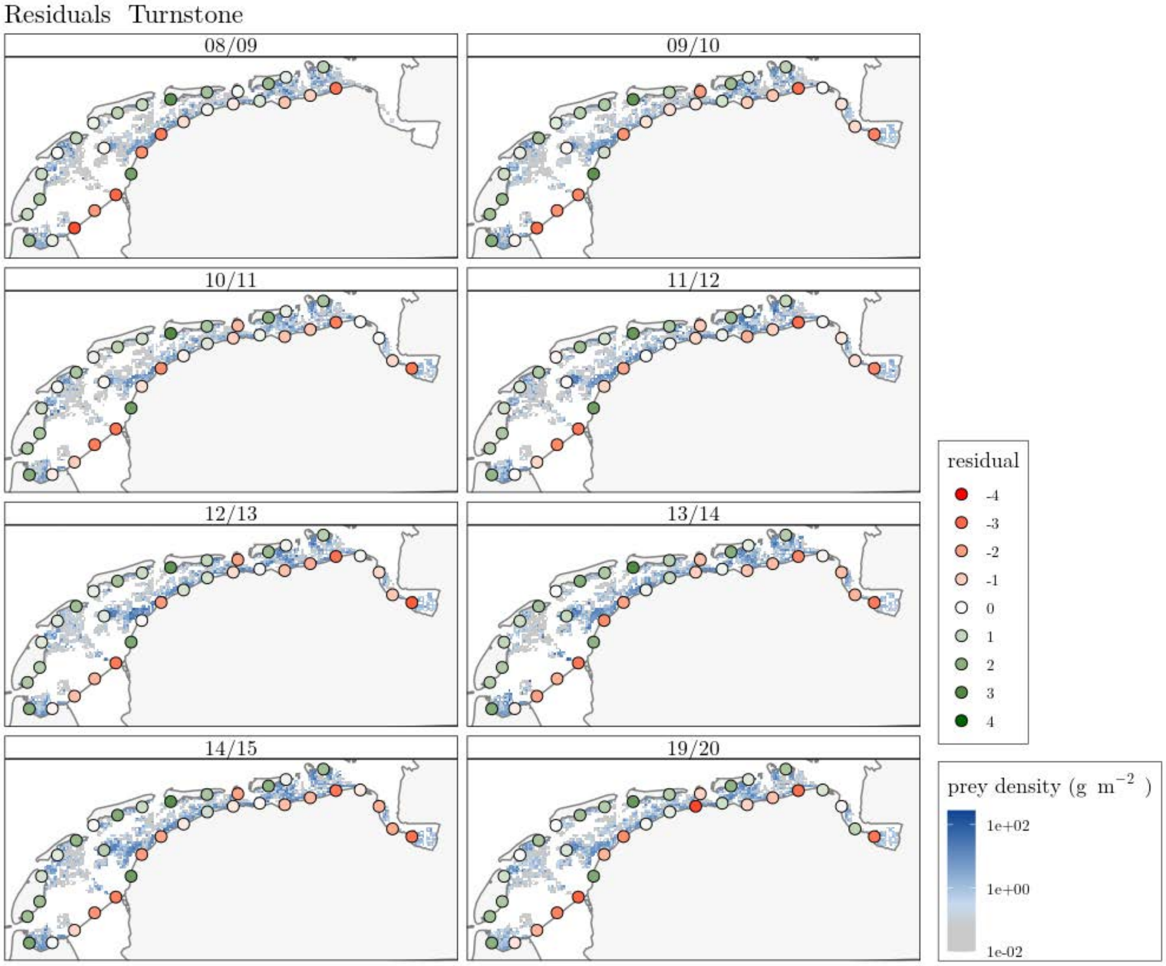


Figure 82: Residuals between the observed and implied number of Turnstones at the virtual roosts.

B.1.10 Ringed Plover

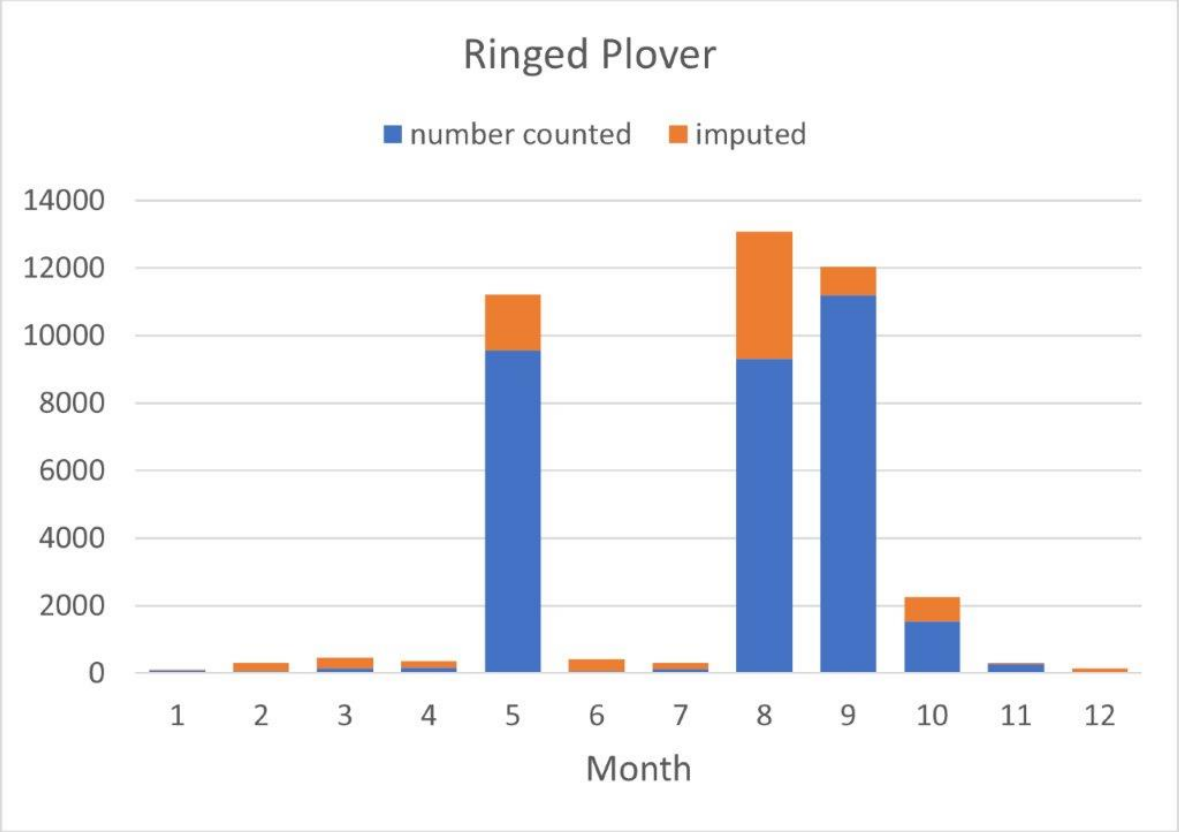


Figure 83: Ringed Plover - seasonal pattern in the number of birds in the Dutch Wadden Sea. See figure 33 for details.

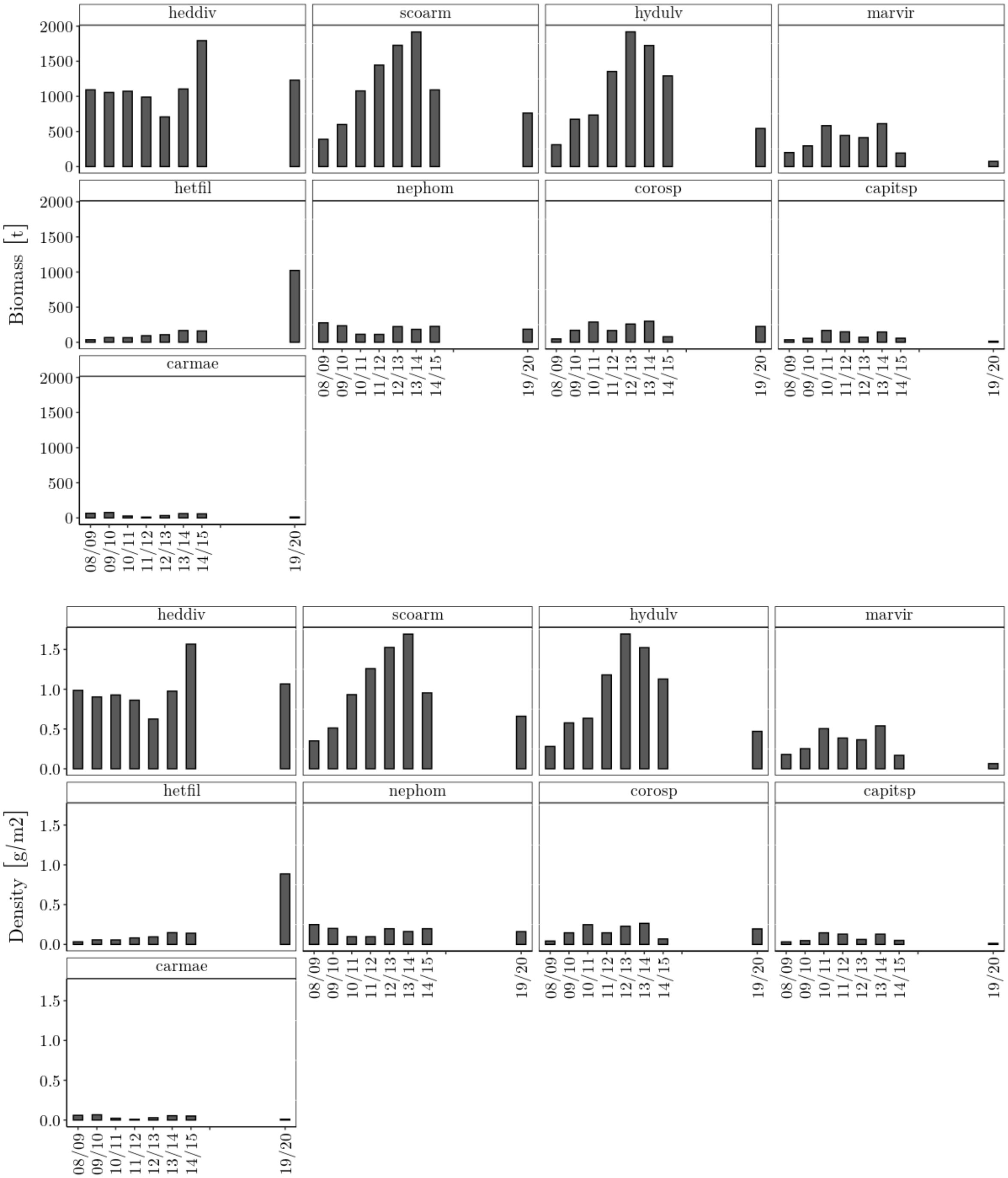


Figure 84: Total biomass (t) and density (g m^{-2}) of Ringed Plover prey for the period 08/09 - 14/15 and 19/20..

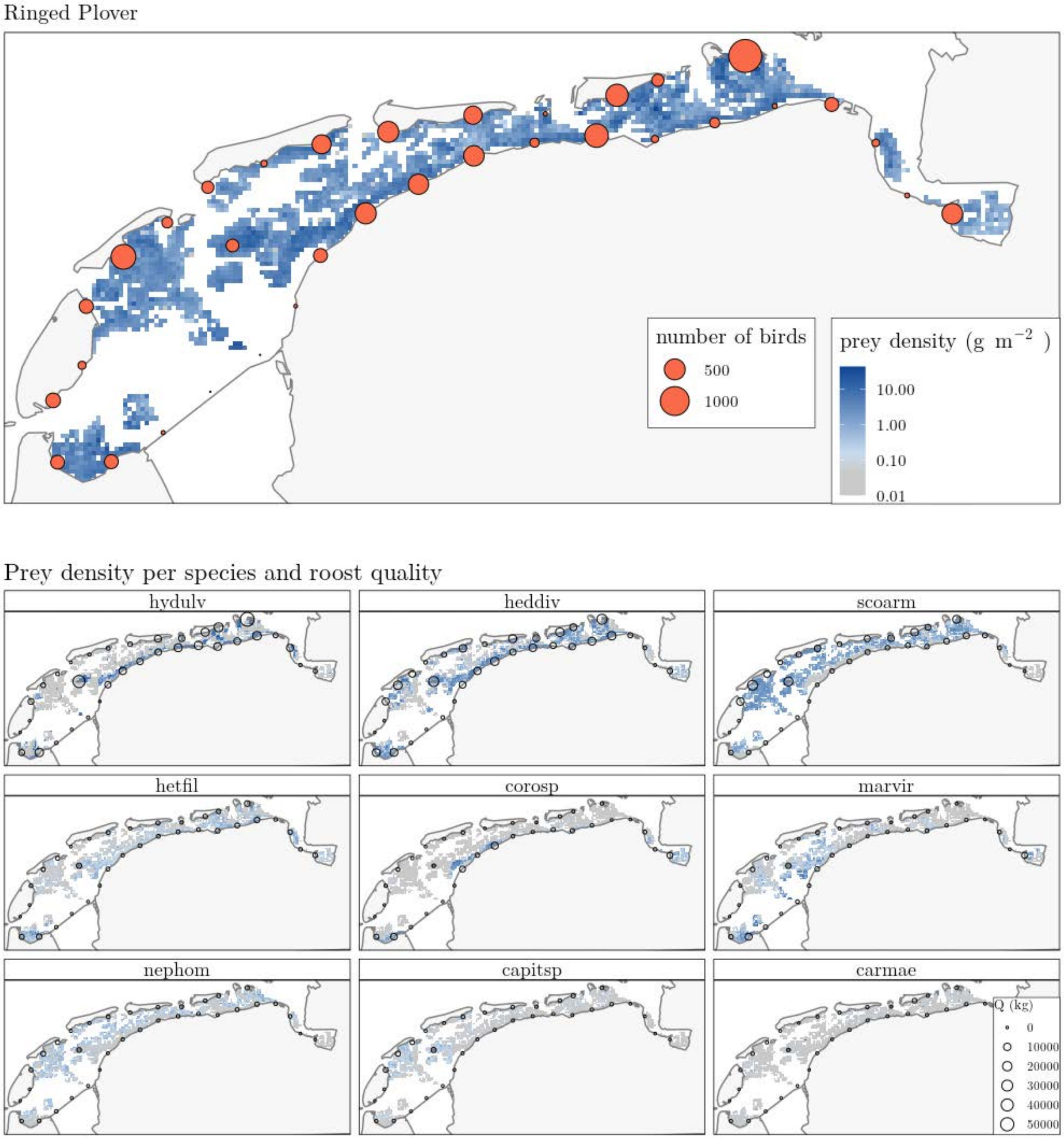


Figure 85: Average number of Ringed Plovers per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

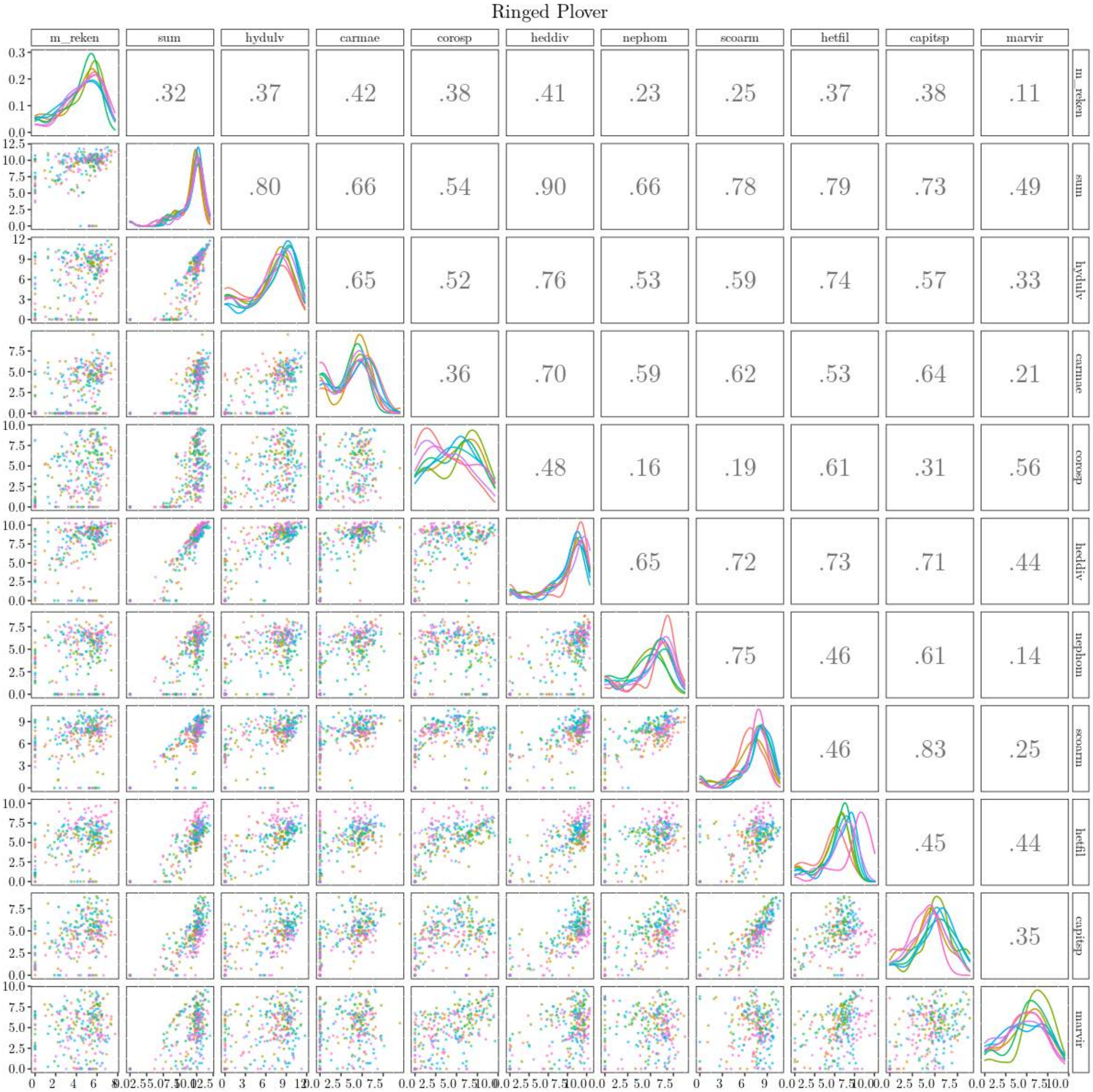


Figure 86: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Ringed Plover. See the caption of Figure 36 for further details.

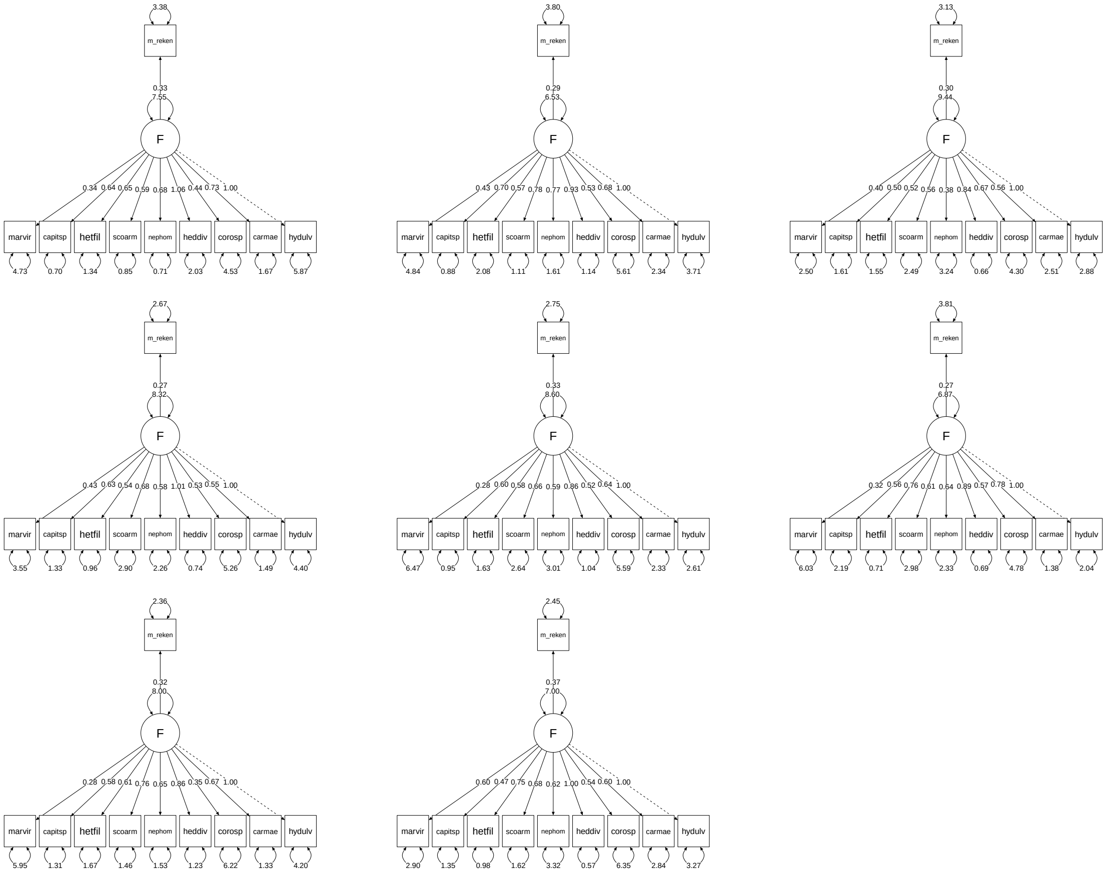


Figure 87: Structural equation model of the number of Ringed Plovers. See the caption of Figure 37 for further information.

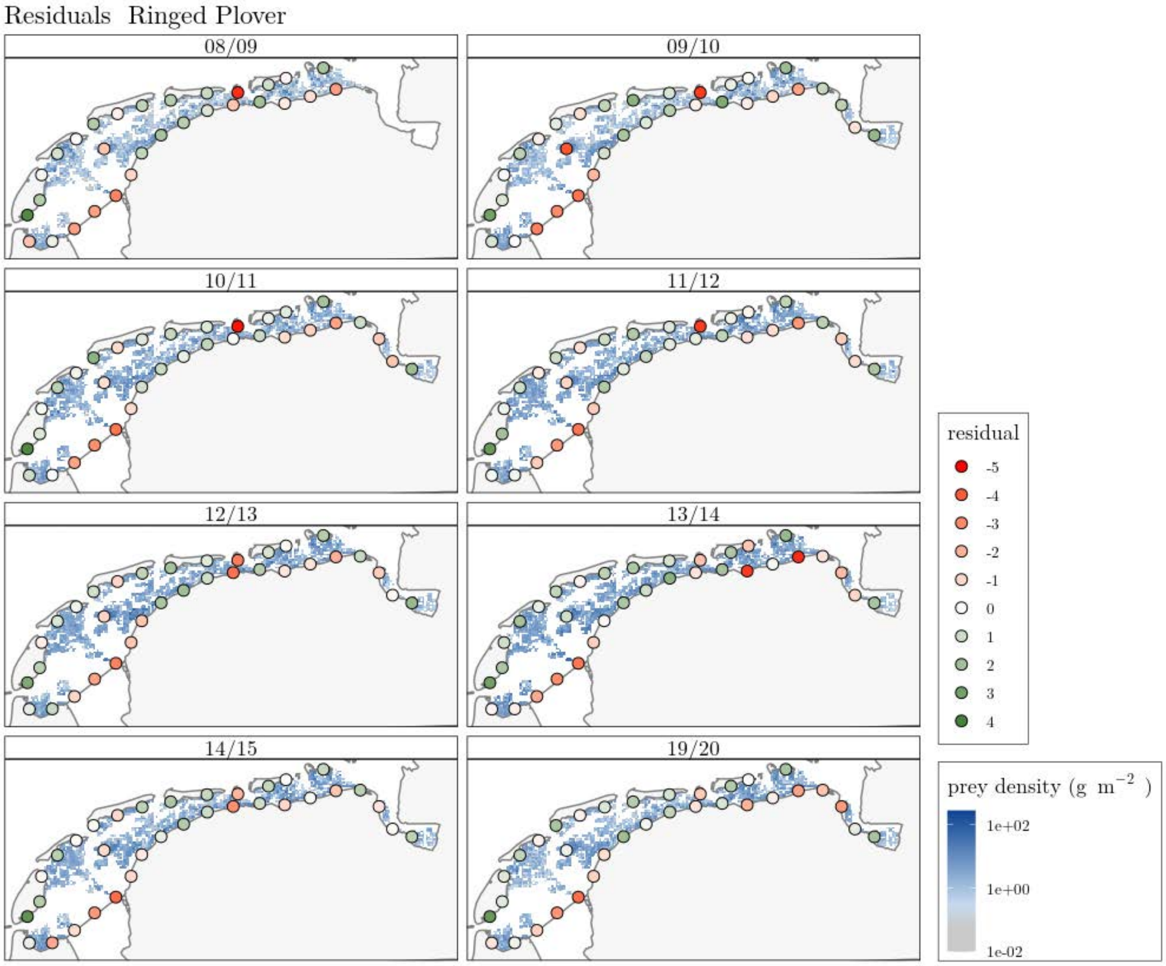


Figure 88: Residuals between the observed and implied number of Ringed Plovers at the virtual roosts.

B.1.11 Redshank - period 1

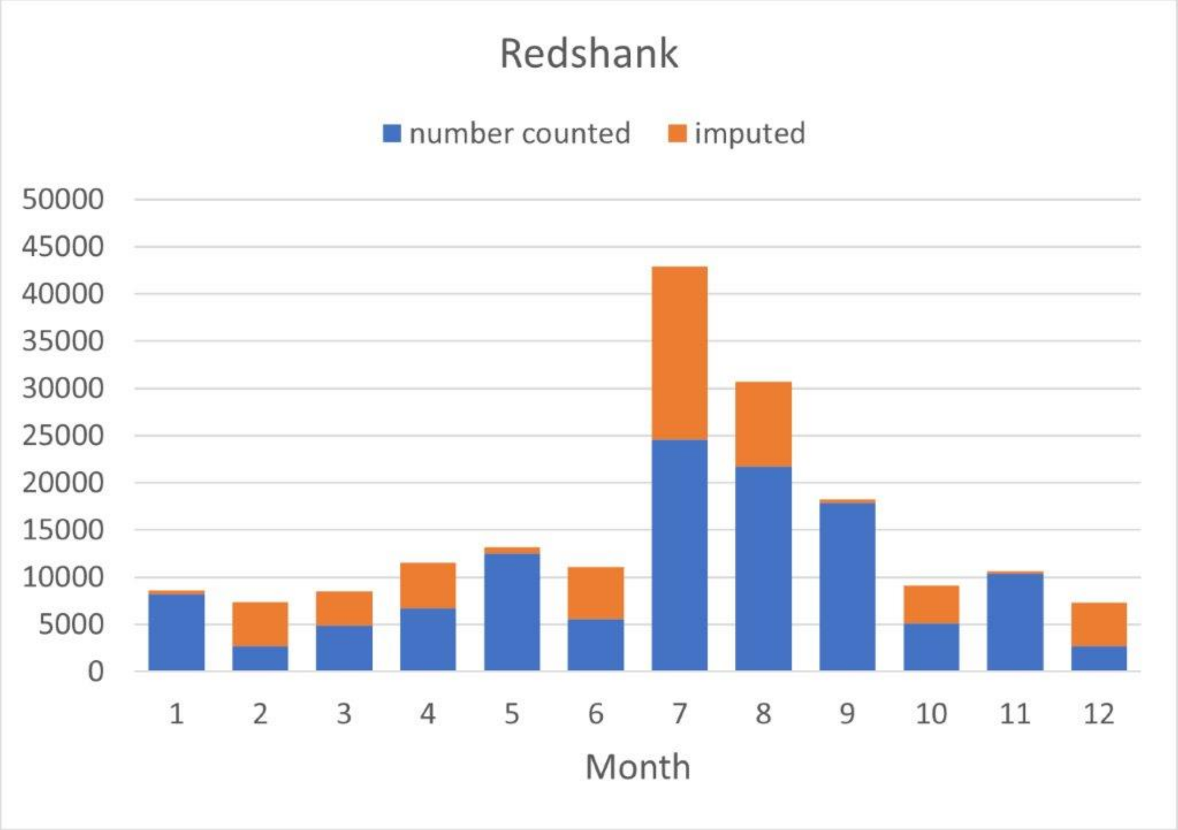
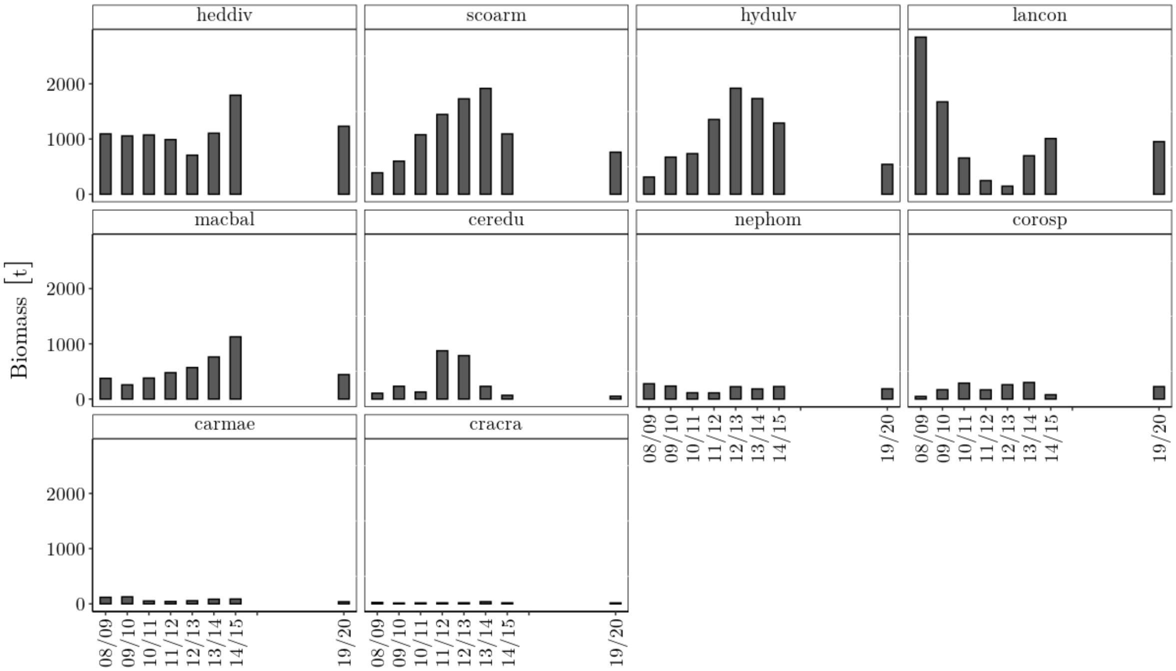


Figure 89: Redshank - seasonal pattern in the number of birds in the Dutch Wadden Sea. See figure 33 for details.



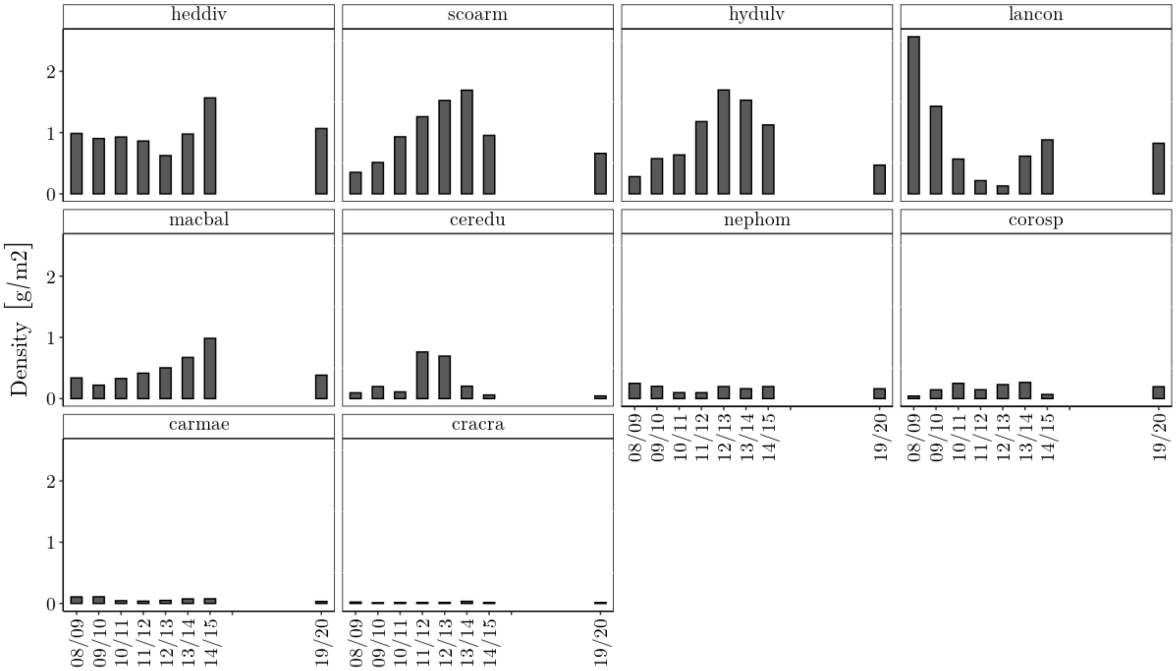


Figure 90: Total biomass (t) and density (g m^{-2}) of Redshank prey for the period 08/09 - 14/15 and 19/20.

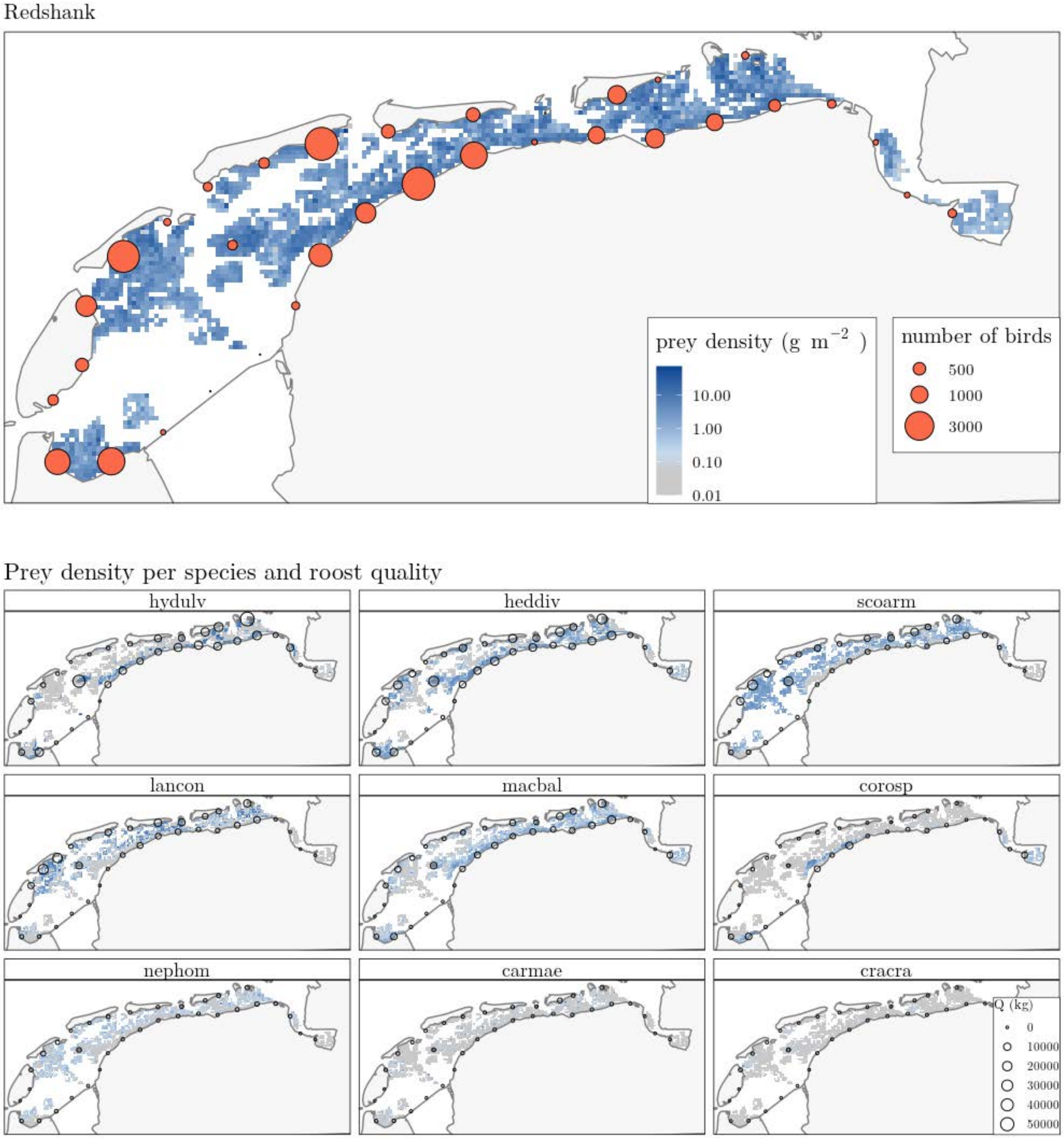


Figure 91: Average number of Redshank per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

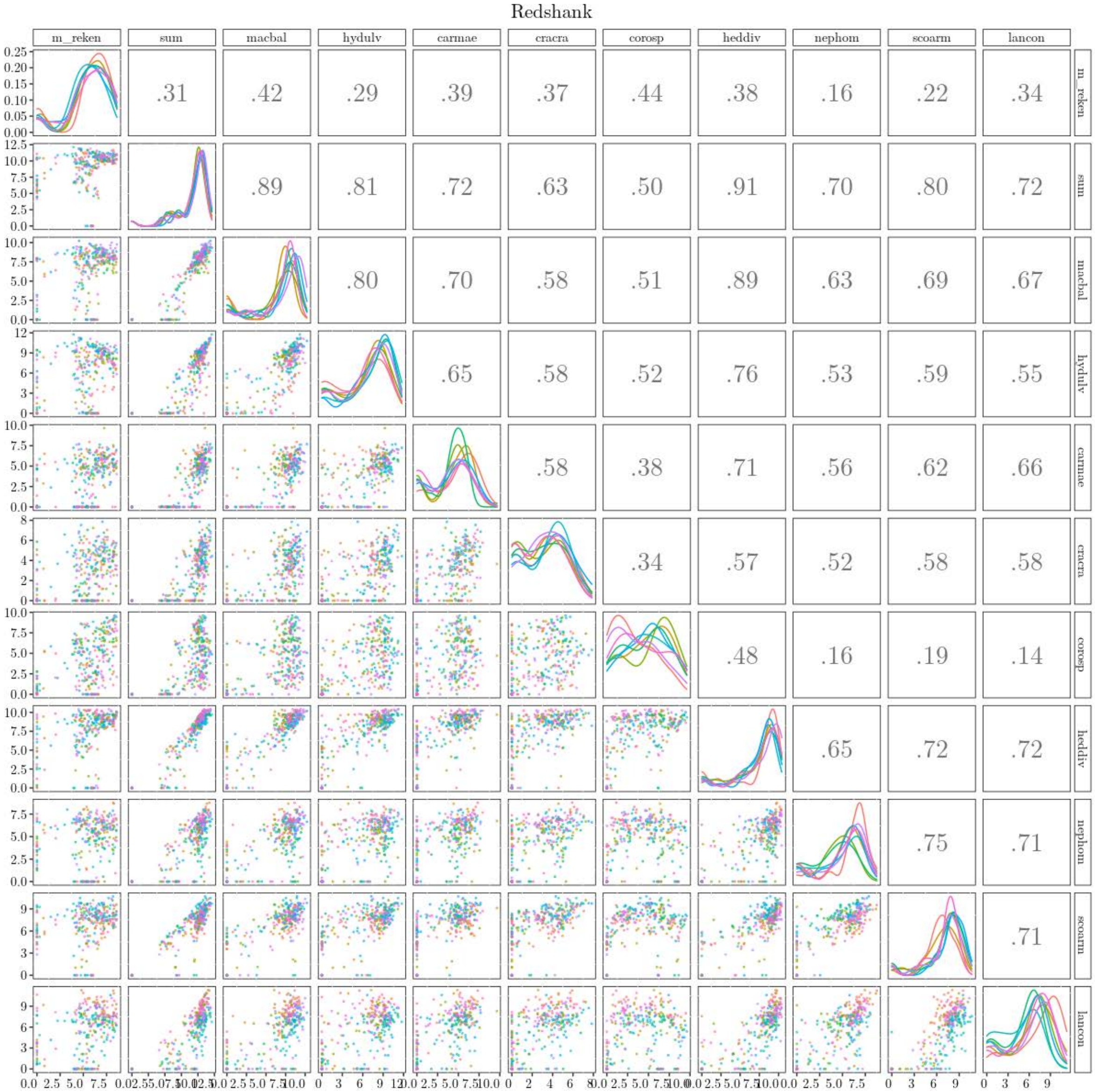


Figure 92: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Redshank. See the caption of Figure 36 for further details.

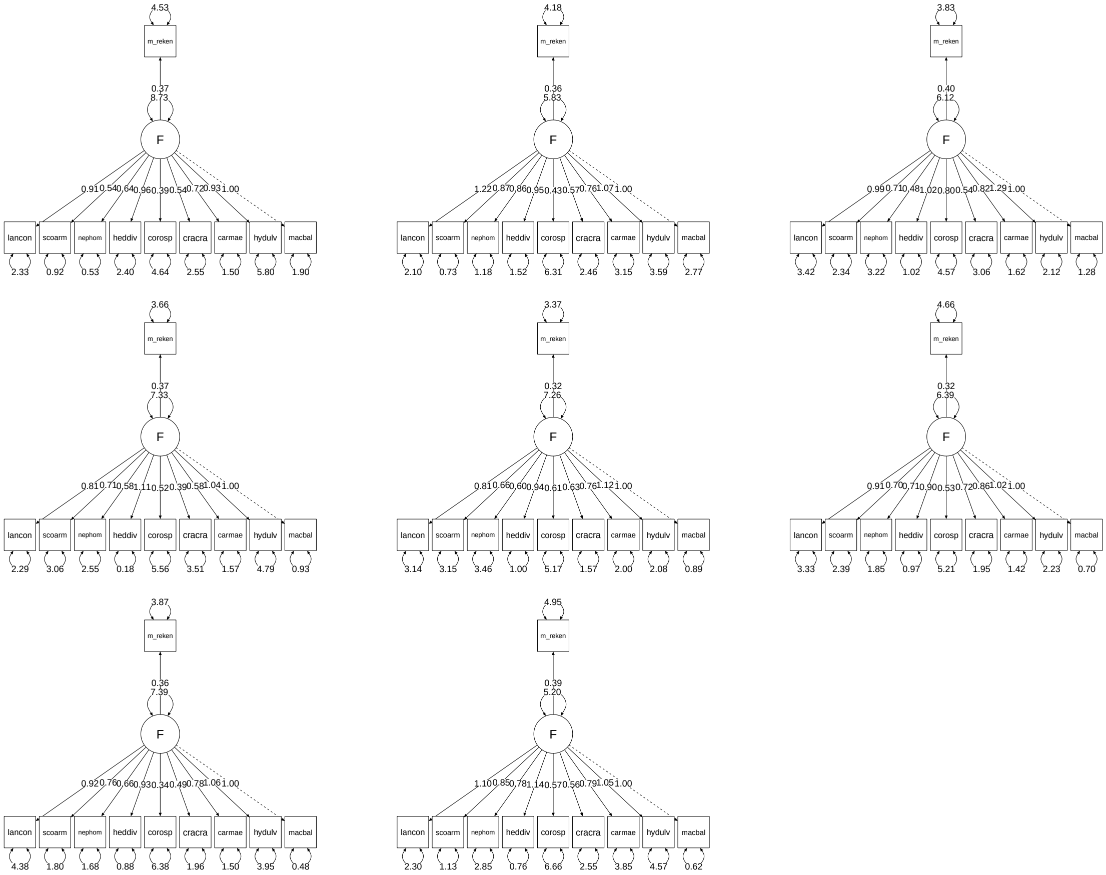


Figure 93: Structural equation model of the number of Redshank during period 1. See the caption of Figure 37 for further information.

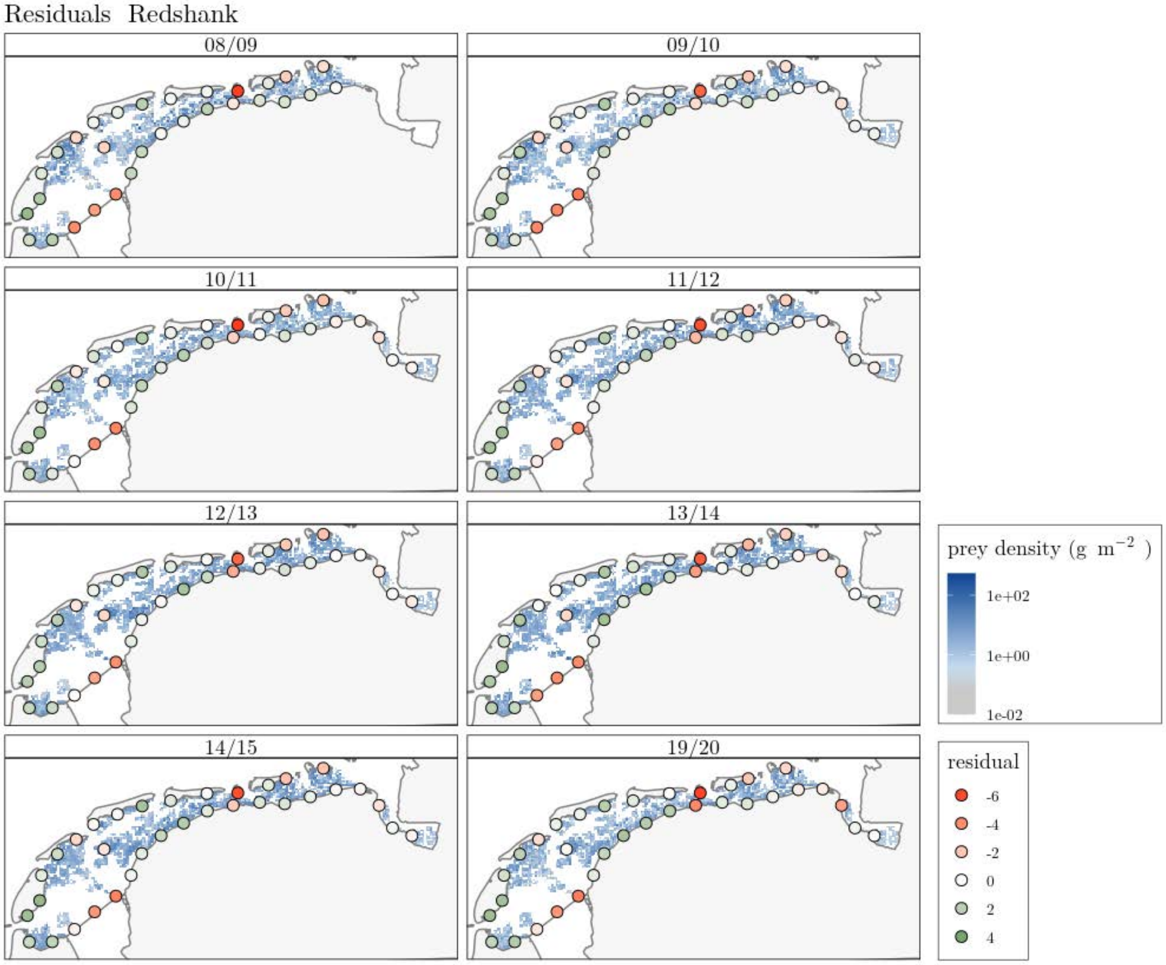


Figure 94: Residuals between the observed and implied number of Redshanks during period 1 at the virtual roosts.

B.1.12 Redshank - period 2

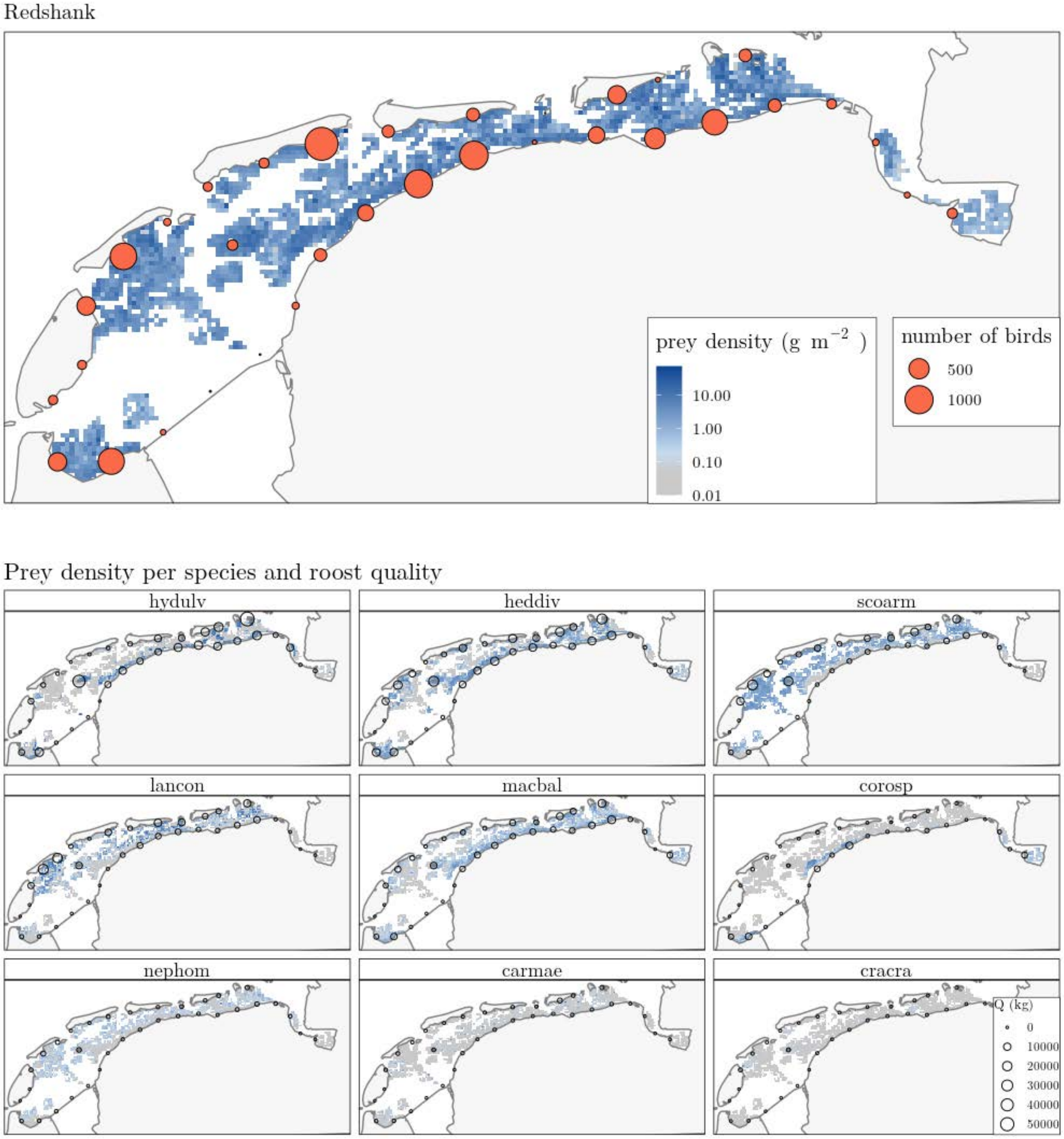


Figure 95: Average number of Redshank per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

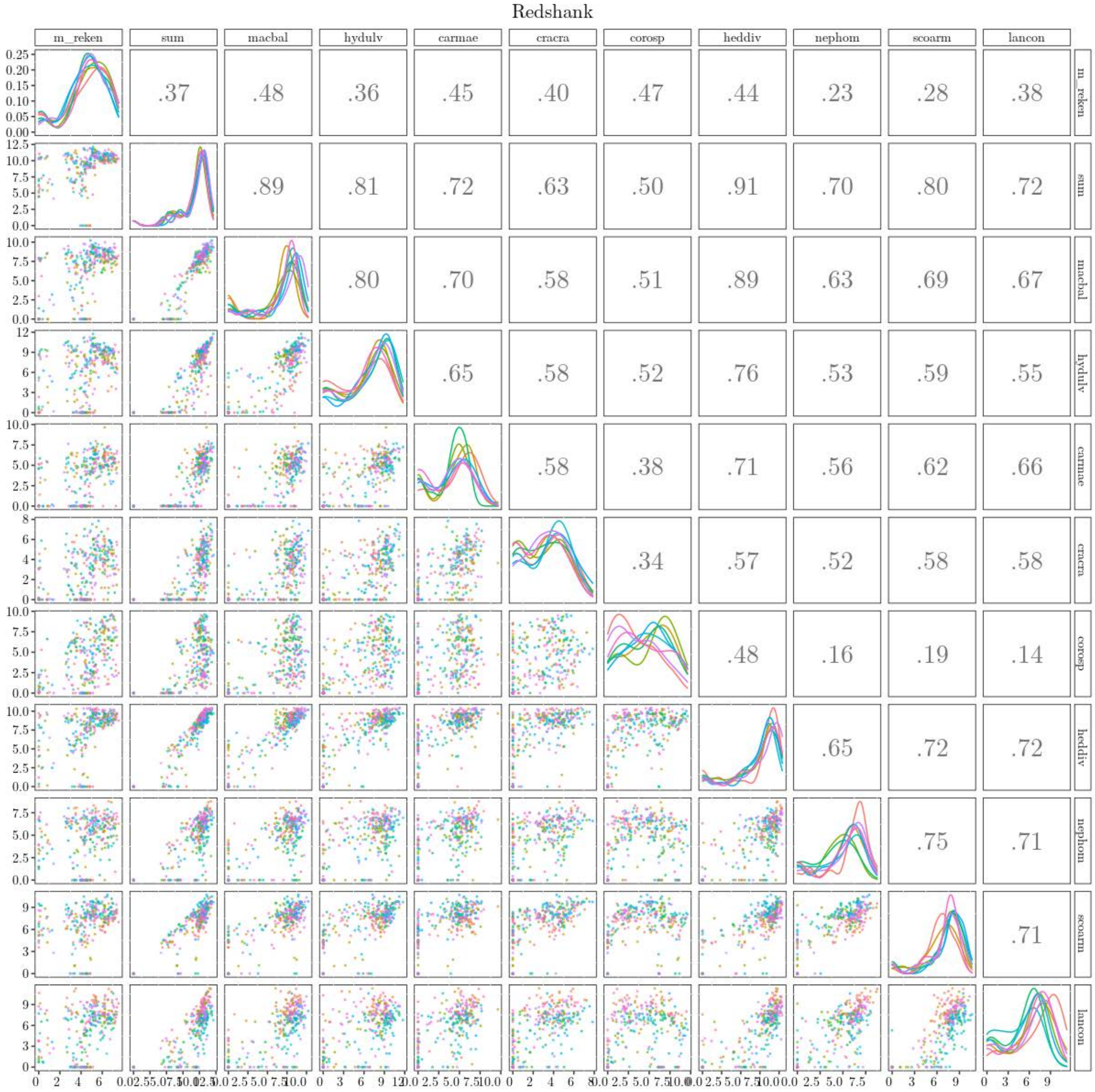


Figure 96: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Redshank. See the caption of Figure 36 for further details.

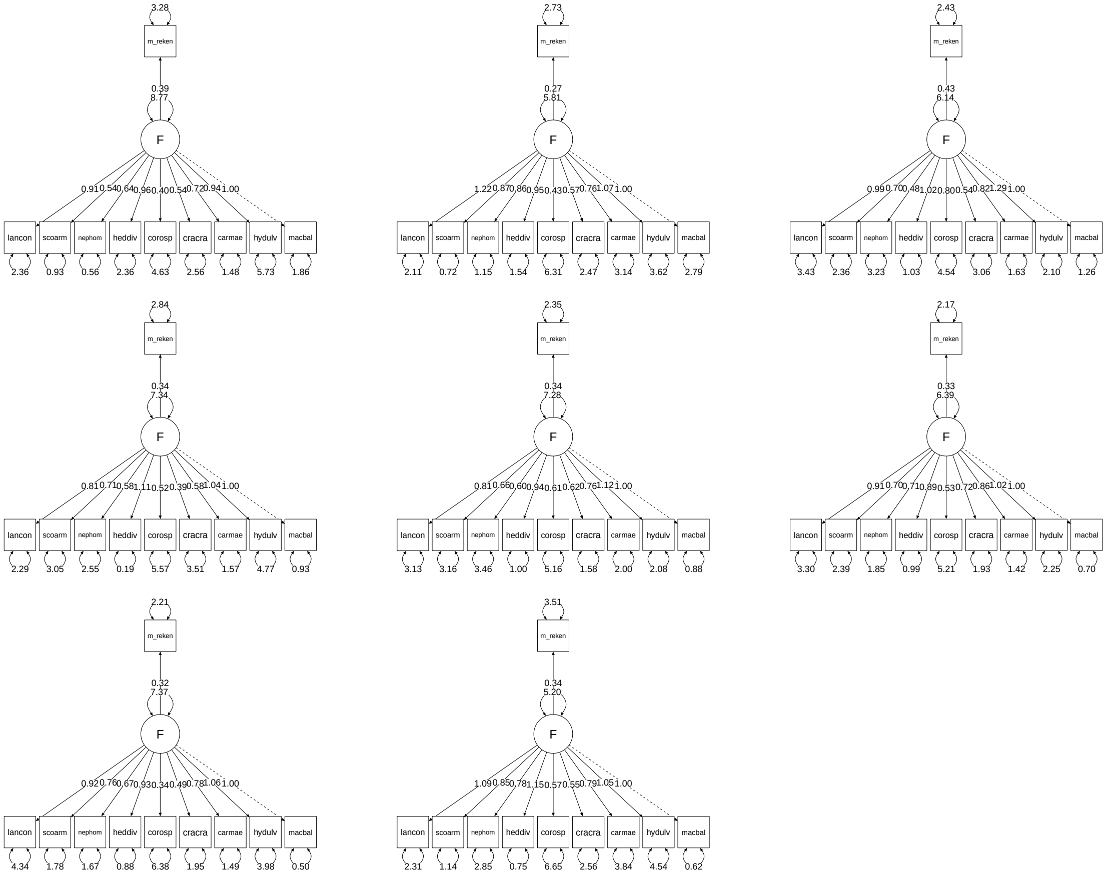


Figure 97: Structural equation model of the number of Redshank during period 2. See the caption of Figure 37 for further information.

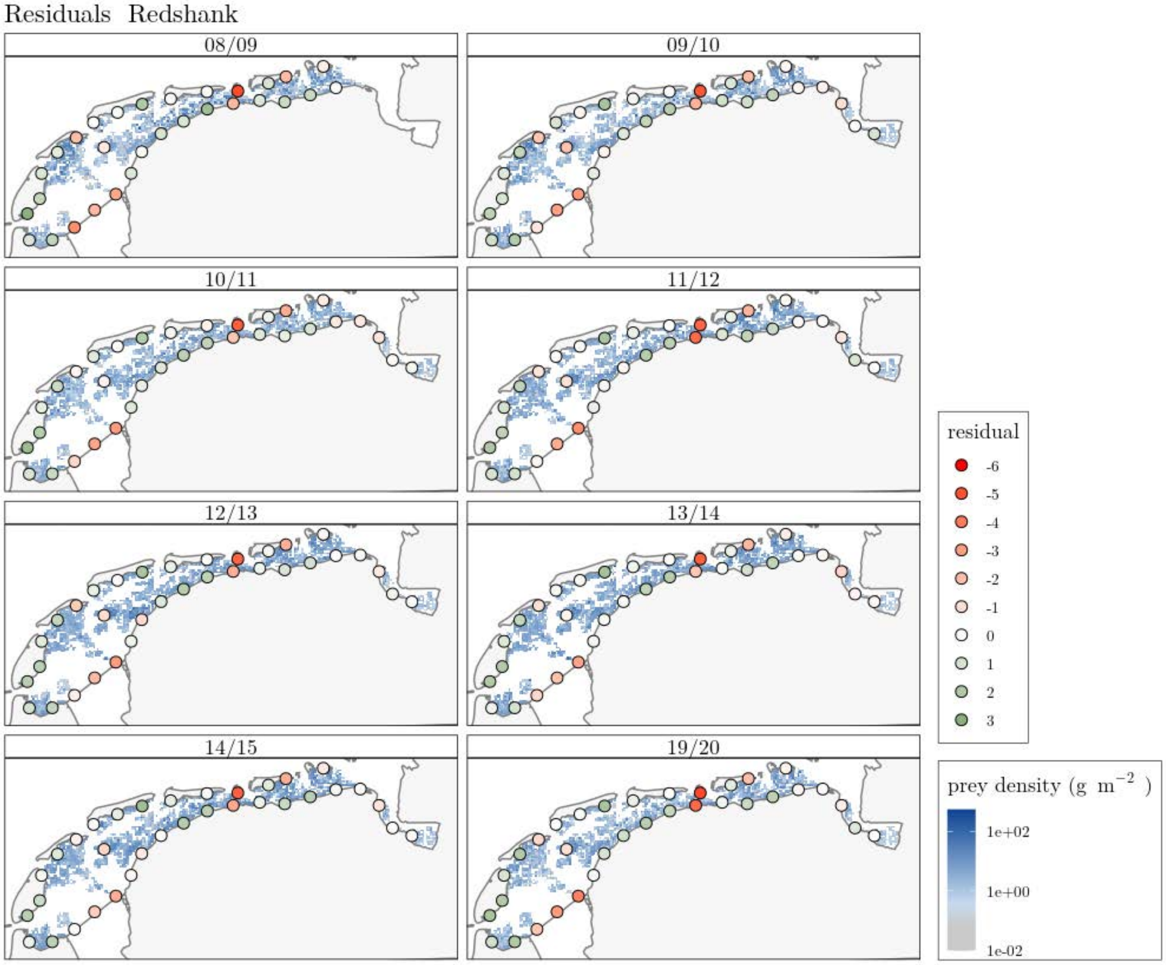


Figure 98: Residuals between the observed and implied number of Redshanks during period 2 at the virtual roosts.

B.1.13 Avocet

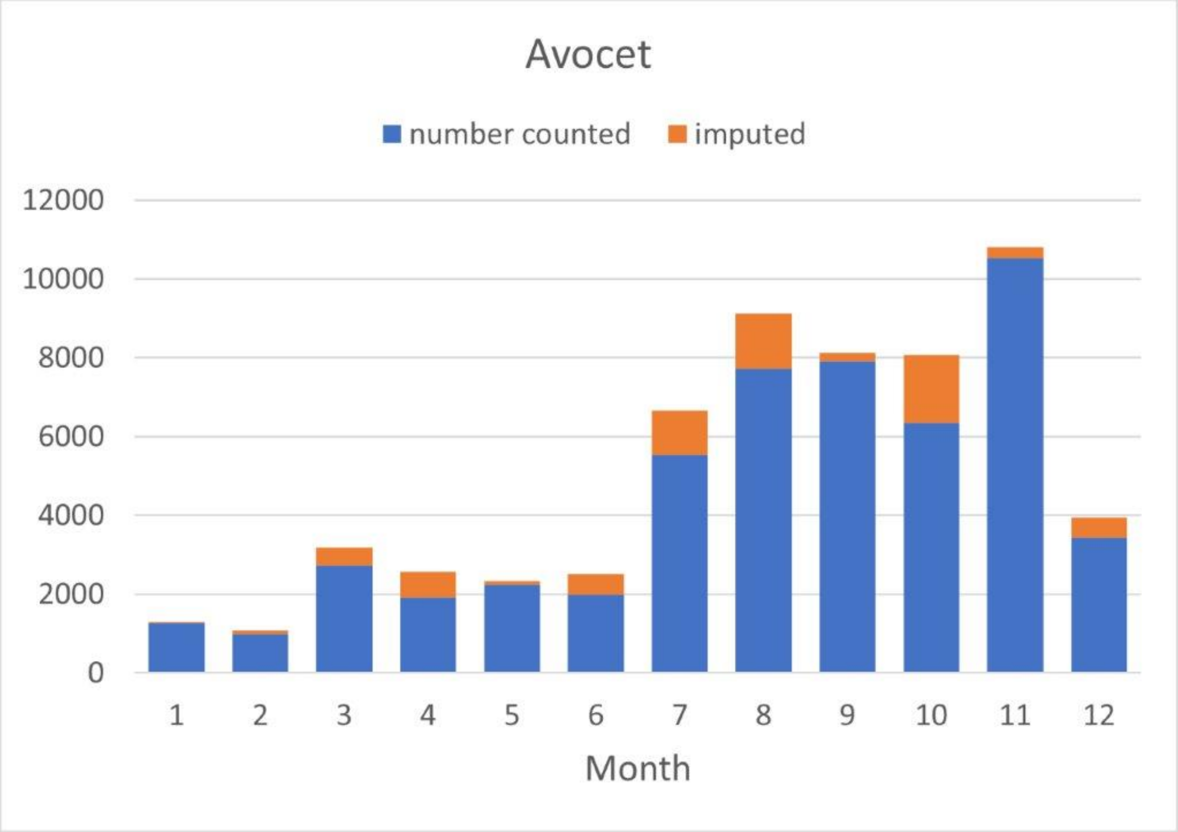


Figure 99: Avocet - seasonal pattern in the number of birds in the Dutch Wadden Sea. See figure 33 for details.

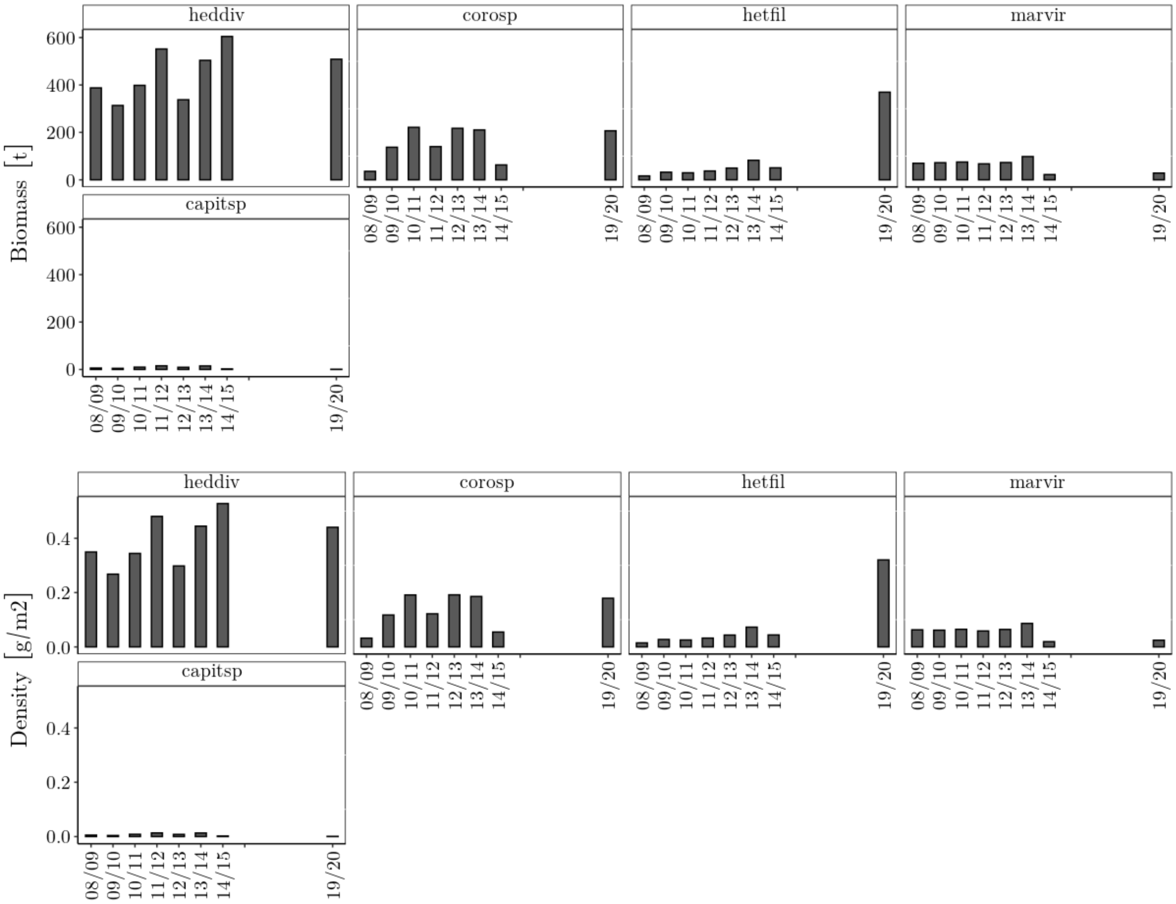


Figure 100: Total biomass (t) and density (g m^{-2}) of Avocet prey for the period 08/09 - 14/15 and 19/20.

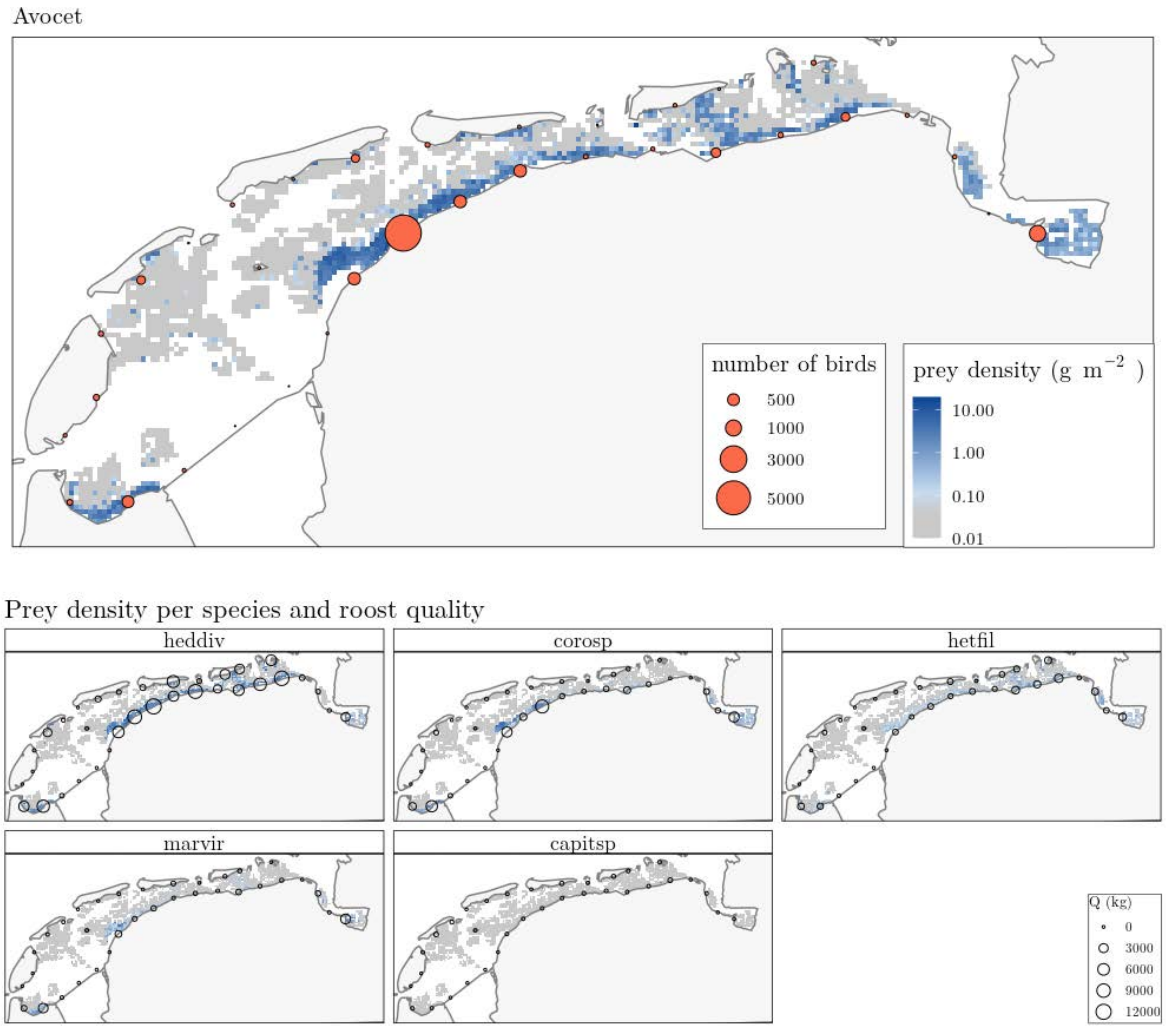


Figure 101: Average number of Avocet per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

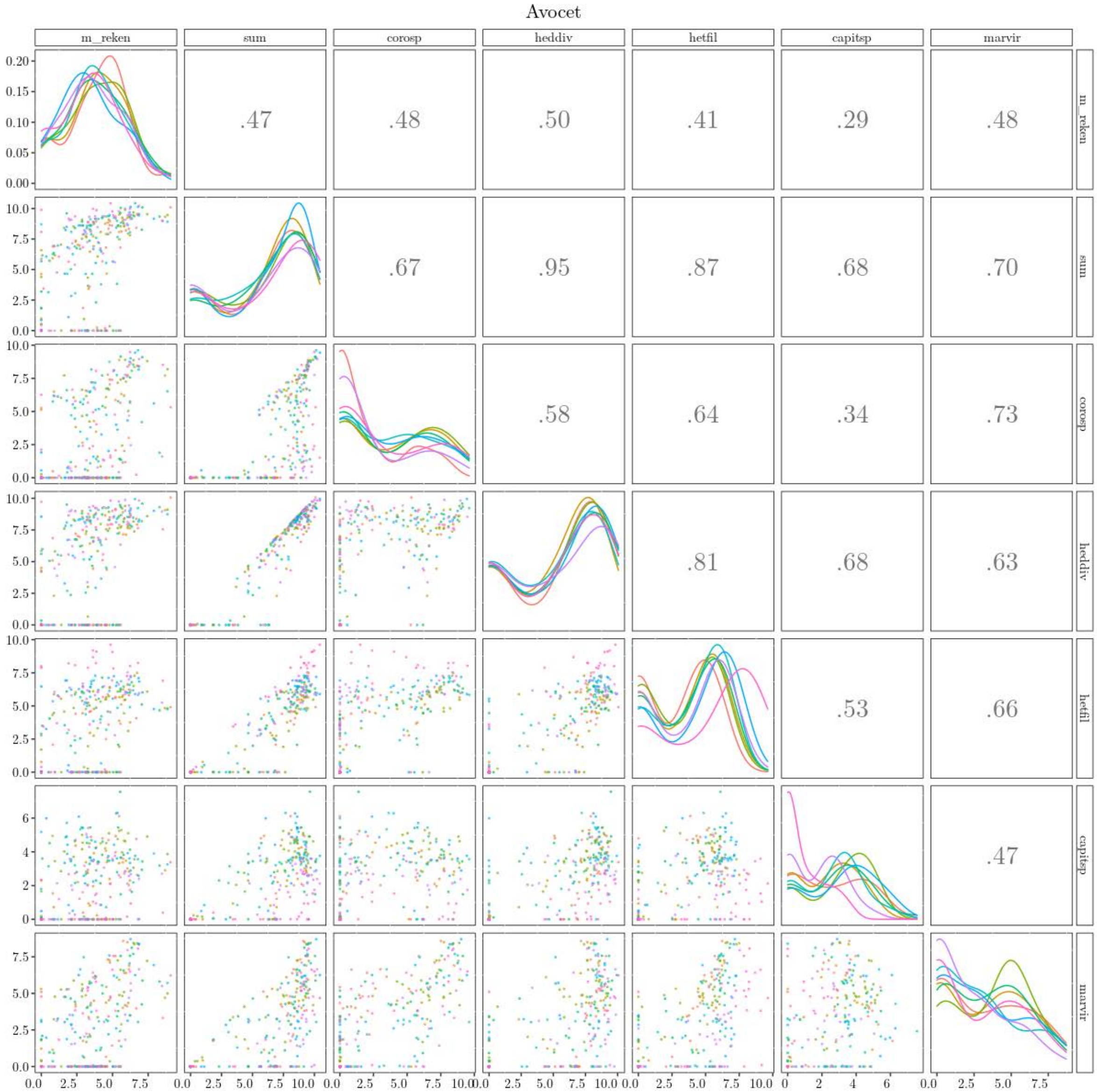


Figure 102: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Avocet. See the caption of Figure 36 for further details.

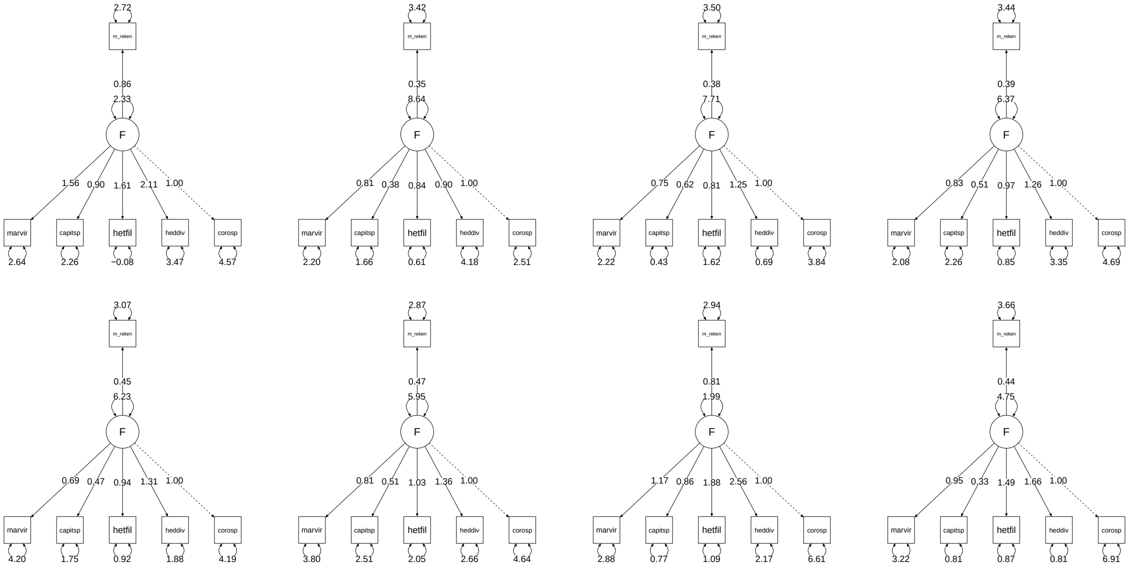


Figure 103: Structural equation model of the number of Avocets. See the caption of Figure 37 for further information.

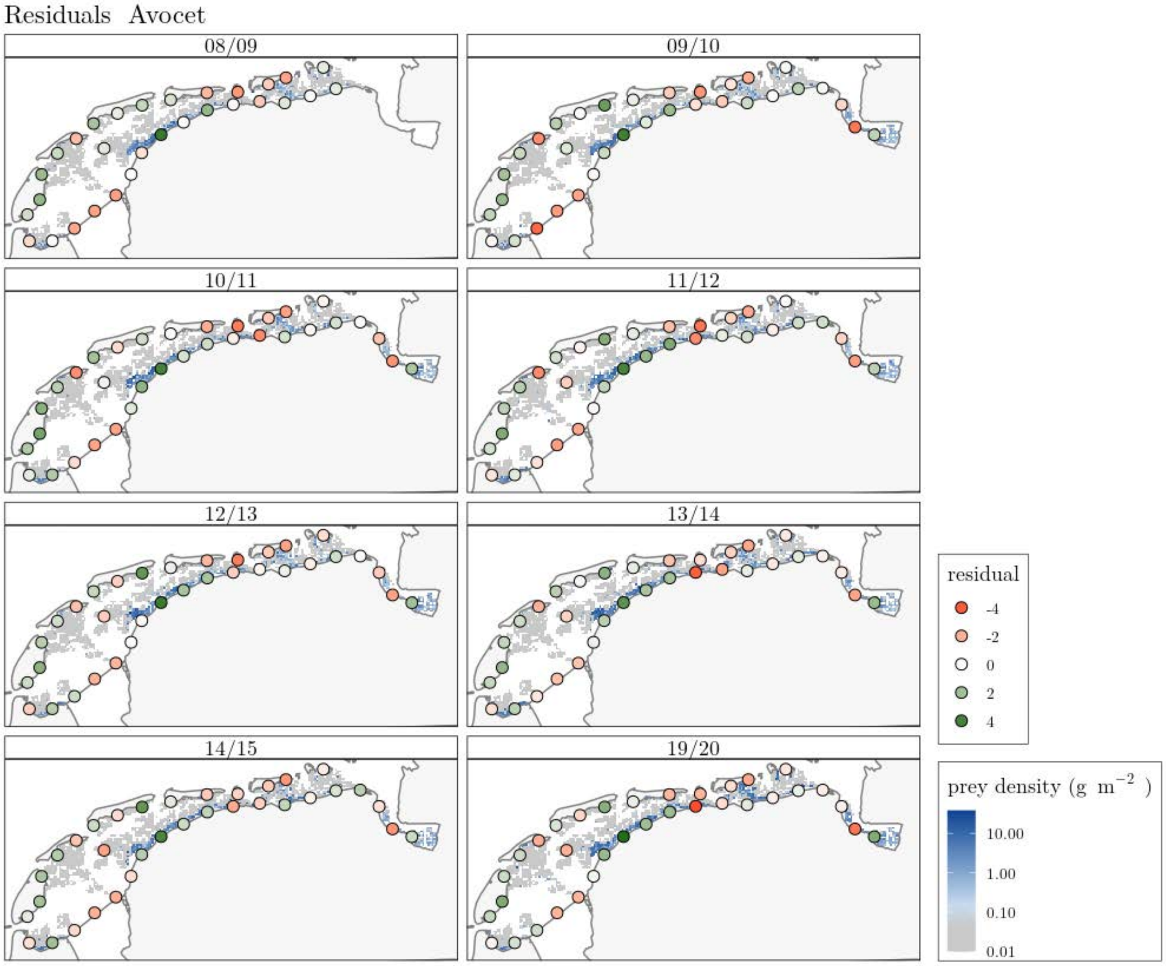


Figure 104: Residuals between the observed and implied number of Avocets at the virtual roosts.

B.1.14 Greenshank

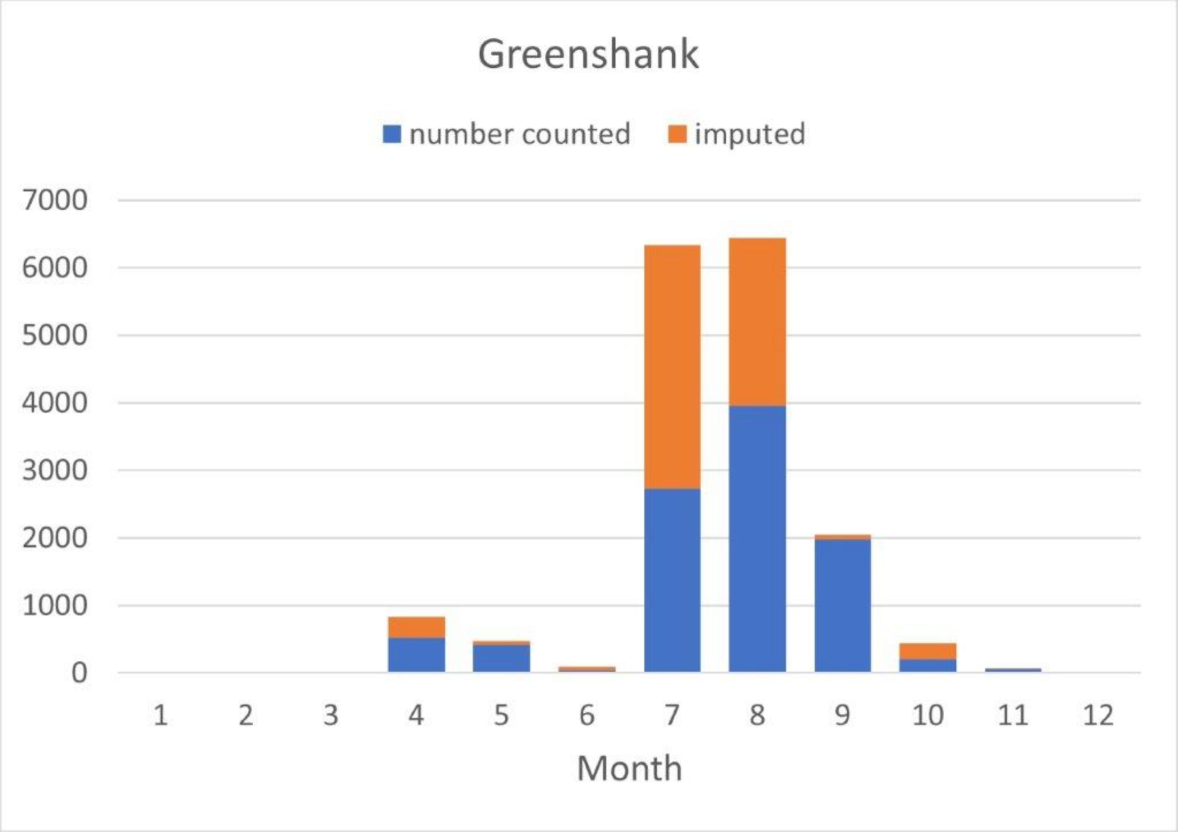


Figure 105: Greenshank - seasonal pattern in the number of birds in the Dutch Wadden Sea. See figure 33 for details.

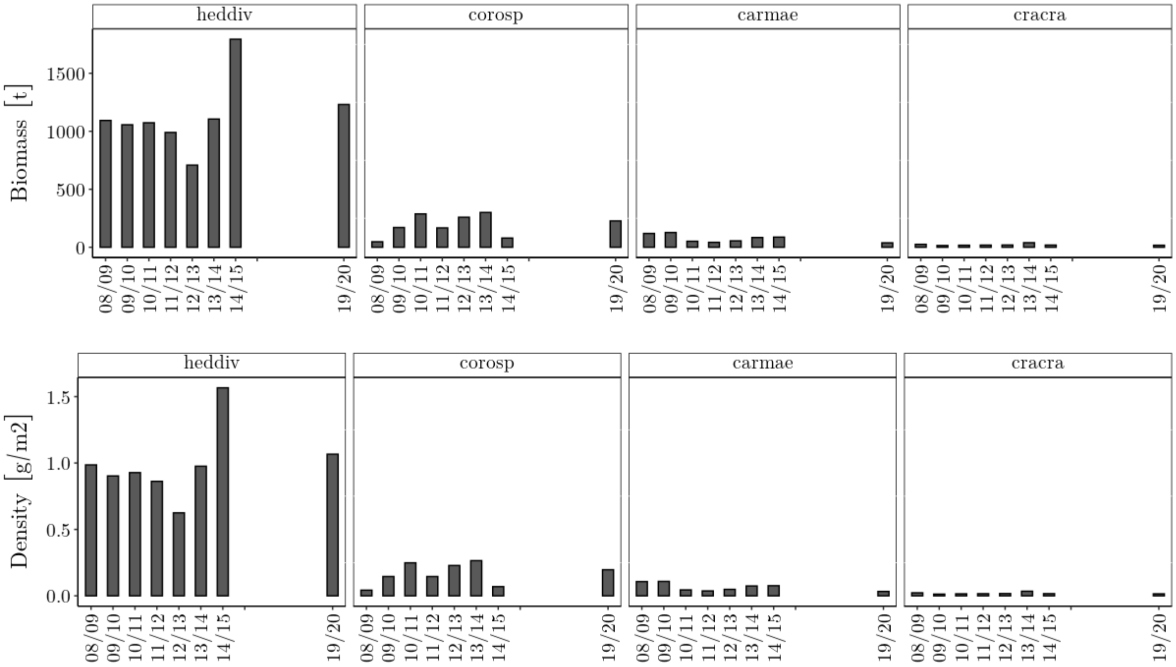


Figure 106: Total biomass (t) and density (g m^{-2}) of Greenshank prey for the period 08/09 - 14/15 and 19/20.

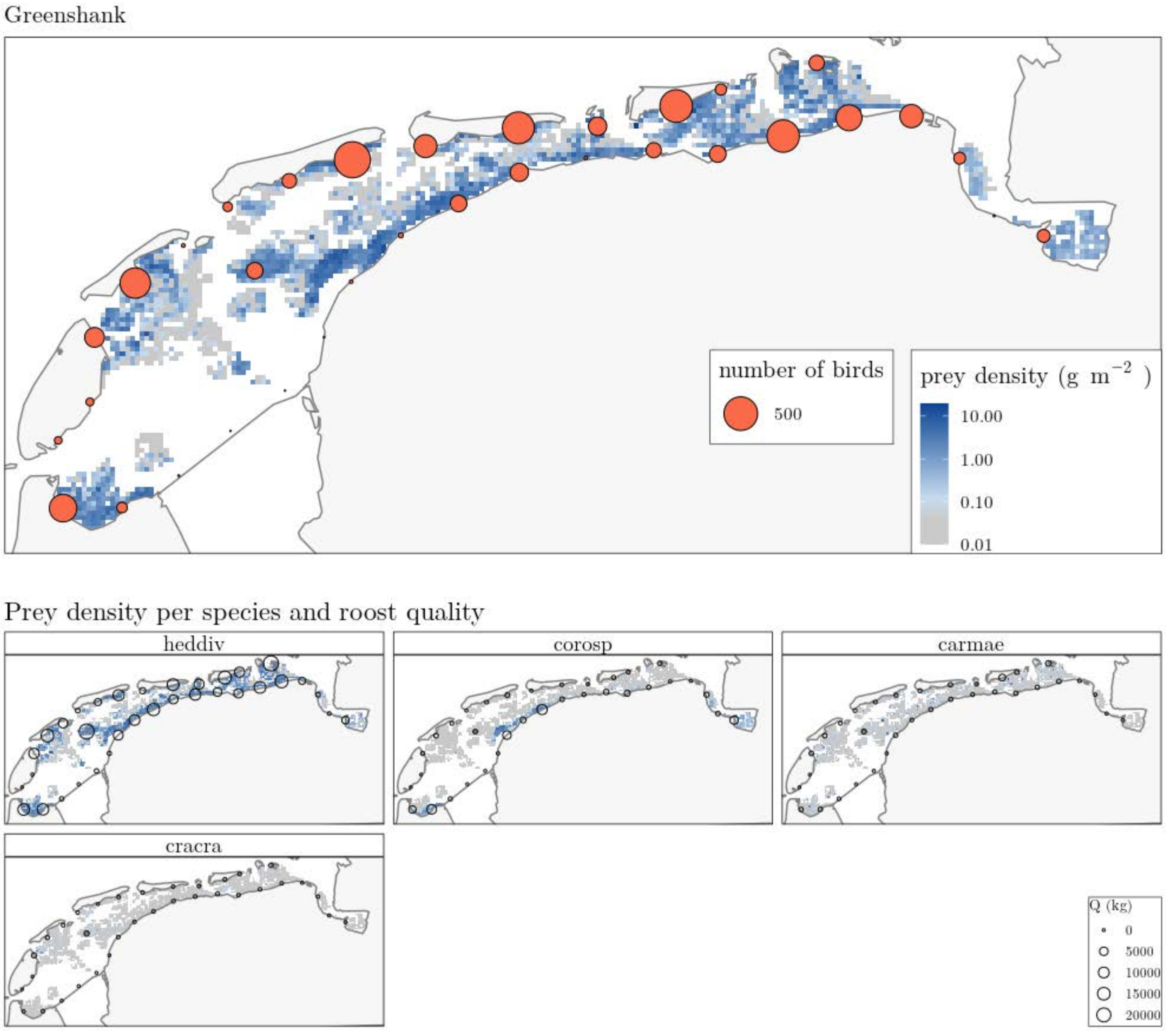


Figure 107: Average number of Greenshank per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

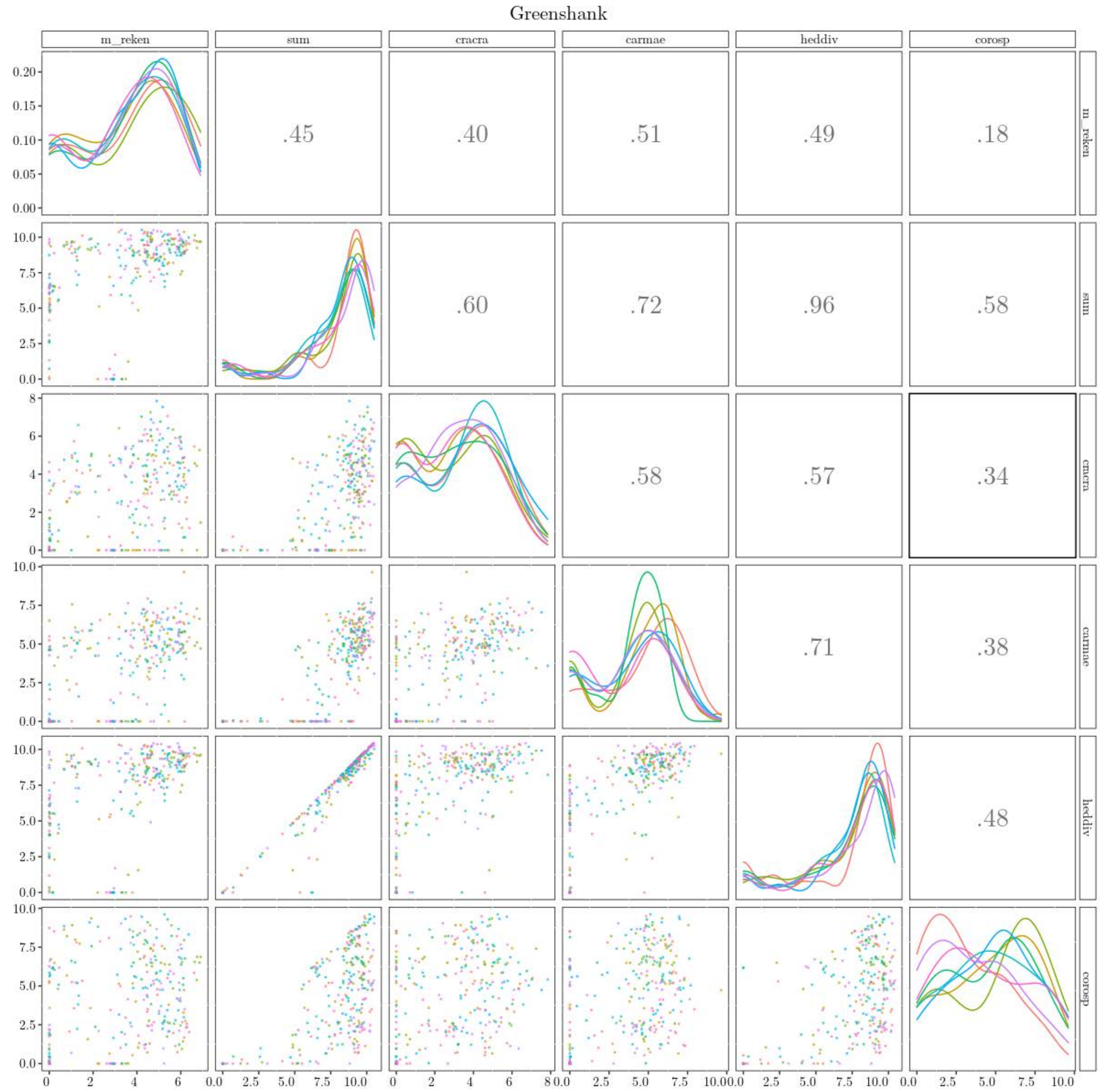


Figure 108: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Greenshank. See the caption of Figure 36 for further details.

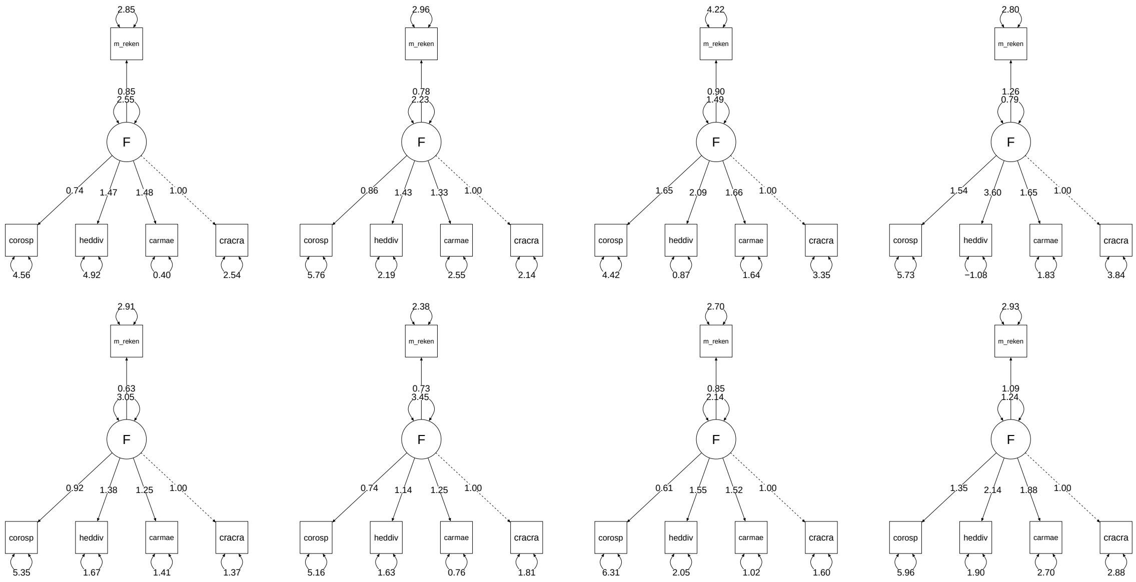


Figure 109: Structural equation model of the number of Greenshank. See the caption of Figure 37 for further information.

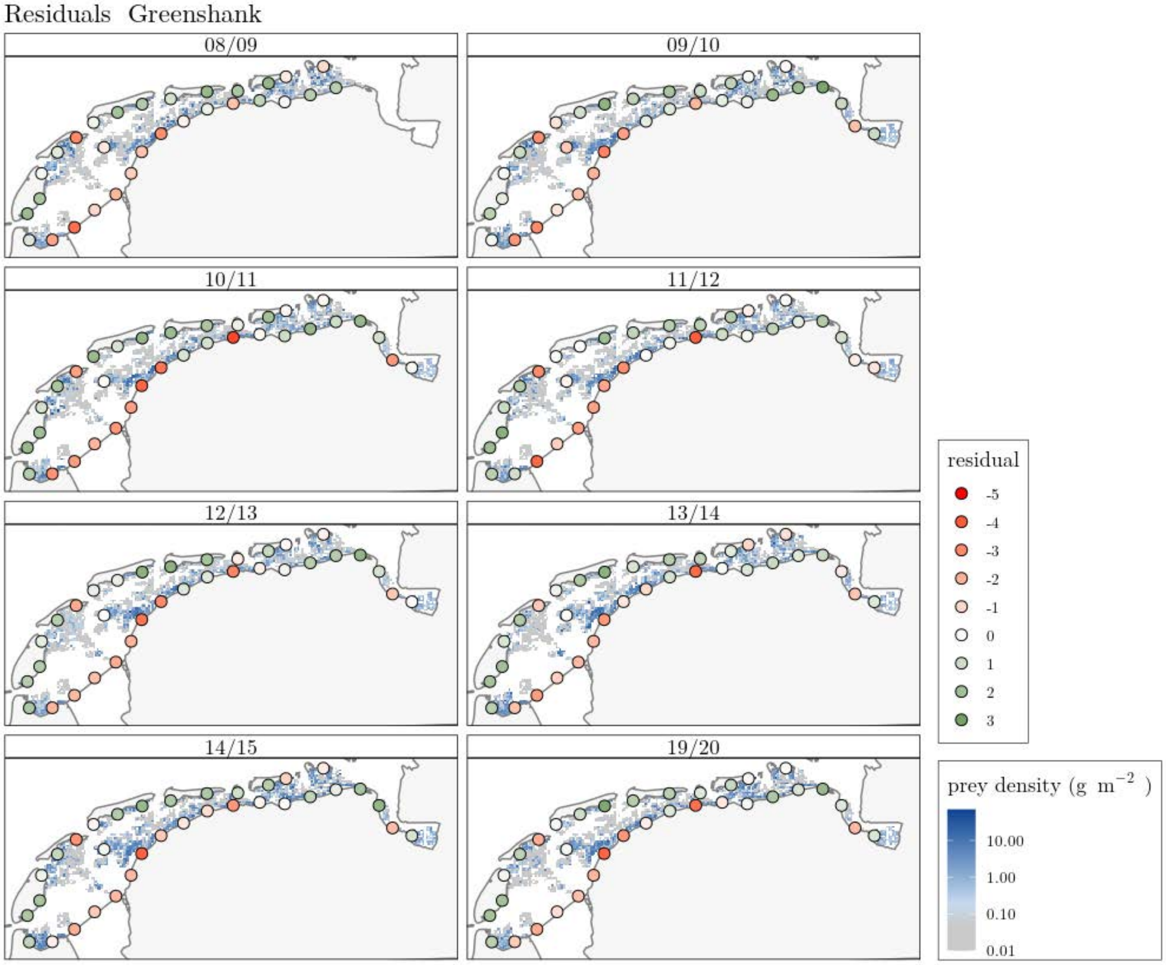


Figure 110: Residuals between the observed and implied number of Greenshanks at the virtual roosts.

B.1.15 Spotted Redshank

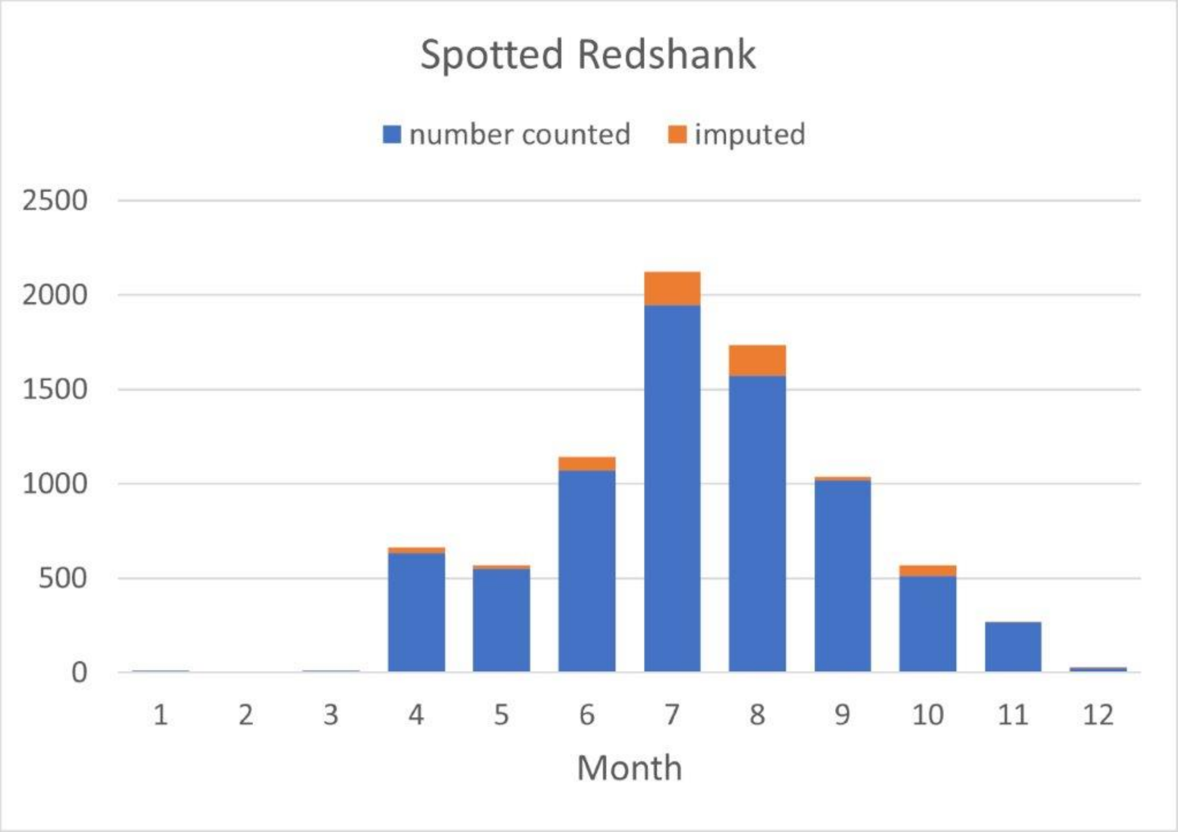


Figure 111: Spotted Redshank - seasonal pattern in the number of birds in the Dutch Wadden Sea. See figure 33 for details.

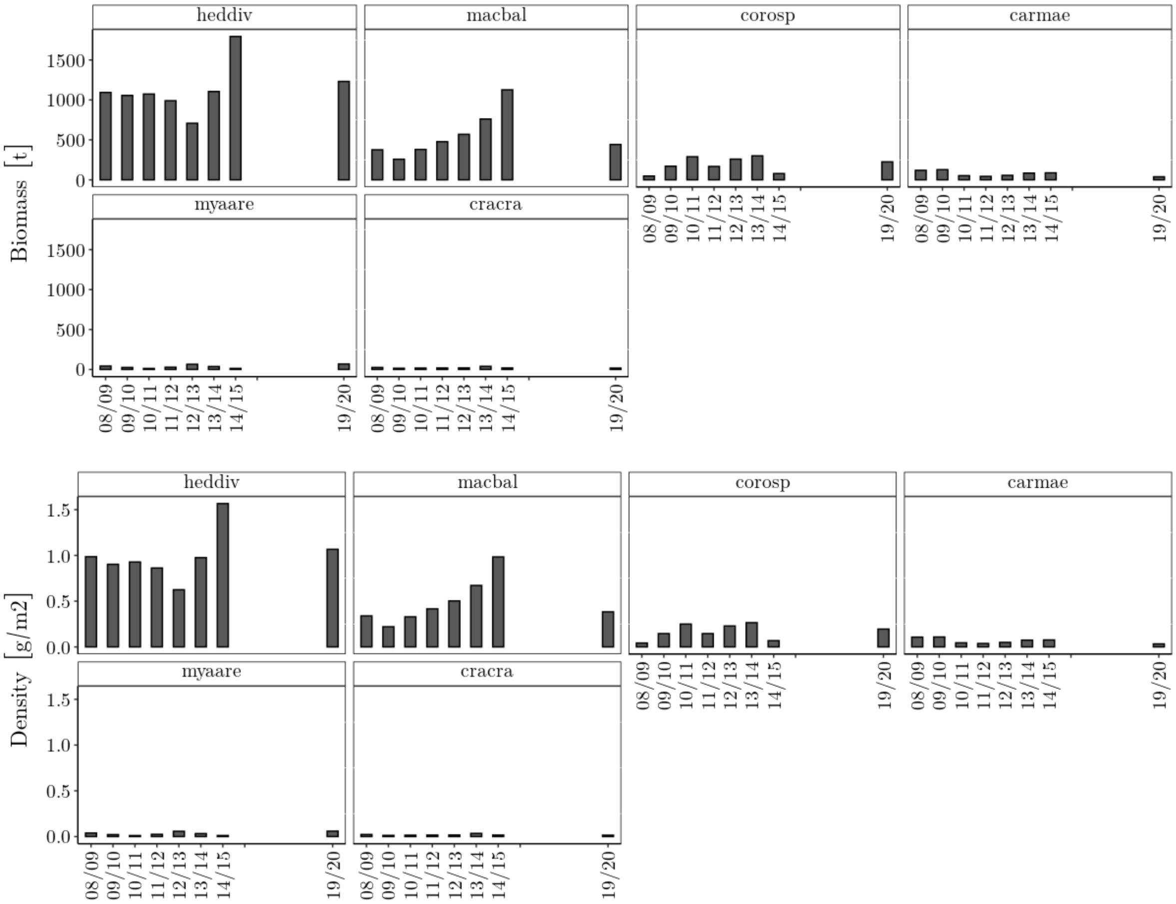


Figure 112: Total biomass (t) and density (g m^{-2}) of Spotted Redshank prey for the period 08/09 - 14/15 and 19/20.

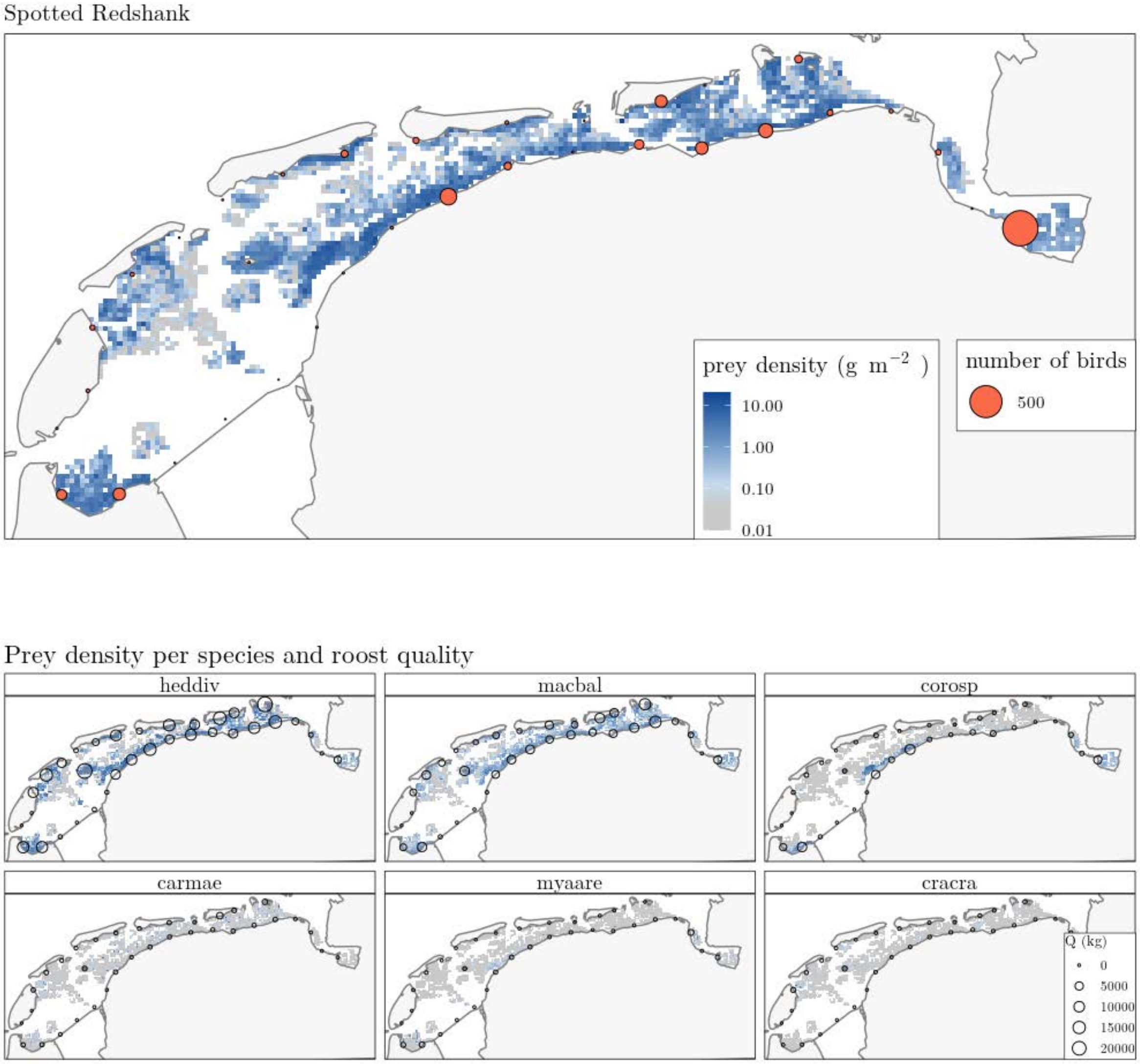


Figure 113: Average number of Spotted Redshank per virtual roost (top panel, red dots) and the distribution of prey. See the caption of Figure 35 for further details.

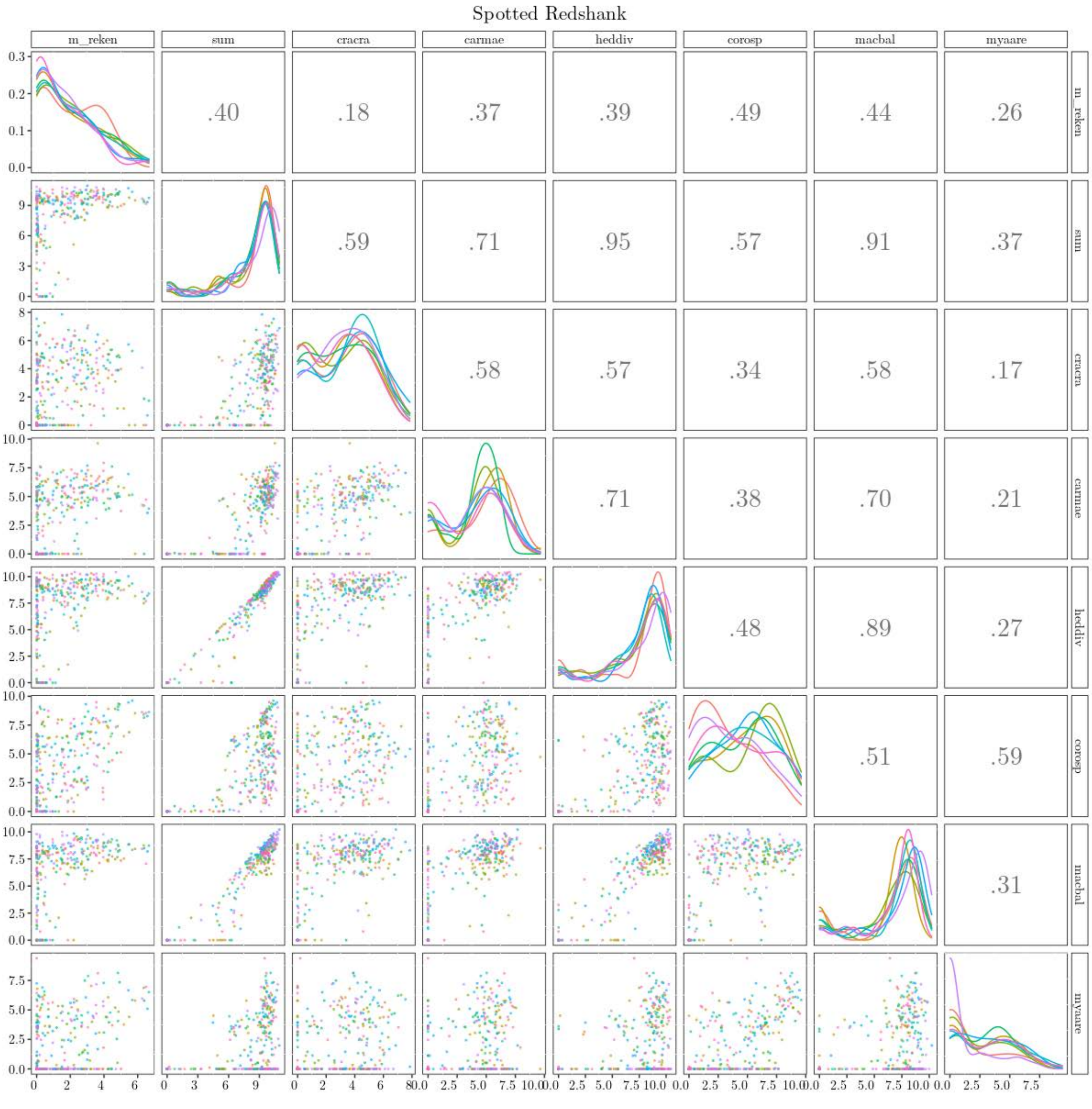


Figure 114: Univariate scatterplots (lower triangle), frequency distributions (diagonal) and correlation coefficients (upper triangle) of the variables used in the structural equation model for the Spotted Redshank. See the caption of Figure 36 for further details.

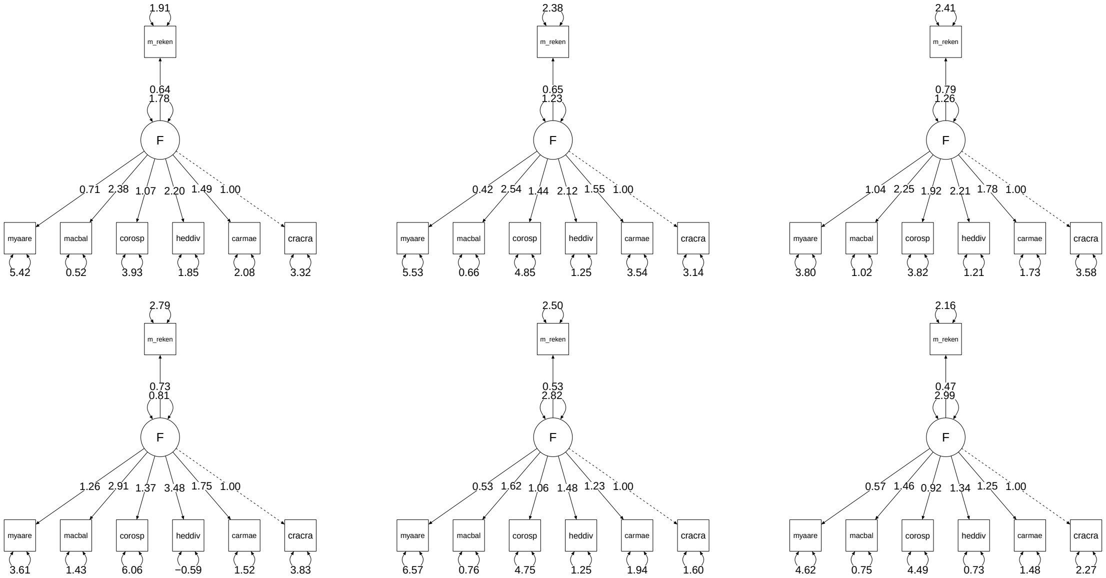


Figure 115: Structural equation model of the number of Spotted Redshank. See the caption of Figure 37 for further information.

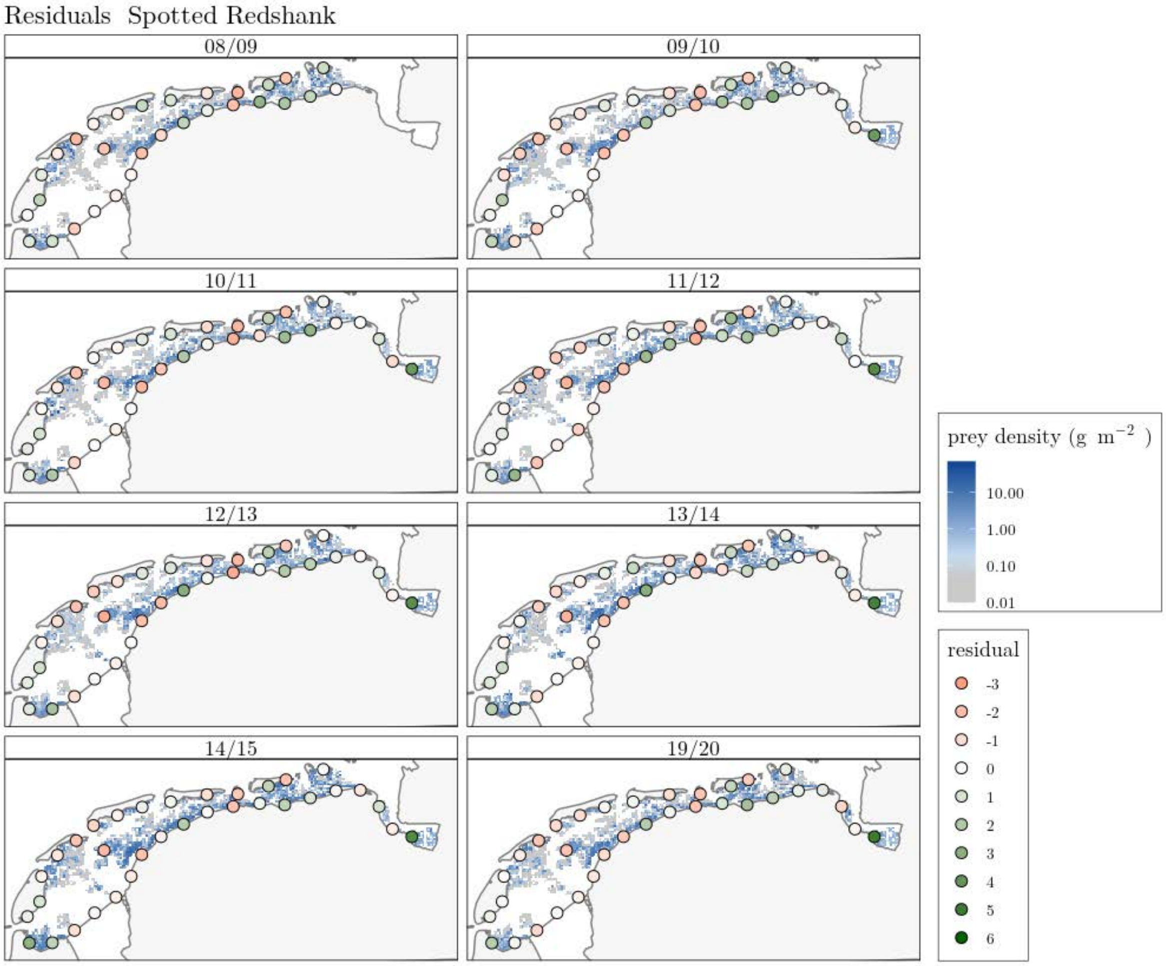


Figure 116: Residuals between the observed and implied number of Spotted Redshanks at the virtual roosts.

B.2 Overview of 12 species: distributions, food and mismatch

This section provides an overview of the spatial distributions of the distributions of the shorebirds along the virtual roosts, the foraging potential and the mismatch. Figures 117 - 120 provide an overview of the annual data which are aggregated in figures 25 and 26.

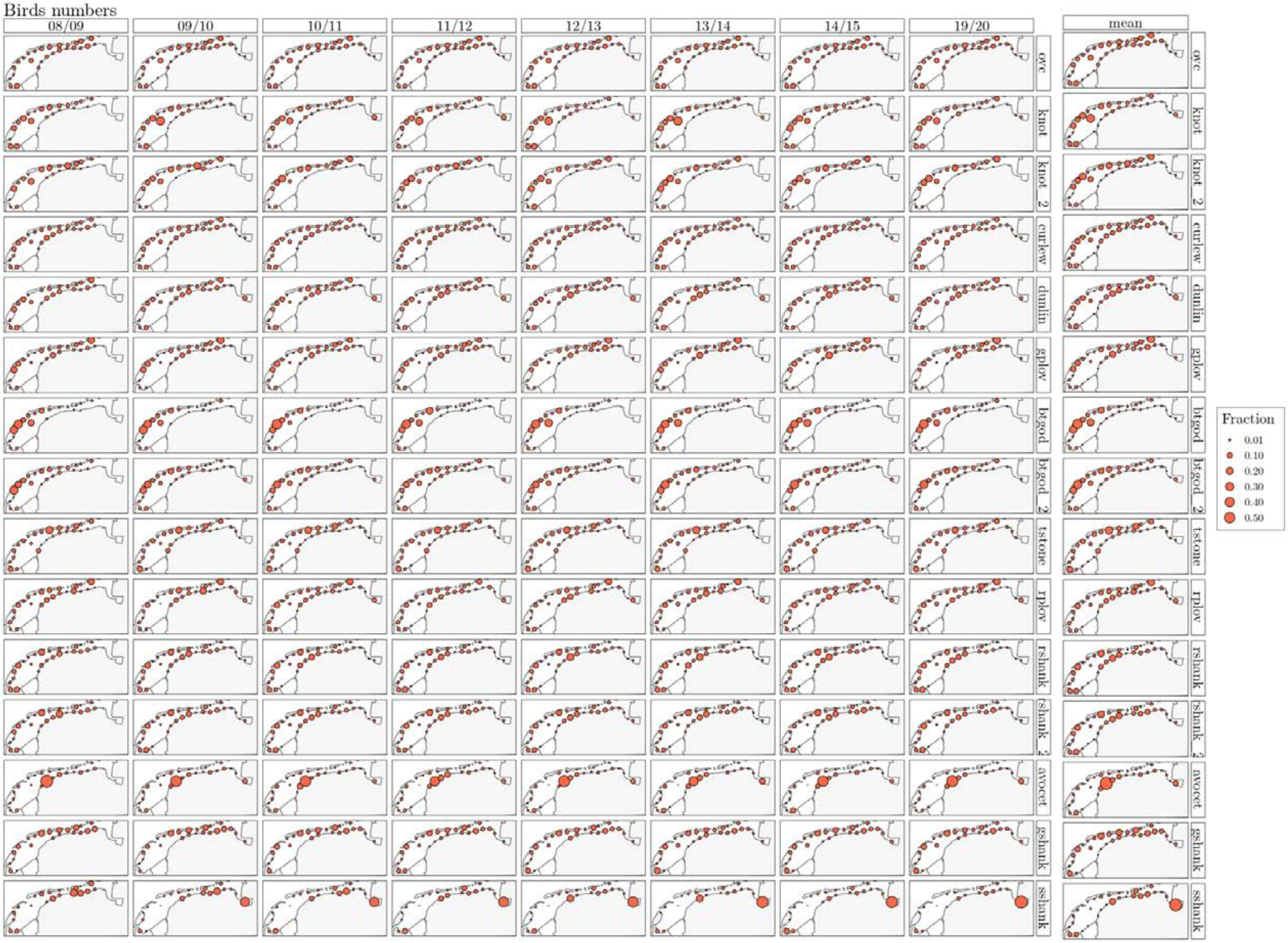


Figure 117: Distribution of birds between virtual roosts. The numbers per species are presented as fractions of the seasonal totals (based on the selection of months (section 2.3)). When in the right margin "_2" is added to the shorebird species, it refers to the second period as defined in section 2.3.

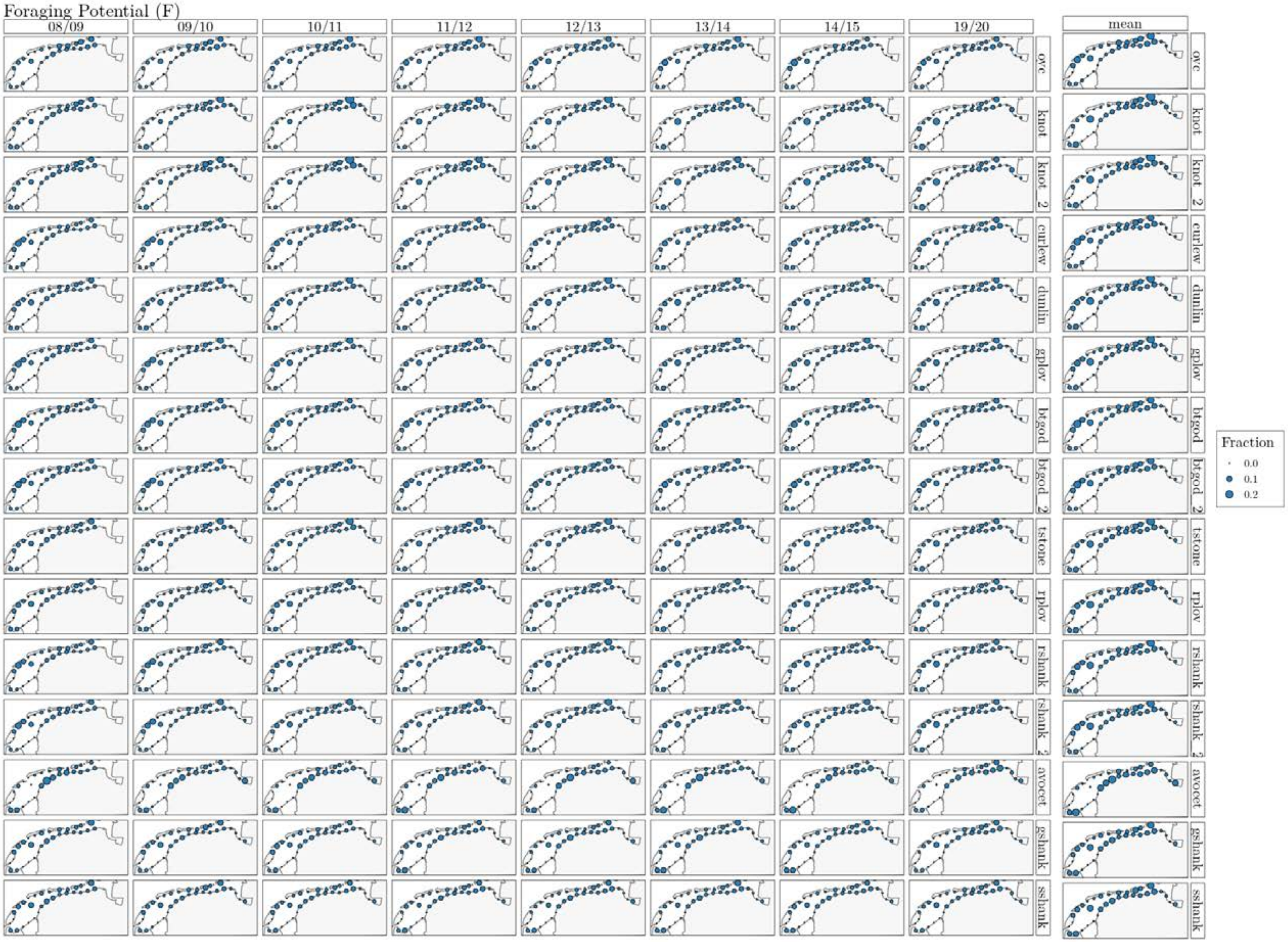


Figure 118: Relative foraging potential along the virtual roosts. Foraging potential is the weighed biomass at the virtual roost, i.e. P_{js} (eqn.1). When in the right margin "_2" is added to the shorebird species, it refers to the second period as defined in section 2.3.

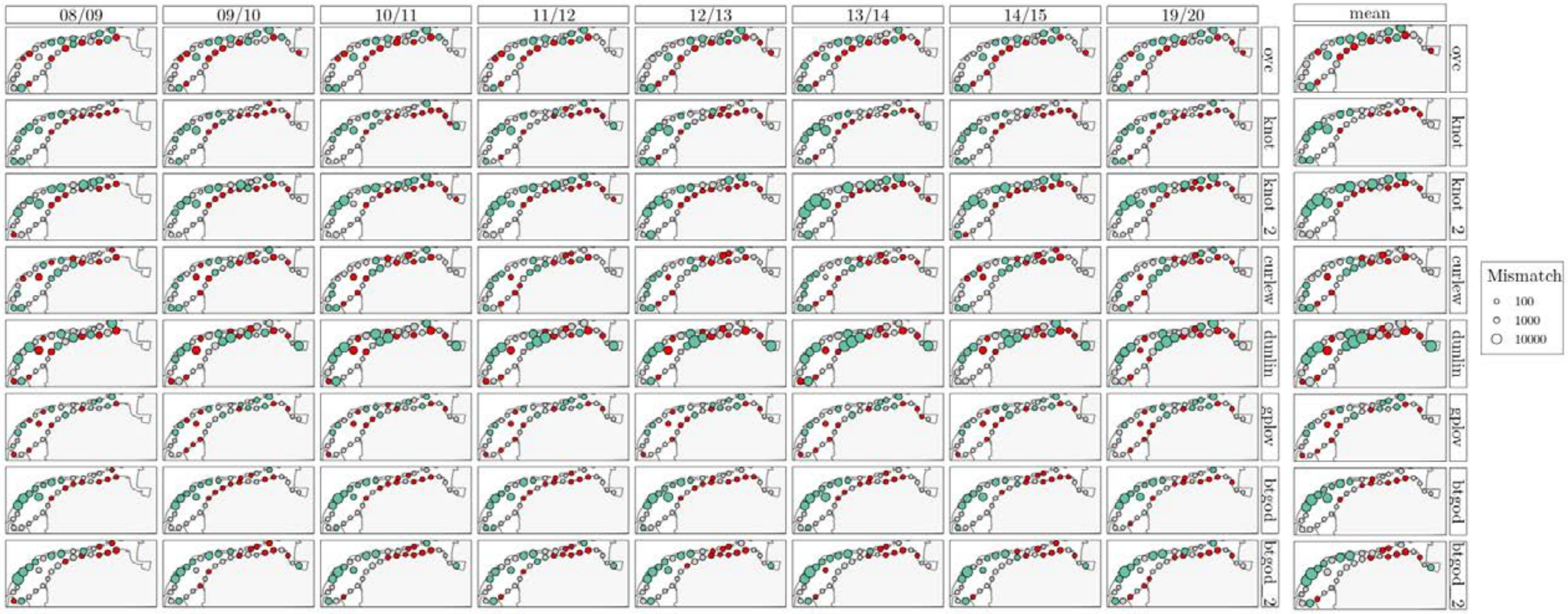


Figure 119: Mismatch between bird numbers and the predicted number of birds on the basis of the overall foraging potential (F). The size of the dot represents the magnitude of the mismatch and the colour whether it is a negative mismatch (red) or positive mismatch (green); the grey dots represent relatively small mismatches and lie between quartiles 2 and 3. When in the right margin "_2" is added to the shorebird species, it refers to the second period as defined in section 2.3.

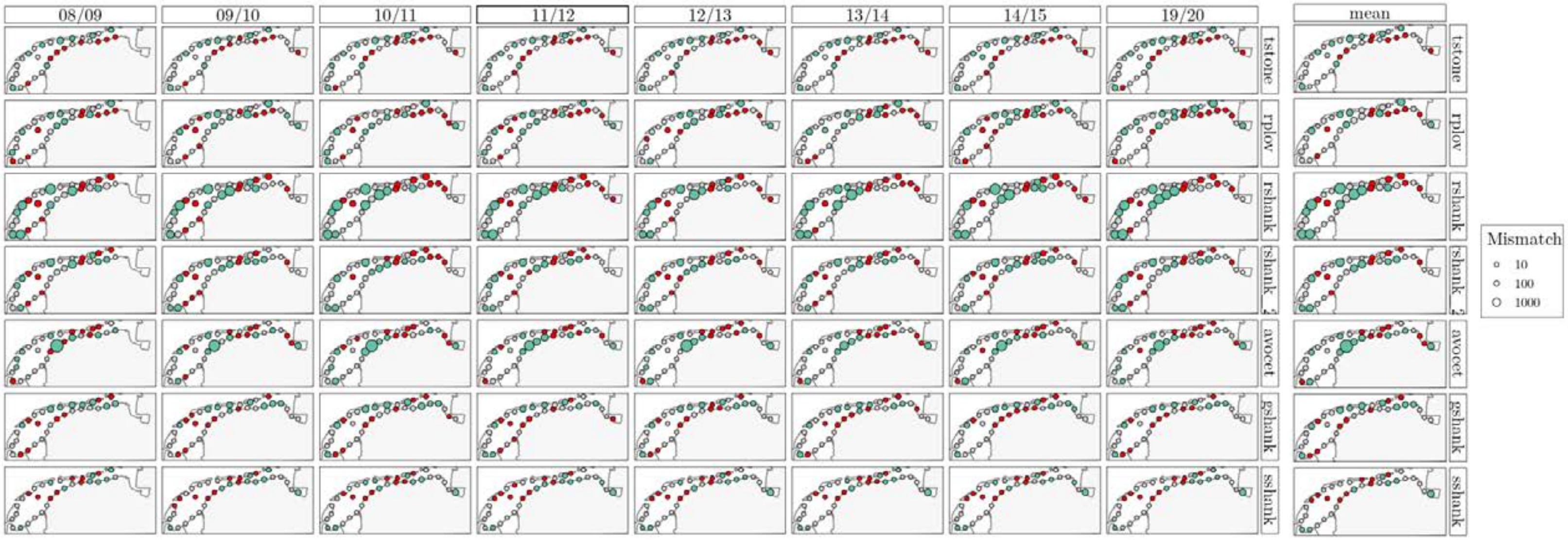


Figure 120: Mismatch between bird numbers and the predicted number of birds on the basis of the overall foraging potential (F). See figure 119 for further details.

C Roosts descriptions / HVP kenmerken

The section below is written in Dutch because the information is mainly relevant for local landmanagers and volunteers.

Beschrijving van hvp-kenmerken (regio's en virtuele hvp's).

C.1 Texel (1-3)

Zuid -1 Op de Razende bol varieert de mate van verstoring. In de winter is de frequentie van verstoring beperkt en als er verstoring plaatsvindt, betreft het een deel van de aanwezig vogels. Voornaamste bron van verstoring zijn dan watersporters. In de zomer en nazomer ligt de frequentie en intensiteit van de verstoring veel hoger door mensen die de plaat op lopen en recreanten met kano's, kleine bootjes en jetski's. Bij zeer hoog tij is de Razende bol soms een alternatieve hvp voor hvp's op Balgzand en Texel met periodiek 10.000en steltlopers. Normaal is de Razende bol vooral in gebruik door Aalscholvers, meeuwen en sterns. Het gebied de Hors wordt weinig als hvp gebruikt, tenzij er zeer hoog water is en vogels bijv. van Balgzand daar heen vliegen. Verstoring in en rond de Mokbaai is tijdens hoog water gemiddeld. Er zijn met enige regelmaat mensen in het gebied. Verstoring tijdens hoog water wordt vooral veroorzaakt door wandelaars (met hond), vogelaars en mountainbikers langs de randen van het gebied. Het Texelpad loopt over de dijk en door de noordrand van kwelder Karhoek. De militaire oefeningen vinden vooral plaats op het terrein van de kazerne en in het centrale deel van het gebied. Oefeningen met helikopters boven het terrein zijn zeer sterk beperkt in vergelijking tot 20 jaar geleden evenals schietoefeningen met zwaardere wapens. Vogels uit dit gebied verplaatsen zich bij verstoring naar andere delen van de Mokbaai. Het traject langs de dijk vanaf het Horntje naar Oude Schild is druk met wandelaars (met hond), fietsers en watersporters. Meeste fietsers blijven op het fietspad, maar wandelaars gaan regelmatig het gesloten gebied in van de Prins Hendrikzanddijk, vaak ook met loslopende honden. Ook zijn er regelmatig kitesurfers die dicht langs het gebied varen. De verstoring is hier geclassificeerd als hoog en de intensiteit van verstoring is middel tot hoog.

C.1.1 Midden-2

Het stuk dijk langs het middendeel van Texel is een populaire fiets- en wandelroute. Alleen Scholekster, Steenlopers en Eidereenden overtijen regelmatig aan de dijkvoet. De dijkvoet is recentelijk wat verbreed waardoor regelmatig iets meer vogels overtijen. De afstand tot fietsers en wandelaars is klein, maar verstoring door fietsers en wandelaars is beperkt. In het gebied rond Zandkes komen veel honden-uitlaters en is de frequentie van verstoring hoog, er zijn bijna altijd wel mensen. Echte HVP's liggen voornamelijk in het gebied Wagejot, ook hier zijn bijna altijd wel mensen in de buurt. De intensiteit van de verstoring is beperkt, vogels worden vooral verstoord als ze dicht bij de rand van de gebieden zitten. Ten noorden van Oudeschild zorgen kitesurfers in dit gebied soms voor verstoring.

C.1.2 Noord-3

Rondom de Vlakte van Kerken is de verstoring beperkt. De Vlakte van Kerken is een belangrijke hvp, bij hoog water zit een groot deel in de kwelder of in het achterland. In het gebied aan de oostkant van de punt van Texel, de westpunt van Vliehors, en bij de Steenplaat zijn regelmatig mensen in het gebied is de verstoring geclassificeerd als gemiddeld door de aanwezigheid van watersporters (kitesurfers, catamarans) en militair oefenterrein.

C.1.3 Texel algemeen

Op het Noordzeestrand is vaak sprake van verstoring. Bijna altijd zijn er wandelaars aanwezig, soms met hond, die er voor zorgen dat vogels opvliegen. Het strand is echter geen belangrijke hvp voor de geselecteerde vogels die in dit rapport worden behandeld. Verstoring van vogels in de polders van Texel is relatief laag. Als er verstoring optreedt, komt dat door agrarische werkzaamheden of jacht. Dit binnendijkse gebied is zo groot dat er bij verstoring alleen verplaatsing optreedt. Maar ook dit gebied is beperkt in gebruik als hvp. Het gebied is vooral uitwijkgebied als reguliere hvp's niet kunnen worden gebruikt door hoge waterstanden of extreme weerscondities. Verstoring door Slechtvalk en andere roofvogels is beperkt en de Vos is niet aanwezig op de eilanden. Op Texel zijn wel veel ratten aanwezig en ook relatief veel (verwilderde) katten, zowel in natuurgebieden als in cultuurgebied. Verruiging van hvp-gebieden is beperkt. Wel is de Kwelder Karhoek deels verruigd en deels veranderd in een zone met Riet. De kwelder dreigt daar te verdrinken waarbij regressie van vegetatie optreedt en verkleining van het areaal kwelder.

C.2 Vlieland (4-5)

C.2.1 West (4)

De Vliehors is militair oefenterrein. Daarnaast rijden er regelmatig auto's over de Vliehors. De frequentie van verstoring is gemiddeld tot hoog, waarbij ook een (groot) deel van de vogels verstoord wordt. Bij zeer hoog water zijn Kroonspolders en Posthuiswad niet in gebruik als hvp.

C.2.2 Oost (5)

Ook hier is het strand druk bezocht met regelmatig wandelaars en auto's. Het dijktraject aan de Waddenzeekant vanaf Lange paal tot aan de Oostpunt van Vlieland kent een hoge mate van verstoring door wandelaars, loslopende honden, vaarrecreanten en (lokaal) surfers. De verstoring is vooral hoog in het hoogseizoen en vakanties. Verstoring op Richel is bij hoog water beperkt doordat het deel van Richel wat bij hoog water nog droog ligt, in gesloten gebied ligt. Verruiging lijkt niet aan de orde op Vlieland. Op Richel zijn slechtvalken aanwezig, maar dit is een groot gebied waardoor niet alles opvliegt bij verstoring door een slechtvalk. Bij zeer hoog water komen de gebieden tussen Lange paal en het dorp in de verdrukking en gaan vogels weg. Richel herbergt juist bij heel hoog water veel vogels, omdat vogels van Griend daar dan heen gaan. Maar bij zeer hoog water (+150 nap), gaan ook hier vogels weg.

C.3 Terschelling (6-8)

C.3.1 West(6)

West-Terschelling is een druk bezocht gebied. Vooral delen van de Noordsvaarder worden veel bezocht door wandelaars (met hond), mountainbikers, vaarrecreanten en watersporters. De frequentie van verstoring is hoog, maar meestel betreft het maar een deel van de vogels. Verstoring door Slechtvalken is beperkt. Verruiging is geen probleem, sommige stukken zijn met heel hoog water niet in gebruik.

C.3.2 Midden(7)

Ook het middendeel van Terschelling kent een relatief hoge verstoring door wandelaars en fietsers langs de dijk en in de polders agrarische werkzaamheden en jacht. Al betreft het vaak maar een deel van de vogels. In de polder treedt lokaal verruiging op door een langer groeiseizoen van de graslanden.

C.3.3 Oost(8)

Het strand van Terschelling wordt regelmatig bezocht door wandelaars en auto's waardoor de mate van verstoring gemiddeld tot hoog is. Er zijn regelmatig tot vaak mensen in dit gebied. De verstoringen door mensen betreffen een (groot) deel van de aanwezige vogels. De verstoring op de Boschplaat is relatief laag. Als er verstoring is, komt dit voornamelijk door wandelaars. Ronde de 4e slenk is er ook verstoring door vaarrecreanten, die daar droogvallen. De oostpunt van de Boschplaat kent wel een relatief hoge mate van verstoring en als er verstoring is tijdens hoogwater heeft dit grote invloed omdat de hvp daar kleiner wordt door het opkomende water. Er is regelmatig verstoring door Slechtvalken. Lokaal kan er sprake zijn van verruiging.

C.4 Ameland (9-10)

C.4.1 West (9)

Verstoring van overtijende vogels op de Blauwe balg is laag in de winter en hoog in de zomer. Gedurende de winter valt het aantal verstoringen mee: af en toe een kitesurfer op of nabij de hvp's. Gedurende de zomer is er een ander beeld. Bootjes varen dan dicht langs de hvp's en af en toe zijn er illegale droogvallers nabij de hvp's. De verstoring is ook sterk afhankelijk van de activiteit. Kitesurfers zorgen voor grote verstoring omdat ze dicht langs de hvp gaan. Vaarrecreanten, rondvaartboten en overige schepen concentreren zich met name aan oostzijde omdat daar de vaargeul langs loopt. Met name in de zomer is dit een drukke route met watersporters, kitesurfers, rondvaartboten, chartervaart, recreatievaart, KNRM (hoge snelheid), peilschepen (hoge snelheid) en illegale robbentochten (reguliere robbentochten zorgen bijna niet voor verstoring omdat die oostelijker blijven). Als er genoeg afstand gehouden wordt tot de hvp, is het effect van de verstoringsbronnen beperkt. Voordeel bij de Blauwe balg is ook dat er een enorm gebied rondom de hvp ook met laagwater gesloten is in het hoogseizoen.

De Vogelpolle is de belangrijkste hoogwatervluchtplaats ten westen van de veerdam van Ameland. De Vogelpolle kent veel verstoring omdat er vaak wandelaars en fietsers in/langs het gebied zijn. Bij hogere vloeden wordt het gebied klein en zijn de vogels gedwongen om vlak bij de dijk te overtijen. Verstoring vanaf de dijk leidt er dan toe dat een groot deel van de vogels het gebied verlaat of komt er niet eens meer naar toe. Met name in de (na)zomer lijken de vogels op deze verstoring te anticiperen en vliegen direct enkele kilometers door, naar de Blauwe Balg, zonder eerst op de kwelder te gaan zitten (Scholekster, Wulp, Rosse Grutto, Kanoetstrandloper, Bonte Stransloper en Zilverplevier). Ook het Groene Strand aan de noordkant van het eiland wordt gebruikt als uitwijkgebied. Bij verhoogde waterstanden komt het voor dat de vogels vliegend moeten overtijen ("een uur rondjes vliegen"). Dat is op zowel Blauwe Balg als Vogelpolle waargenomen. Bij lagere vloeden is de verstoring geringer, maar mensen (met honden) gaan af en toe ook tijdens hoogwater de kwelder op. Sinds de recente dijkverhoging zijn er ook weer verbindingen tussen de dijk en de kwelder aangebracht waarover mensen (met honden) de kwelder en het wad eromheen kunnen bereiken. Daardoor worden ook bij wat lagere vloeden de hoogwatervluchtplaatsen elke dag wel een keer verstoord. Incidenteel wordt gevliegerd op de dijk.

In de polder west is de frequentie van verstoring ook hoog, maar vogels worden daar maar deels verstoord door wandelraars fietsers. Vogels in de polder worden enkele keren per tij verstoord. In de polder midden is weinig tot gemiddeld verstoring. Het fietsen op de dijk maakt het overtijen bij hoogwater overdag hier vrijwel onmogelijk. Dat gebeurde vroeger wel, toen er op de dijk niet gefietst kon worden, maar tegenwoordig dus alleen tijdens nachtelijk hoogwater.

C.4.2 Oost (10)

In de polder oost is de frequentie van verstoring hoog, waarbij een deel van de vogels wordt verstoord. Wandelaars en fietsers in het gebied Nieuwlandsreid-Zoute weide zijn regelmatig tot vaak aanwezig. Fietsers en wandelaars langs de rand van dit gebied (Stuifdijk, Oerd) geven weinig verstoring, maar wandelen en vooral fietsen (mountainbikers) dwars door het gebied vormt een toenemend probleem. Bij verstoring vliegen Wulpen en Tureluurs vanuit dit gebied naar de Hon. Zonder verstoring zouden de aantallen in het gebied naar verwachting hoger zijn.

De oostelijke wadkant van de Hon is de belangrijkste hoogwatervluchtplaats voor de Amelander wadvogels die foerageren ten oosten van de veerdam. Op de Hon is te verstoring laag tot gemiddeld. Bij hoogwater zijn de hoogwatervluchtplaatsen op de oostelijke Hon slecht bereikbaar voor mensen via de wadkant vanwege enkele diepe geulen dwars over het eiland. De meeste wandelaars komen dus vanaf het strand en "ronden het eiland". Bij springtij of verhoging leidt dat wel tot verstoring. Er zijn hier veel minder mensen aanwezig dan bij de Vogelpolle en op de Zoute Weide. Sinds het gesloten natuurgebied is, overtijen Wulpen ook overdag op de Hon.

C.4.3 Ameland algemeen

Tijdens springtij midden op de dag, maar ook bij licht verhoogde waterstanden is er eigenlijk geen goede hoogwatervluchtplaats meer aan de wadkant onder West-Ameland. Vroeger fungeerde het weiland binnendijks als uitwijkgebied, maar ook daar lijkt de verstoring toegenomen. Overtijen op het Groene Strand of op de Blauwe Balg betekent een aanzienlijk aantal extra extra kilometers vliegen. Bij de jachthaven in Nes is de afgelopen 20 jaar een kweldertje ontstaan. Hier kunnen enkele duizenden Scholeksters en (in mei) Rosse grutto's overtijen. Tijdens de recente dijkversterking in 2018 is het kweldertje met opzet vergroot en met een steenrichel beter van het havengebied gescheiden. Desondanks is hier dagelijks verstoring door mensen en honden die het kweldertje betreden. Verder wordt er 's zomers in de buurt van de veerdam gevliegerd. Een paar infopanelen of toegangsbeperking rond hoogwater is wenselijk. Zorgelijk is het toenemend aantal fietsers ("mountain bikers") over de kwelder. Die verplaatsen zich relatief snel en zorgen daardoor voor onevenredig veel verstoring, ook van broedvogels. Het gaat soms om tientallen fietsers op een dag. Veel gaan vanaf de Kooiduinen langs de zuidkant in de richting de Oerdsloot monding, zien dat ze niet verder kunnen en gaan dan terug of naar de stuifdijk ten noorden van het gebied. Dus vooral het gebied westelijk van de oerdsloot wordt ernstig verstoord. Verstoring door Slechtvalken is toegenomen en aantallen zijn relatief hoog bij de Vogelpolle en op de kwelders.

C.5 Engelsmanplaat & Het Rif (11)

De frequentie van de verstoring is hier gemiddeld, maar als er verstoring is, gaan wel alle vogels de lucht in. Wadlopers komen hier met enige regelmatig. Bezoekers van passagiersschepen nam de laatste jaren toe, maar was het afgelopen jaar een stuk lager door de Corona-maatregelen. Belangrijkste verstoringsbron die voor de grootste reactie bij vogels zorgt, zijn wind en kite-surfers die afkomstig zijn van de Friese wal en incidenteel een zeil-motorjacht/kajakker. Hoewel het aantal surfers laag is, zorgen ze er vaak voor dat alle vogels opvliegen en mogelijk zelfs het gebied vermijden als verstoring vaker achter elkaar optreedt.

Op Engelsmanplaat en Rif zit vaak een Slechtvalk. Bij zeer hoog water vliegen vogels van Engelsmanplaat naar de hoger gelegen zandplaat Rif. Het Rif is meer verruigd door jaren heen, maar nog steeds grotendeels geschikt.

C.6 Schiermonnikoog (12-13)

C.6.1 West (12)

In het Westelijke deel van Schiermonnikoog is de frequentie van de verstoring laag tot gemiddeld. Wandelaars en fietsers zijn de voornaamste bron van verstoring. Bij verstoring betreft het een deel van de vogels.

C.6.2 Oost (13)

Ook hier is de frequentie van verstoring laag tot gemiddeld, met name door wandelaars en fietsers. Kanoërs die langs kwelder varen met hoog water zijn verstorend, mogelijk wordt dit een probleem als dit een vaste route wordt en het gebruik toeneemt. De Slechtvalk is in aantal toegenomen, hoge aantallen zitten met name op de Oosterkwelder van de 4e slenk en Balg. Verwilderde huiskatten zijn mogelijk ook een bron van verstoring. Het Noordzeestrand wordt weinig gebruikt als hvp. Bij hoger tij zitten hier wel Kanoeten, Drietenen, Zilverplevieren en Bontbekplevieren. Ze worden dan op het strand regelmatig verstoord, ook omdat ze bij heel hoog water gevoeliger zijn voor verstoring.

Simonszand is enorm veranderd toen een jaar of zes geleden het wantij is doorgebroken. Daarna is het oude Simonszand snel verdwenen en daarmee ook de hvp-functie van dat gebied. Een 'nieuwe' zandplaat die een jaar of dertig terug in de Noordzee voor Simonszand ontstond (Simonsrif) is na een periode voor groei de laatste jaren ook veel kleiner en lager geworden en afgevlakt. Wadlopers en recreatieboten hebben we hier de laatste drie jaar niet tot nauwelijks gezien. Bij vlagen en als er onrust op de Balg van Schier is, willen er nog wel eens een paar duizend steltlopers overtijen, maar het is gebied heeft nu dus veel minder betekenis dan het twee decennia terug had.

C.7 Rottums (14)

Verstoring is gering. Er is af en toe verstoringen door watersporters en vliegtuigjes. Wel is er natuurlijke verstoring door Slechtvalk.

C.8 Noord-Holland (15-16)

C.8.1 Balgzand (15)

De frequentie van de verstoring is laag, maar door geringe grootte heeft een verstoring hier veel impact waardoor soms veel vogels de lucht in gaan. Voornaamste verstoringen komen door het vliegverkeer van De Kooy. De belangrijkste hvp zit op de buitenrand van de schor op de overgang van wad naar begroeing. De schor zelf is vrij ruig. Bij zeer hoog water zitten met name Scholeksters op het dijktalud. De Balgzanddijk is zowel binnen- als buitendijks niet toegankelijk voor recreanten. Vanaf de ‘natuurpunten’ vogelkijkscherm ‘Balgzandpolder’ en natuurinformatiecentrum ’t Kuitje is de Balgzanddijk op afstand te zien.

C.8.2 Stroe (16)

De frequentie van verstoring is hier hoger dan bij Balgzand. Laatste jaren neemt het uitlaten van honden langs de dijk toe. Rondje Vatrop is ook erg populair bij hondenuitlaters, wandelaars en mountainbikers. Bij harde NW-NO wind zijn hier soms illegale kitesurfers aanwezig. De dijk is hier in gebruik door bergeenden, meeuwen, kanoeten en ijslandse grutto’s. Scholeksters gebruiken de verharde dijk aan de oostkant meer. Door het recentelijke weghalen van de hekken bij Normerven-Vatrop is de oostkant nu meer verstoord. En ook de West-Schor bij Den Oever is populair bij hondenuitlaters, recreanten, wadlopers en kitesurfers. Af en toe komen hier ook mensen met drones. Er is een uitkijkpunt en een waddenbelevingspunt. Het is aan te raden hier een bord te plaatsen zodat mensen met hoog water niet de pier aflopen, waardoor de 1e en 2e schor beter functioneren als hvp. Verstoring door Slechtvalken is hier beperkt. Bij zeer hoog water zijn delen hier niet in gebruik.

C.9 Afsluitdijk (17-19)

Er vinden al enige grootschalige werkzaamheden aan de afsluitdijk plaats, waardoor de tellers geen toegang krijgen tot de dijk. Goede recente gegevens ontbreken daardoor. Er liggen nauwelijks goede voedselgebieden in de directe omgeving van de afsluitdijk.

C.10 Friese kust (20-26)

C.10.1 Zurich- Harlingen (ZH-20)

Als hoogwatervluchtplaats biedt het Hegewiersterfjild tijdens hoge vloed een rustplaats aan talloze wadvogels. Vanuit de vogelkijkhut in het gebied zijn de vogels goed te bekijken en is verstoring beperkt.

C.10.2 Harlingen-Westhoek (H-WK 21)

Op het traject langs de dijk direct ten noorden van Harlingen zijn bijna altijd mensen aanwezig, maar verstoring betreft vaak maar een (klein) deel van de vogels. Het gaat met name om verstoring door fietsers en/of wandelaars (met hond) en hengelaars. Het is vooral op vrije dagen druk, doordeweeks is het uitgestorven. Buitendijks is hier geen kwelder en er is weinig ruimte voor hvp's. Binnendijks is de verstoring beperkt, hierbij gaat het vooral om akkerbouwactiviteiten. Het stuk vanaf Koehool naar Westhoek is druk met fietsers en/of wandelaars (met hond) en vooral Westhoek is druk.

C.10.3 Westhoek-Zwarte haan (WK-ZH 22)

De verstoring tussen Westhoek en Zwarte haan is beperkt, binnendijks gaat het voornamelijk om akkerbouwactiviteiten. Op de kwelder bij Zwarte haan zijn wel vaak mensen (fietsers, wandelaars (met hond)) aanwezig en verstoring heeft hier effect op een deel van de vogels. De kwelder is bij heel hoog water (deels) niet in gebruik.

C.10.4 Friesland buitendijks west (FBW-23)

De verstoring op de kwelder is beperkt. Het aantal mensen in het gebied is overwegend laag, alleen in gebied rondom Noarderleech wordt de kwelder vaker bezocht. Dit zijn voornamelijk fietsers en wandelaars (met hond). Dit gebied is ook onderdeel van de aanvliegroute van straaljagers naar de vliegbasis, wat tot verstoring leidt.

C.10.5 Friesland buitendijks oost (FBO-24)

In dit deel zijn regelmatig mensen, maar verstoringen die optreden betreffen een klein deel van de vogels. De kwelder ten oosten van de veerdam bij Holwerd is vooral op vrije dagen druk met wandelaars.

C.10.6 Wierum (25)

Kwelder(tjes) rondom Wierum zijn klein en er zijn vaak mensen in het gebied, waardoor veel vogels opvliegen bij verstoring door fietsers en wandelaars (met hond). Verruiging is niet aan de orde. De kweldertjes zijn niet in gebruik met zeer hoog water. Door het kleine oppervlak kan er ook veel verstoring zijn van Slechtvalken.

C.10.7 Paezumerlannen (26)

Er is hier vaak verstoring, waarbij ook een groot deel van de vogels opvliegen. Het gaat vooral om verstoring door fietsers, wandelaars (met hond), crossmotoren, kitesurfers en windsurfers. Vooral op vrije dagen druk, door de week is het rustiger. Ten noorden van Paesens wordt veel (wad)gelopen. Bepaalde soorten (o.a. Rosse grutto, Wulp) uit dat gebied verplaatsen naar een andere locatie.

C.10.8 Friesland algemeen

Voor alle kwelderstukken geldt eigenlijk dat het gebied te groot is om alle vogels door een Slechtvalk in de lucht te krijgen. Binnendijks beperkt verstoring zich tot landbouwactiviteiten. De gebieden Zwarte Haan, Westhoek, Koehool, Holwerd, Schoor en Moddergat zijn druk, maar vooral op mooie dagen in weekenden en vakanties en daarbuiten is het uitgestorven of rustig.

C.11 Groninger kust (27-29)

C.11.1 West (27)

Bij de Westpolder buitendijks zijn regelmatig mensen aanwezig op het laarzenpad. De kwelder bij Julianapolder is erg diep en daar is bijna geen verstoring. In omliggende binnendijkse gebieden is ook weinig verstoring.

C.11.2 Midden (28)

Ook hier is de verstoring laag. Rondom Noordpolderzijl komen vaker mensen en is de verstoring hoger door fietsers, wandelaars (met hond) en wadlopers. De kwelder ter hoogte van Westernieland, heeft plaatselijke verruiging en is een betrekkelijk hoge kwelder. Globaal kan worden gesteld dat bijna alle binnendijkse telgebieden bestaan uit akkerbouw percelen. De aantallen vogels die hier voorkomen zijn over het algemeen laag. In de Klutenplas bij Den Andel zitten de meest uiteenlopende soorten en bij extreem hoogwater (als de kwelders zijn overstroomd), puilt de Klutenplas uit van de vogels. Verstoring treedt regelmatig op als voorbijkomende fietsers stoppen om te kijken. In de afgelopen zomers is de Klutenplas bijna compleet drooggevallen en dan zit er bijna niks.

C.11.3 Oost (29)

Langs het oostelijk deel van de Groninger kwelders is de verstoring laag. Soms zijn er wandelaars (met hond), fietsers en boeren (met quad).

C.12 Eems-Dollard

C.12.1 Eemshaven (30)

In de haven zelf is altijd wel activiteit, maar de vogels zitten hier voornamelijk onderaan de dijken en trekken zich hier weinig van aan. Op het strandje bij de Eemshaven zitten vaak wel wat vogels, die bij verstoring op strekdammen gaan zitten. Soms varen vissersschepen kort langs de dijk, vogels gaan dan verderop zitten. Verstoring in de Eemshaven is beperkt, maar ook de waarde als hvp is beperkt.

C.12.2 Watum - Delfzijl (31&32)

Het stuk dijk ten zuiden van de Eemshaven wordt vaker verstoord. Vooral met mooi weer komen hier enkele wandelaars, fietsers of brommers langs. Vogels lijken dan allemaal op het broedeiland te gaan zitten wat recent is aangelegd. Langs de dijk komen vossen, maar die zitten niet op het recent aangelegde eiland.

C.12.3 Dollard (33)

De verstoring is gemiddeld tot hoog, er zijn altijd wel andere mensen aanwezig. Die blijven echter vrijwel altijd bij de dijk omdat de toegang van de kwelders grotendeels verboden is. Hierdoor gaan mensen ook op plekken waar dat niet verboden is, niet de kwelder op. Bij de Duitse grens, aan de oostkant van de Dollard bij de vogelkijkhut, komen relatief veel mensen, maar daar zijn geen hvp's (vanwege de hoge rietvegatie). Ook bij de Punt van Reide, aan de Westkant van de Dollard komen relatief veel mensen. Hvp's van steltlopers liggen hier in het algemeen ver van de dijk en worden daardoor niet niet vaak verstoord door mensen. De menselijke verstoringsbronnen betreffen vooral wandelaars en fietsers. De verstoring door Slechtvalken is matig tot groot, de vogels vliegen even op, maar gaan snel weer zitten. Het effect van verstoring door zeearenden lijkt veel groter. Dan kunnen met name eenden en ganzen bepaalde dagen minder aanwezig zijn in het hele telgebied dan verwacht. De waterhoogte heeft tot gevolg dat de hvp's verder naar het westen verschuiven, omdat daar meer buitendijkse hogergelegen kwelders zijn. Bij zeer hoog water (> 200 cm boven NAP) overtijen veel vogels in het binnenland.

C.13 Griend (34)

Op Griend is weinig verstoring. Naast onderzoekers en vogelwachters zijn er geen andere mensen op Griend. De meeste verstoring komt van vliegverkeer (helikopters en straaljagers). Op Griend is regelmatig een Slechtvalk aanwezig, maar het gebied is groot en bij aanwezigheid van een Slechtvalk vliegt niet overal alles weg. De omvang van de verstoring door een Slechtvalk is sterk afhankelijk van de waterhoogte en de mate van concentratie van de vogels. Het gevolg is vaak dat Kanoeten, Bonte strandlopers, Rosse grutto's en Wulpen naar de Richel vliegen. Op Griend is deels sprake van verruiging en dat kan een probleem vormen. Bij hoge waterstanden boven de + 100-110 nap komt het water tot aan de vegetatie. Hierdoor vliegen op dat moment veel vogels naar Richel. Dit geldt vooral voor Kanoet, Bonte strandloper en Rosse Grutto. Het afvlakken van de Noorddijk in 2016 lijkt voor sommige vogels positief, maar moet verder uitgezocht worden.