Spatial and Temporal Wader Distribution Related to the environment on an Intertidal Shoal in the Oosterschelde

By

D.H.J. Dekker

July, 2020

Utrecht University

WAGENINGEN
UNIVERSITY & RESEARCH

Spatial and Temporal Wader Distribution Related to the Environment on an Intertidal Shoal in the Oosterschelde

Master Thesis

In Partial Fulfilment of the Requirements for the Degree of
Master of Science

in

MSc Marine Sciences
at the Faculty of Geosciences of Utrecht University,
the Netherlands

at

Wageningen Marine Research,
Yerseke, the Netherlands

Submitted by

D.H.J. (Dennis) Dekker

Supervised by

Prof. Dr. Katja Philippart, Utrecht University and NIOZ
and
Dr. Brenda Walles, Wageningen Marine Research

from Zierikzee, the Netherlands

July, 2020

Abstract

Intertidal areas in the Oosterschelde estuary decreases due to a disturbed sediment-balance caused by construction of a storm surge barrier and two compartmentalization dams. The intertidal area provide valuable foraging ground for the benthivore wader populations of the East-Atlantic Flyway. In 2019 seven nourishments were constructed at the Roggenplaat intertidal shoal to mitigate loss of foraging area and preserving wader populations. We study abundance of waders at the Roggenplaat prior to nourishment construction in a spatial and temporal manner and its relation with environmental factors to be able understand natural distribution of the waders and to evaluate the selected nourishment locations regarding interference with natural wader distribution. Relation between wader abundance and environmental factors like exposure time, food availability, and sediment composition increases understanding of the impact of drivers behind natural patterns in wader abundance.

This study uses intertidal shoal covering bird counts that are obtained by counting from a boat that makes three two-hour tours (period 1, 2 and 3) around the Roggenplaat on 25 counting days. Bird counts were executed from one hour after high tide up to one hour after low tide. All waders that are protected by Nature2000 regulations for the Oosterschelde are studied. Environmental data of the Roggenplaat were obtained by combining tide gauge and LIDAR measurements for exposure time and collecting field samples at 113 stations for benthic infauna abundance and sediment composition. Spatial hotspot maps of foraging wader density were created for each period to find most important foraging ground of each species. Hotspots of foraging behavior were related to spatial differences in environmental conditions by comparing mapped data.

The results show that significant temporal differences are present within a tidal cycle since less birds are counted from one hour after high tide up to three hours before low tide (period 1) than from three hours before low tide up to one hour after low tide (period 2 and 3). Spatial density hotspots and the periodic movement over the intertidal shoal of each species are divergent. Moreover, environmental factors show different relations with each species. Significant higher densities in areas with short exposure time are found for Dunlin, Bar-tailed godwit, Grey Plover, Sanderling and Common Redshank during low tide. Furthermore, there is an overlap between Oystercatcher, Red Knot, and Sanderling distribution and peak biomass or density of their preferred prey, which was not observed for the remaining wader species. Also sediment composition distribution shows a relation with wader hotspots since Sanderling mainly forage in area with larger d50 sediment grain size, while other species generally ignore this area and use foraging ground with smaller d50 sediment grain size and higher mud fraction.

Wader behavior differs in a temporal manner since tidal dynamics prevent waders from foraging in low lying intertidal area during ebbing tide. The remaining differences in spatial distribution of wader species are primarily caused by the relation of each species with environmental factors. No obvious relation between benthic infauna biomass or density peaks and wader density has been found for several species. Their distribution is however affected by food availability in another way. Tide-following behavior increases prey accessibility, which has been observed for Dunlin, Sanderling and Common Redshank. Distribution of Bar-tailed godwit and Grey Plover shows a relation with polychaeta dominated area despite low total biomass. This indicates the relation between wader distribution and benthic infauna goes further than a direct relation with peak density and biomass.

Considerable parts of the nourishments at the Roggenplaat overlay valuable foraging ground of most of the studied wader species, which changes the local environmental conditions. It is therefore recommended that selection criteria for suitable nourishment locations should include avoidance of foraging wader hotspots in the future. The impact of these nourishments on the value of foraging ground for wader populations can be defined by studying spatial wader abundance at the Roggenplaat also for the modified situation after construction of nourishments. The outcome should be compared to the natural wader distribution as perceived by our study to identify changes in behavior. Understanding of wader distribution in a spatial and temporal manner and incorporate this knowledge in future nourishment design approach will increase success of human interventions to preserve the deteriorating intertidal area and its valuable foraging ground.

Contents

1. Introduction

Millions of water birds migrate in an annual cycle between stopover-sites along the eastern shore of the Atlantic ocean. This network of sites is named the East Atlantic Flyway and stretches from the Arctic to Southern Africa. Different stations are used for resting, breeding and wintering purposes. The estimated total flyway population however decreased over the last decades. Especially, benthivore wader populations (*Charadriiformes*) show a significant decline, while species with another diet remain stable or even increase in numbers (van Roomen et al., 2017). During low tide waders use exposed intertidal area to feed, while they move to permanently exposed high water residences to rest during high tide (Pitelka, 1979). As intertidal mud and sand flats are rich of benthic species they provide valuable foraging ground for waders. Sea level rise, modified infrastructure, and change in sediment transport by large structures results in a decrease or even disappearance of these valuable intertidal foraging grounds (Galbraith et al., 2002; van Zanten & Adriaanse, 2008). As most waders are specialized foragers that require minimum refueling rates during their stopover before migrating over long distance, decline of the wader population over the last decades strongly depends on the deterioration and decrease of foraging grounds (Baker et al., 2004; Schellekens et al., 2013; Studds et al., 2017). The Wadden Sea and southwestern Delta are two essential wintering and resting sites along the East Atlantic Flyway in the Netherlands (Figure 1). The Oosterschelde (Nature2000 area) is one of the most important foraging sites in the southwestern Delta (Arts et al., 2019). Waders visit the Oosterschelde in autumn and spring as stopover, but it is also used as wintering site by many individuals (Troost & Ysebaert, 2011).
Forty years ago, annual peak numbers of estuarine shorebirds in the Oosterschelde were counted in January and reached 190.000 individuals on average. Population size however started to decline after suitable foraging area decreased (Schekkerman et al., 1994). Intertidal shoals in the Oosterschelde are eroding at a mean net erosion rate of 1 cm per year as a result of the construction of a storm surge barrier and compartmentalization dams (Santinelli & de Ronde, 2012). The construction of the storm surge barrier was completed in 1986 and induced a reduction of tidal range by narrowing the inlet between the North sea and Oosterschelde. Moreover, two upstream compartmentalization dams that were built in approximately the same period blocked all fluvial influences of the Scheldt river, so only a tidal embayment remained. Reduced tidal flow decreases sediment transport to the intertidal zone, while storm events still cause erosion (Mulder & Louters, 1994). The disturbed sediment balance resulted in a gradual erosion process named ‘Sand Starvation’. This process causes a reduction in exposure time due to lowering of the intertidal area heights and a decline in total surface of suitable foraging habitat (Hesselink et al., 2003).

The Roggenplaat is among the largest intertidal shoals in the Oosterschelde and provides important foraging ground for waders. Waders mainly forage in areas that emerge <80% of the time (Zwarts et al., 2011). At the Roggenplaat the areas with 40 to 80% exposure time (~1000ha) are expected to decrease by 80% between 2010-2060 (de Ronde et al., 2013). Areas that emerge <40% of the time are expected to be less affected due to sediment input from the higher located erosive intertidal areas. This has a large impact on the foraging ground of waders. Nature2000 management objectives for the Oosterschelde prescribe conservation of the habitat of bird populations that are affected by Sand Starvation (Rijkswaterstaat, 2016).To mitigate loss of the area with a 40 to 80% emersion time sand nourishments were constructed at the Roggenplaat in the autumn of 2019. These nourishments are expected to preserve the foraging ground by compensating for 25 years of erosion (van der Werf et al., 2019). To determine if the nourishments on the Roggenplaat actually improve foraging grounds as intended a long-term monitoring program is executed in which spatial and temporal use of the Roggenplaat by bird populations was monitored four years prior to the construction of the nourishments and will be monitored for several years after the construction (Ysebaert et al., 2016).

Macrobenthic resources are well-studied as key explanator of spatial wader distribution, but sediment composition and exposure time also influence spatial patterns (Fretwell, 1969; Nehls & Tiedemann, 1993; Granadeiro et al., 2006; VanDusen et al., 2012; Ponsero et al., 2016). All these factors are artificially modified when new foraging areas with sufficient exposure time are constructed by means of a nourishment (Baptist et al, 2009). Most benthic live is killed after addition of a thick sediment layer on top of the intertidal shoal, which causes little to no benthic live just after construction of a nourishment (Speybroeck et al., 2006). It can take several years before benthic communities recolonize the nourished areas transforming it into a rich foraging ground again and there might even be different benthic communities than before (van der Werf et al., 2015; Boersema et al., 2018). Impact of a nourishment on the foraging ground for waders and the use of this foraging ground by waders is not well-studied. Strategic placement of nourishments to improve foraging areas is therefore a complicated process with large uncertainty. In order to perform an impact assessment, insight is needed in how birds spatial and temporal used the foraging area prior to the nourishments. Birds are generally counted in plots that only cover small parts of a large intertidal shoal (Ysebaert & Troost, 2011; Zwarts et al., 2011). This method was used for bird counting on a pilot-nourishment at the Galgeplaat (van der Werf et al., 2015). The plot-counting method provides an overview of the amount of birds on a specific location of the intertidal shoal, but gives no indication of bird presence in the disregarded area. This method is not sufficient to obtain insight in the spatial distribution of birds on the intertidal shoal. In this study we investigate spatial distribution patterns of waders by bird counting's covering a complete intertidal shoal. This is the first study looking at the spatial distribution of waders over an entire intertidal shoal in the Oosterschelde. Holistic monitoring of bird distribution on an intertidal shoal is required to be able to identify spatial patterns. Initially, understanding natural spatial patterns in wader distribution is necessary to determine where waders are exhibiting their foraging activities. The relationship between natural spatial wader distribution and location specific environmental factors like food availability, exposure time, and sediment characteristics is essential to understand the importance of these factors for foraging waders. It is also relevant to analyze whether patterns in foraging activities are constant in a temporal manner.

This study focus on spatial and temporal patterns in wader distribution at the Roggenplaat. Continuous holistic bird counts during low tide were done to determine spatial use of the intertidal shoal by waders. This data was used to investigate (1) how waders spatially and temporal used the Roggenplaat as foraging and resting area, (2) how wader distribution relates to exposure time, (3) food availability and (4) sediment composition. Relation between potential driving factors (exposure time, food availability and sediment composition) and wader distribution were analyzed by comparing mapped data.
The observed spatial and temporal patterns in bird distribution can be used as reference scenario for a future impact assessment. Effect of the constructed nourishments on bird distribution will be assessed in a future study by comparing results of this study to bird counts obtained after construction of the nourishments. Relations between wader distribution and environmental factors can help explain differences between the distribution before and after nourishment. Understanding key drivers behind spatial distribution of waders can help coastal managers to strategic design future nourishments aimed at improving foraging grounds for waders. In the next decades improvement of intertidal foraging areas will be more frequently needed as deterioration of habitat continues.

2. Methods

2.1 Study area

The Oosterschelde estuary is a 251 km^2 semidiurnal tidal basin located in the southwest of the Netherlands (Figure 1). The basin is separated from the Scheldt river by two compartmentalization dams and from the North sea by a storm surge barrier (constructed in 1986). Mean tidal amplitude is 2.47m near the storm surge barrier to 2.98m in the northeastern part and 3.39m in the southern end (Nienhuis & Smaal, 1994). The Roggenplaat is an intertidal shoal located in the western part of the Oosterschelde (Figure 1). During neap low tide a total surface of 15,2 km^2 emerges. The Roggenplaat is a bare intertidal shoal, but natural established dense Pacific oyster reefs cover 62 hectares (van den Ende et al., 2020). Human activities are only allowed in a small area at the eastern side of the Roggenplaat. The exposed shoal is intensively used by waders as foraging area. Most of the shoal is submerged during high tides, which induces tide-dependent availability of foraging grounds. Mean net erosion rates of 10mm per year caused a strong reduction of foraging area with 40-80% exposure time (Santinelli & de Ronde, 2012). Construction of 7 sand nourishments that compensate for the expected erosion between 2010-2035 to preserve foraging ground started in October 2019 and was finished at the end of December 2019 (van der Werf et al., 2019).

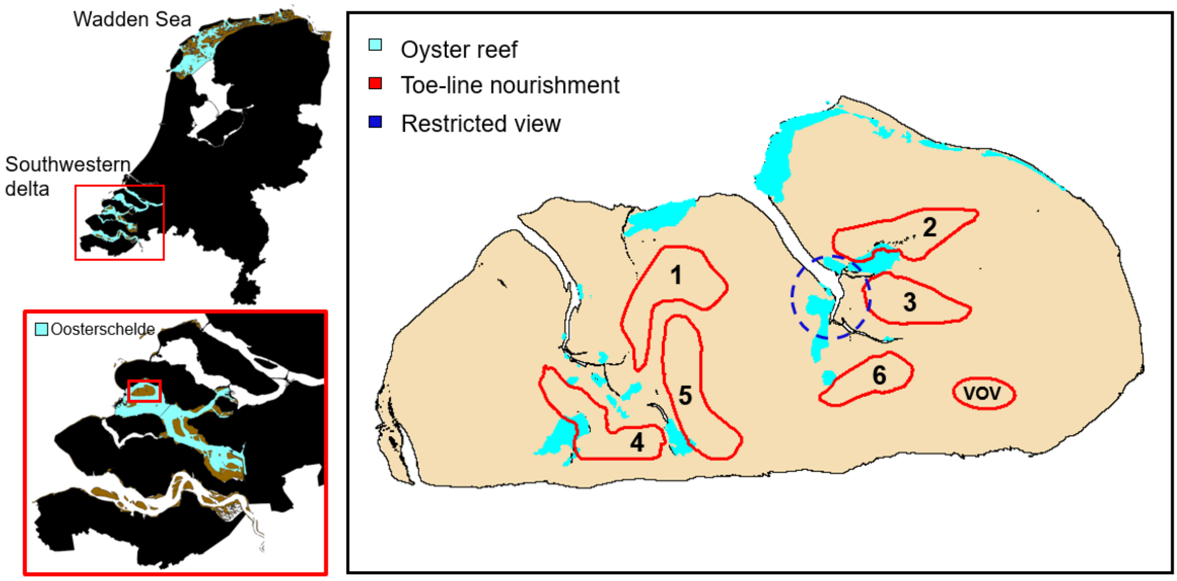


Figure 1: Overview of the Netherlands (upper left) and southwestern delta with the Roggenplaat (bottom left). Intertidal area is shown in brown. Top view of the Roggenplaat (right) includes shellfish reefs (mixed reef, but mainly Crassostrea gigas) of 2019 (van den Ende et al., 2020) and nourishment locations. Boundaries of the Roggenplaat are represented by the low water line of 2019. The blue dotted circle indicate the location which was difficult to view from the boat.

2.2 Bird counting

To investigate how birds use the intertidal shoal as foraging habitat, birds were counted on the Roggenplaat during low tide for a period of 4 years before the planned nourishments were executed. Birds were identified, counted, and foraging or resting behavior identified during low tide from a boat. The boat started at the middle of the southern side of the Roggenplaat and moved in counter-clockwise direction around the intertidal shoal (Figure 2). One round took exactly two hours. Three tours were done on every counting-day, hereafter also referred to as Period 1, 2 and 3, with the first tour starting one hour after high tide (Figure 3). Most species visiting the Roggenplaat are migratory species. To count these migratory birds, counts took place during daylight at monthly intervals between October and February. Other months were monitored with lower frequency (Table 1). Counting only took place when predicted wind force did not exceed 7 Beaufort. Counts were executed both during dry and rainy days.

Two experienced counters were positioned on a high location of the boat that provides them an overview of at least half of the intertidal shoal. This ensures that the entire Roggenplaat surface could be counted during one completed tour. Only birds at the center of the flat near the middle gully could not be determined accurately due to a restricted view (Figure 1). To count and identify the birds Swarovski BTX 35x95 telescopes on sturdy tripods and tally counters were used. To investigate the spatial distribution of the birds on the intertidal shoal, polygons were drawn on a map during the counts indicating where the birds were approximately located. For each tour a new map with polygons was made. Polygon size and location was determined by uninterrupted emerged surface, bird presence, and type of habitat. Counters determined bird species, amount of individuals, and their behavior at the moment of passing by and noted this on prepared forms. Foraging and resting were distinct as different types of behavior. Bird distribution within a polygon is not taken into account. Bird migration between different parts of the Roggenplaat during one counting tour possibly causes inaccuracy of the cumulative amount of individuals of the total population. However, migration of large numbers of individuals within a counting tour was barely observed (Deltamilieu Projecten, personal communication, February 18, 2020). As birds were counted during three two-hour tours insight in the spatial migration of the birds on the Roggenplaat was obtained between one hour after high water and one hour after low water. By identifying bird behavior, differences in use over time could be studied. Counters divided tasks of counting individuals of different species to manage the count of individuals accurately within the timeframe of passing. Birds arriving shortly after counting were not included. A maximum error-margin of 10% is expected for the estimated amount of individuals (Deltamilieu Projecten, personal communication, July 6, 2020). Uncertainty increases with larger amounts of individuals, while extent of the error also differs between species. No disturbed behavior of birds that was caused by the boat itself has been observed. However, circumstances that potentially could influence behavior of birds on the Roggenplaat, such as presence of predators or humans, were mentioned in daily reports.

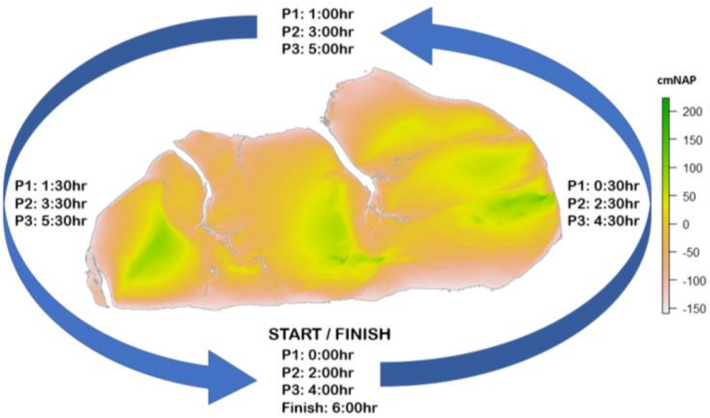


Figure 2: Counting cycles (arrows) at the Roggenplaat. Elapsed time after start of a counting day is shown for passing specific locations during Period 1 (P1), Period 2 (P2), and Period 3 (P3). Background: a digital elevation map in cmNAP of the Roggenplaat.

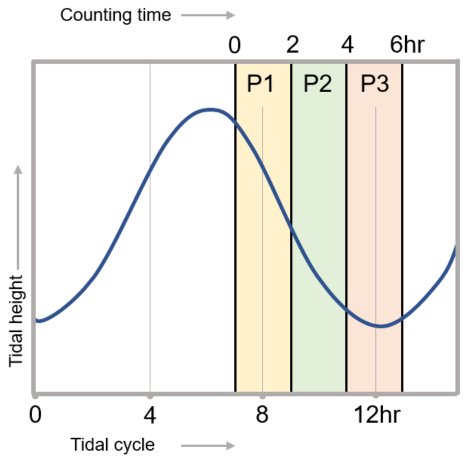


Figure 3: Time range of Period 1 (P1), Period 2 (P2), and Period 3 (P3) of a counting day in a tidal cycle.

Table 1: All 25 bird counting days, including time of measured highwater level (HW), start of each counting tour (Period 1, 2 and 3), weather conditions and human disturbance.

#	Date	HW	P1	P2	P3	Weather	°C	Wind	Note
1	19 / 11 / 2015	8.10	9.00	11.00	13.00	Drizzly	10	WSW 7	
2	18 / 12 / 2015	7.50	8.45	10.45	12.45	Dry	12	SW3 4	
3	16 / 01 / 2016	7.50	8.35	10.30	12.30	Rain / Hail	5	NW 6	
4	01 / 02 / 2016	8.00	9.00	11.00	13.00	Dry	10	WSW 6	
5	12 / 05 / 2016	7.25	8.50	10.50	12.50	Dry	18	ENE 3-4	
6	09 / 08 / 2016	7.30	8.30	10.30	12.25	Dry / P2: Rain	20	NW 3-4	
7	03 / 03 / 2017	6.30	7.55	9.25	11.25	Dry / P2: Rain	10	SSW 4	
8	31 / 03 / 2017	5.40	8.15	9.45	11.40	Dry	14	S 1 / SW 4	
9	03 / 05 / 2017	8.50	10.30	12.20	14.20	Rain	10	ENE 3-4	

10	28 / 08 / 2017	7.25	9.25	11.25	13.25	Dry	25	NNE 0-1	
11	26 / 10 / 2017	7.00	8.45	10.45	12.45	Drizzly	13	WSW 3	Disturbance P2/P3
12	28 / 11 / 2017	9.30	11.50	13.20	15.00	Dry	5-10	NW 4	
13	28 / 12 / 2017	10.00	10.45	12.45	14.45	Dry	5	NW 4-5	
14	10 / 01 / 2018	9.30	10.05	12.05	14.05	Dry	5-7	SW 3	
15	07 / 02 / 2018	8.00	9.00	11.00	13.00	Dry	5	NE 3	
16	09 / 03 / 2018	8.00	9.20	11.20	13.00	Dry	3-9	SSW 2-3	
17	09 / 05 / 2018	9.50	11.35	13.35	15.35	Dry	11-18	NW 3-4	Disturbance P1
18	16 / 08 / 2018	7.00	8.55	10.55	12.55	Dry	21	SW 3-4	
19	01 / 10 / 2018	7.10	9.00	11.00	13.00	Drizzly	7-12	NW 6-7	
20	02 / 11 / 2018	10.00	11.00	13.00	15.00	Dry	10	WNW 3	
21	14 / 12 / 2018	7.20	8.45	10.15	12.05	Dry	0-4	E 3-4	
22	14 / 01 / 2019	8.00	9.05	11.00	12.55	Drizzly	5-7	NW 5	
23	13 / 02 / 2019	8.30	9.20	11.20	13.20	Dry	6	SW 2-3	
24	23 / 05 / 2019	6.20	8.15	10.00	12.00	Dry	12-18	SW 2-3	
25	06 / 08 / 2019	7.20	9.10	11.10	13.10	Dry	17-21	SW 5 / W 4	

2.3 Environmental factors

Data of environmental conditions at the Roggenplaat were collected so it could be compared with bird distribution. Three types of conditions were taken into account: exposure time, food availability and sediment composition.

2.3.1 Exposure time

Exposure time is an important factor since the emersion of the Roggenplaat occurs gradually during ebb tide. Not all area of the intertidal shoal are therefore available for foraging at the same moment in time. Studies showed that time-dependent emersion of intertidal area has an effect on movement of foraging birds (Granadeiro et al., 2006). Bird presence in different exposure time zones are studied to determine if there are exposure time effects on bird distribution at the Roggenplaat. Tide gauge data of *Rijkswaterstaat* at location 'Roompot Binnen' (2014) were used as representative water level for the western part of the Oosterschelde. For every 1 cm bin within the measured water level range it was determined how many other water level measurements were equal to or smaller than the level of a particular bin throughout the whole year. Thereafter, exposure time was derived as a percentage of time by dividing the number of water level samples that were equal to or smaller than a particular water level-bin by the total number of water level samples. The outcome provides percentage of water level measurements that were larger than the chosen bin. This percentage is also representative for the percentage of time that the area that is positioned above this water level-bin is emerged because of the regular recurrence of tide gauge measurements. Bed level height of the Roggenplaat was obtained from LIDAR (2019) measurements. LIDAR determined distances between a small airplane and the surface by sending laser pulsus and measuring laser return times. Water level height with corresponding exposure times could be compared directly to bed level height of the Roggenplaat to determine to which exposure time zone an area belongs.

2.3.2 Benthic infauna

Benthic infauna are the main food source for the investigated Nature2000 target species. Individual bird species however can be foraging on different types of benthos. Therefore, spread in benthos species and density could be an important factor in explaining bird abundance (Nehls & Tiedemann, 1993; Leopold et al., 2004; VanDusen et al., 2012). Quantitative data of the macrobenthic infauna communities was used to create maps that could be compared to wader distribution. This data was collected by triploid sampling with a 10 cm i.c. corer that reached up to 35cm depth at 113 stations on the Roggenplaat (autumn 2015 and 2019) (Figure 4). Every sample was sieved through a 1mm mesh sieve where after the residue was preserved in 4% buffered formaldehyde solution. Moreover, *Arenicola marina* densities were counted in-situ using quadrants of 0.25m^2. Determination of preserved species was done in the laboratory. Yielded numbers of individuals were used to calculate density (ind. per m^2). Thereafter, biomass was determined in ash free dry weight (g AFDW per m^2) using species specific wet weight to AFDW conversion rates as prescribed by Craeymeersch &

Escaravage (2014). Additionally, annual inventory of cockles in the Oosterschelde takes place by order of the Dutch Ministry of LNV (WOT-cockle survey 1990-2019). Troost et al. (2019) describes monitoring method for this database. Sediment samples that cover a surface of 0.1 m^2 and reach up to 7 cm depth are sieved by 5mm mesh at monitoring locations that are representative for 26.67ha intertidal area each. Thereafter, all fish, crustacea and polychaeta were removed. Cockles were grouped by age classes based on growth rings (van Asch et al., 2019).

2.3.3 Sediment composition

Sediment composition is known for its indirect-effect on shorebirds by influencing macrobenthic infauna communities. However, studies suggest there is also a direct effect of sediment characteristics on shorebird distribution (VanDusen et al., 2012). Sediment composition is therefore taken into account while studying explanatory factors of patterns in bird distribution. Measurements were done at the same 113 locations and on the same days as macrobenthic infauna sampling in autumn 2015 and 2019 (Figure 4). The top 3 cm sediment layer was sampled by a syringe with 1.4 cm sampling diameter. Particle sizes were determined by laser diffraction (Malvern Mastersizer 2000) after storing the samples three days at -20°C and freeze drying for four days. The analysis derived the d50 median grain size (µm) and sediment size distribution (percentage coarse, medium, fine sand, very fine sand, and silt).

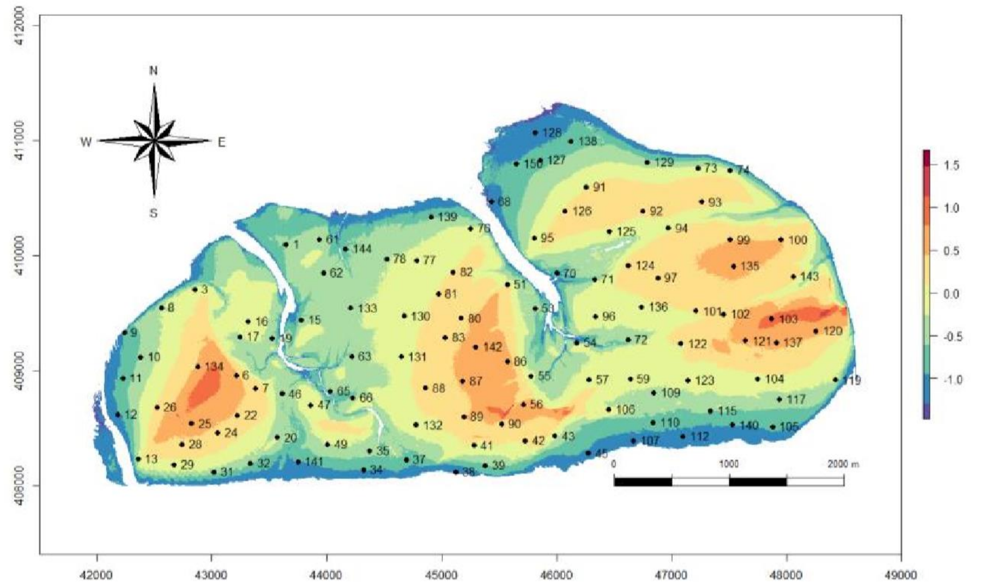


Figure 4: Map with 113 sample locations for benthic infauna and sediment grain size at the Roggenplaat in autumn 2015 and 2019. Background: digital elevation map with bed level height in mNAP (figure derived from Walles et al., 2019).

2.4 Data analysis

Bird counts were analyzed to identify patterns in temporal and spatial distribution of different bird species during low tide and how this relates to environmental factors. Only bird counts from before construction of the nourishment were used as we focus within this study on the natural distribution patterns on the Roggenplaat. Initially, all birds present each counting day were included to gain insight in the amount of birds that make use of the Roggenplaat and which behavior they express. Shorebirds classified as bottleneck species by Nature2000 management objectives for intertidal habitat of the Oosterschelde were selected for further analysis of their low-tide foraging behavior (Rijkswaterstaat, 2016). These species were selected since nourishments are primarily constructed to maintain foraging grounds for preservation of their populations. All these Nature2000 bottleneck species in intertidal habitat rely on benthic communities as main food source. Based on data from the benthos survey we studied the relation between bird distribution and food availability by looking at bird species specific patterns in distribution in relation to availability of its preferred prey species. To look at temporal differences in dispersions within a tide the three counting tours (period 1, 2, and 3) were analyzed separately. Seasonality was only investigated in relation to the total number of birds visiting the Roggenplaat, but not in relation to distribution patterns on the intertidal shoal. Four different seasons can be distinguished in which birds show different types of behavior: summer (June-July, n = 0; breeding season), autumn (Aug-Nov, n = 9; migration), winter (Dec-Feb, n = 9; wintering), spring (Mar-May, n = 7; migration). Spatial distribution was based on the number of birds present in the polygons which were identified in the field during bird counting. All selected birds were studied individually to be able to identify differences between species.

Data analysis was done using R software (R Core Team, 2019). Comparison of means were executed for the number of birds for the different periods, species, and behavior. Differences in population composition was investigated by looking at species richness at different periods and seasons. Spatial distribution per bird species was visualized by making heat maps of the averaged daily amount of birds per hectare of the Roggenplaat. A grid, with grid-cells of 2 by 2 m, covering the whole Roggenplaat was created. For each polygon, identified in the field, the total number of observed birds were divided over the grid-cells within the polygon to obtain per grid-cell a number of birds per 4 m^2. This was done for all counting days (n=25) after which the average bird densities per grid-cell was calculated. This method was applied for each period, species, and behavior. A heat map with bird density distribution was obtained using these calculated average bird densities per grid-cell. These maps show averaged daily density of birds at different locations of the Roggenplaat at a particular moment during low tide and for different behaviors. To identify which areas are used most by the birds a hotspot map was created. An independent hotspot-selection was done for each species per period. To select grid-cells with the highest daily bird presence we looked at the number of counting days in which at least one bird has been counted. First all cells that had less than 50% of the maximum number of day that a specific bird species was counted, on the whole Roggenplaat, were removed. The remaining cells exceeding the 2-quantile (median) of the maximum bird density were used to create hotspot maps. The obtained map shows for foraging or resting birds, per species and period its hotspot.

Bird hotspot maps were combined with exposure time, benthic infauna and sediment composition to identify corresponding patterns between bird distribution and environmental factors. Density of individual birds per exposure time zone were determined for each period to study bird movement during ebb tide. Sample point-based visualization was done for benthic infauna and sediment grain size distribution. Diet of investigated Nature2000 species was derived from literature. Every species main prey were grouped per individual bird species to investigate the relation between food availability and bird distribution. Moreover, dominant type of prey (Polychaeta or Bivalvia) was determined for each sample point to study if spatial difference in dominant prey type has an effect on spatial bird densities.

2.5 Statistics

Statistical tests accompany visual data analysis to confirm whether observed variation can be accepted as significant deviation. To check if the number of individual birds or number of species were normally distributed a *Shapiro-Wilk test* was executed (Shapiro & Wilk, 1965).
Species richness was normally distributed. To test which period has highest species richness a *one-way ANOVA* was used followed by a post-hoc *Tukey's range test* if a significant difference has been perceived (Tukey, 1949). Number of individual birds were not normally distributed. For not normally distributed data nonparametric tests were executed to test periodic difference in number of individual birds, expressed behavior and bird densities in exposure time zones. Nonparametric tests like the *Kruskal-Wallis test by ranks* followed by a *Mann-Whitney U test* in case of significant differences perceived by the Kruskal-Wallis test were used (Mann & Whitney, 1947). False discovery rate of the Mann-Whitney U test was controlled using the Benjamin & Hochberg (1995) method.

3. Results

3.1 Temporal abundance of shorebirds

3.1.1 Population dynamics

A total of 67 unique bird species were counted, of which 40 species were observed ten times or more (Table 2). An overview of all unique species is shown in Appendix 1. The Dunlin, Bar-tailed godwit, Oystercatcher, Eurasian Curlew, Grey Plover, Red Knot, and Sanderling are present in large numbers and observed at all counting days (n = 25). These species are classified as Nature2000 bottleneck species. The Common Shelduck, Common Redshank, Common Ringed Plover, Ruddy Turnstone, Common Greenshank, and Spotted Redshank are less frequently observed Nature2000 bottleneck species.

Table 2: All bird species with at least 10 individuals counted over all 25 counting days combined. Number of individuals counted shows the largest periodic number of birds of each day summed for all counting days. Daily mean shows the daily average of the maximum periodic number of individuals counted on each counting day. Nature2000 bottleneck yes/no indicates whether a species is classified as a bottleneck species for intertidal area in the Oosterschelde.

Common name	**Taxa**	**Individuals counted**	**Daily mean**	**Range daily numbers**		**Nature2000 bottleneck**
				Min	**Max**	
Dunlin	*Calidris alpina*	120949	4838	100	12341	Yes
Bar-tailed Godwit	*Limosa lapponica*	67245	2690	510	5417	Yes
Oystercatcher	*Haematopus ostralegus*	67209	2688	426	5811	Yes
Eurasian Curlew	*Numenius arquata*	48887	1995	114	5216	Yes
Grey Plover	*Pluvialis squatarola*	44679	1787	26	3309	Yes
Black-headed Gull	*Larus ridibundus*	33451	1338	0	8668	No
Red Knot	*Calidris canutus*	26399	1056	10	8705	Yes
European Herring Gull	*Larus argentatus*	18226	729	0	2661	No
Sanderling	*Calidris alba*	9276	371	21	1581	Yes
Brant	*Branta bernicla*	5783	231	0	1418	No
Common Gull	*Larus canus*	3330	133	0	511	No
Common Eider	*Somateria mollissima*	3268	131	0	530	No
Common Shelduck	*Tadorna tadorna*	1701	68	0	815	Yes
Great Cormorant	*Phalacrocorax carbo*	1511	60	0	542	No
Common Redshank	*Tringa totanus*	1081	43.2	0	174	Yes
Common Tern	*Sterna hirundo*	947	37.9	0	230	No
Common Ringed Plover	*Charadrius hiaticula*	709	28.0	0	144	Yes
Eurasian Spoonbill	*Platalea leucorodia*	476	19.0	0	144	No
Ruddy Duck	*Oxyura jamaicensis*	470	18.8	0	470	No
Great Black-backed Gull	*Larus marinus*	463	18.5	0	72	No
Sandwich Tern	*Sterna sandvicensis*	361	14.4	0	120	No
Barnacle Goose	*Branta leucopsis*	332	13.0	0	330	No
Greylag Goose	*Anser anser*	268	10.7	0	130	No
Lesser Black-backed Gull	*Larus fuscus*	268	10.7	0	130	No
Eurasian Wigeon	*Anas penelope*	214	8.6	0	89	No
Ruddy Turnstone	*Arenaria interpres*	208	8.0	0	40	Yes
Mallard	*Anas platyrhynchos*	186	7.4	0	74	No
Eurasian Magpie	*Pica pica*	130	5.2	0	130	No
Eurasian Whimbrel	*Numenius phaeopus*	109	4.4	0	54	No
Common Greenshank	*Tringa nebularia*	95	3.8	0	31	Yes
Northern Pintail	*Anas acuta*	91	4.0	0	60	No
Red-breasted Merganser	*Mergus serrator*	87	3.0	0	34	No
Little Egret	*Egretta garzetta*	57	2.3	0	14	No
Black-tailed Godwit	*Limosa limosa*	51	2.0	0	39	No
Peregrine Falcon	*Falco peregrinus*	17	0.68	0	3	No
Common Goldeneye	*Bucephala clangula*	15	0.60	0	15	No
Spotted Redshank	*Tringa erythropus*	15	0.60	0	3	Yes
Horned Grebe	*Podiceps auritus*	13	0.52	0	12	No

Great Crested Grebe	*Podiceps cristatus*	12	0.48	0	11	No
Mediterranean Gull	*Larus melanocephalus*	12	0.48	0	11	No

We investigate whether there is variation within the population between periods (timing in the tidal cycle) and for expressed behavior (foraging or resting). Figure 5 shows the sum of all daily bird counts per period to increase understanding of the bird population that visits the Roggenplaat at low tide. Peak number of individuals were present in Period 2 of March 3, 2017. Both other periods of that day contain a smaller number of birds. This pattern is observed more often since Period 2 has generally highest daily numbers. Largest proportion of resting birds are counted during Period 1, while Period 2 and 3 are dominated by foraging birds. Regular daily fluctuation in total number of individuals is shown, but no seasonal pattern can be recognized.

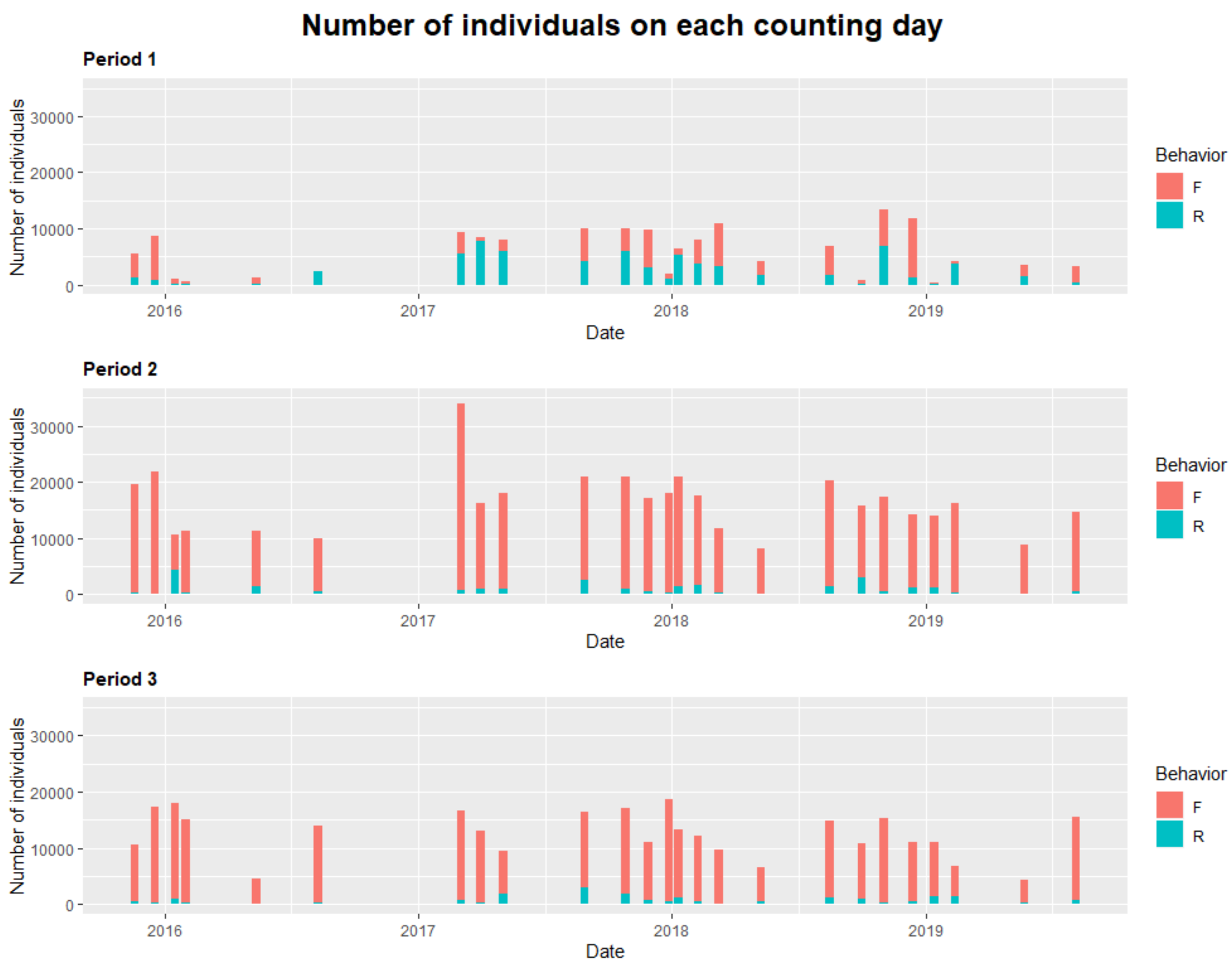


Figure 5: Total number of individuals and their behavior (red: Foraging (F) and blue: resting (R)) each counting day per period (1, 2, and 3).

Number of individuals significantly differed between periods (H(2) = 38.98, $p < 0.01$) with higher counts in Period 2 (M = 17313, SD = 6698), followed by Period 3 (M = 13929, SD = 4344) and Period 1 (M = 6017, SD = 3973), as shown in Figure 6. Period 1 significantly differs from both Period 2 ($p < 0.01$) and Period 3 ($p < 0.01$). Period 2 and 3 however did not significantly differs ($p = 0.10$). Similar patterns were observed for species richness, with significant difference between periods (F(2, 72) = 6.04, $p = 0.004$) and significant higher species richness in Period 2 ($p = 0.02$) and 3 ($p < 0.01$) compared to Period 1, but no significant difference between Period 2 and 3 ($p = 0.85$).

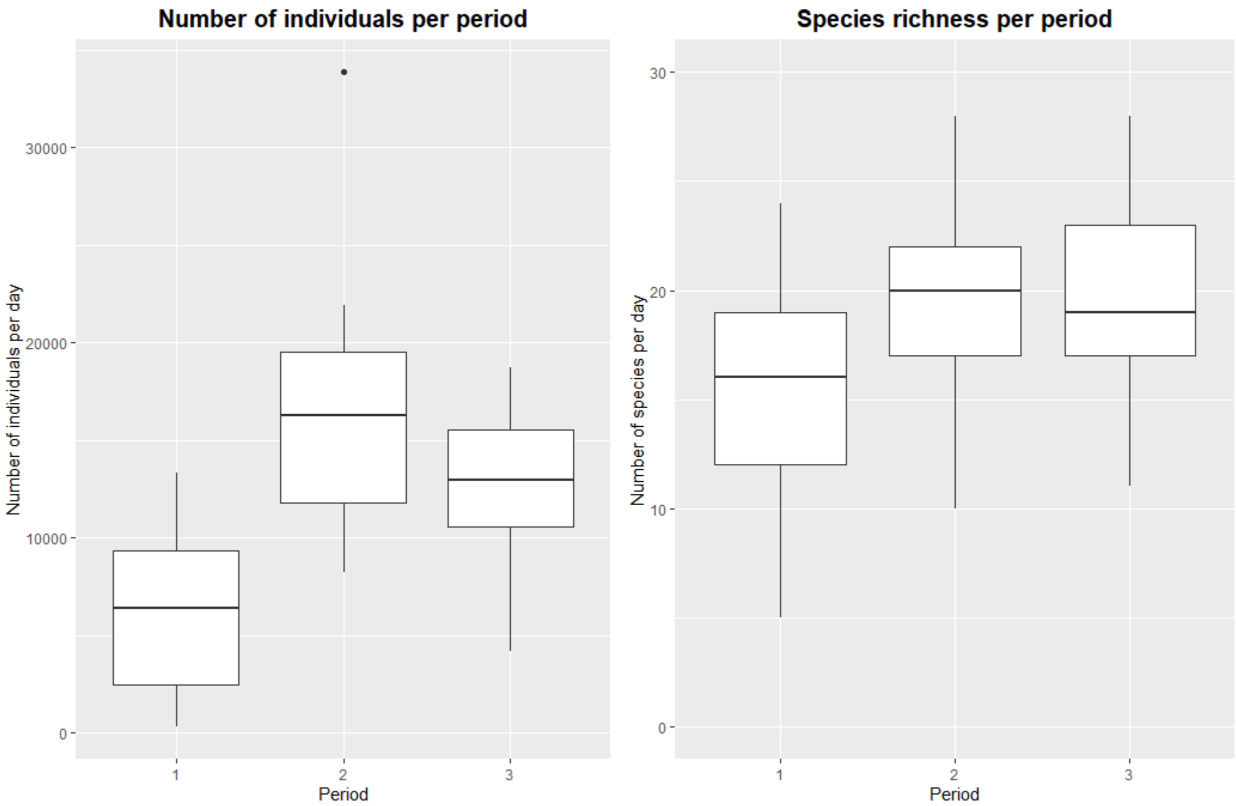


Figure 6: Total number of individuals (left) and species richness (right) per period (N = 25 per period).

Seasonality in abundance was investigated by comparing seasonal means (Table 3). Highest mean number of individuals were counted in autumn, and slightly lower means in winter and spring. These differences were however not significant. Species richness was also highest in autumn and slightly lower in spring. Winter had lowest mean species richness despite high number of individuals were counted in this season. Also here no significant differences between seasons was observed.

Table 3: Mean (standard deviation) number of individuals and species richness observed within winter, spring, and autumn per period. P-value shows significance of seasonal differences (p < .05). Seasonal differences in number of individuals were tested by a Kruskal-Wallis test (H-test, df = 2). Differences in species richness were tested by a one-way ANOVA (F-score, df = 2, 72).

No. of individuals	**Winter**	**Spring**	**Autumn**	**H-test**	***p*-value**
Period 1 *(StDev)*	4758 *(4157)*	6502 *(3583)*	6899 *(4192)*	1.857	0.395
Period 2 *(StDev)*	17180 *(5331)*	16450 *(10415)*	18118 *(4840)*	2.111	0.348
Period 3 *(StDev)*	14122 *(3103)*	11321 *(5823)*	15764 *(3432)*	1.683	0.431
Species richness	**Winter**	**Spring**	**Autumn**	**F score**	***p*-value**
Period 1 *(StDev)*	12.3 *(3.46)*	15.7 *(3.81)*	16.2 *(2.73)*	1.940	0.168
Period 2 *(StDev)*	17.3 *(6.16)*	20.1 *(3.89)*	20.6 *(4.12)*	2.702	0.089
Period 3 *(StDev)*	17.0 *(4.36)*	21.4 *(4.19)*	22.6 *(4.03)*	1.382	0.272

Behavior differed per period (Figure 7). Significant more birds are foraging during Period 2 ($H(1) = 36.31$, $p < 0.01$) and 3 ($H(1) = 33.46$, $p < 0.01$), while during Period 1 comparable numbers of individuals are either foraging or resting ($H(1) = 0.502$, $p = 0.48$). Resting behavior was not significantly different between periods ($H(2) = 2.29$, $p = 0.32$). Foraging behavior however significantly differed between periods ($H(2) = 45.58$, $p < 0.01$). Significantly more individuals foraged during Period 2 ($p < 0.01$). Most foraging individuals are observed during Period 2, followed by Period 3 and Period 1.

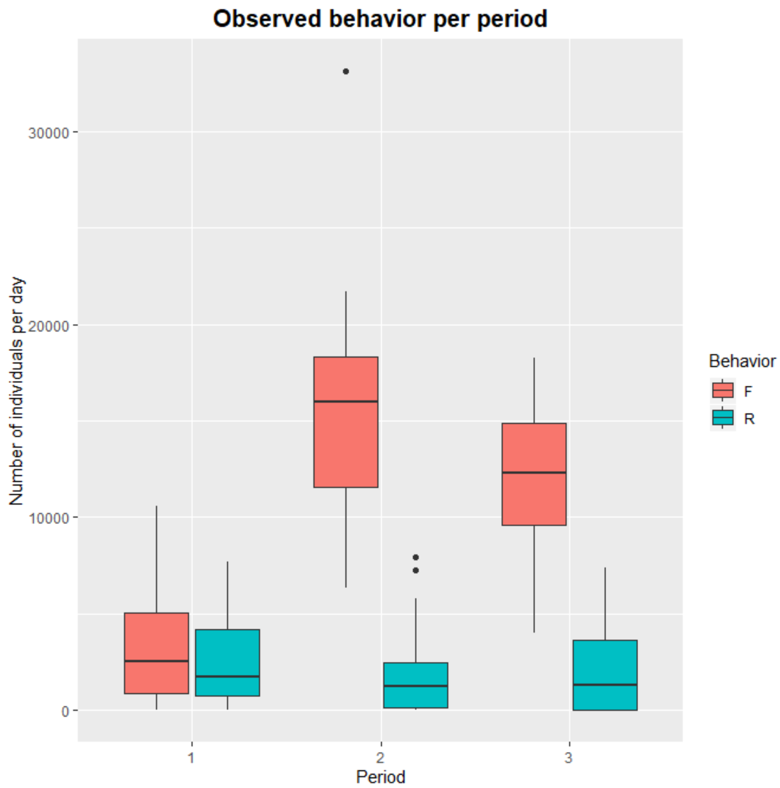


Figure 7: Distribution of daily number of individuals that express foraging (F) or resting (R) behavior per period.

3.1.2 Nature2000 bottleneck species

We want to investigate whether individual shorebird species show the same pattern in periodic abundance and behavior as was observed for the population. Table 4 shows all Nature2000 bottleneck species. Mean Dunlin population at the Roggenplaat is largest for all periods. Period 2 has highest amount of individuals, followed by Period 3. This periodic pattern is observed for most of the species, which corresponds to observations of the Roggenplaat-population. Only numbers of Shelduck, Common Redshank, Common Greenshank, and Spotted Redshank are largest during Period 3. For all species' lowest amount of individuals were counted during Period 1. Ratios between foraging and resting behavior (F/R ratios) indicate that most individual start foraging in Period 2 and 3. Only the Common Redshank has a relatively high ratio of foraging individuals in Period 1, but even higher ratios in Period 2 and 3. This indicates that the Common Redshank doesn't frequently express resting behavior if it is present at the Roggenplaat. Common Greenshank and Spotted Redshank individuals are not even observed during Period 1, while the individuals that are counted during Period 2 and 3 are only expressing foraging behavior.

Table 4: All Nature2000 bottleneck shorebird species that were observed at the Roggenplaat, including mean number of individuals, standard deviation and Foraging/Resting behavior ratio. Species name include common name and Dutch name.

Species	Period 1			Period 2			Period 3		
	Mean	StDev	F/R	Mean	StDev	F/R	Mean	StDev	F/R
Dunlin *Bonte Strandloper*	1887	1709	1.6	4430	3355	99.05	3007	2350	782
Oystercatcher *Scholekster*	847	792	1.51	2607	1381	40.36	2170	1270	6.51
Bar-tailed godwit *Rosse Grutto*	819	755	0.3	2421	1399	8.87	1779	1094	22.93
Eurasian Curlew *Wulp*	731	779	2.39	1851	1258	10.87	1352	901	17.28
Grey Plover *Zilverplevier*	415	435	0.7	1708	873	18.46	1079	710	20.6
Red Knot *Kanoetstrandloper*	159	226	0.53	989	1696	328.73	520	651	87.41
Sanderling *Drieteenstrandloper*	116	168	2.4	261	368	28.25	195	318	96.3
Common Shelduck *Bergeend*	20	35	0.84	22	36	8.03	61	162	9.31
Common Redshank *Tureluur*	3	10	9.43	26	36	644/0	33	45	815
Common Ringed Plover *Bontbekplevier*	6	15	2.92	27	41	7.28	9	14	7.68
Ruddy Turnstone *Steenloper*	2	3	4.56	7	10	45.25	2	5	61/0
Common Greenshank *Groenpootruiter*	0	0	-	2	5	51/0	3	7	74/0
Spotted Redshank *Zwarte Ruiter*	0	0	-	0.12	0.44	3/0	0.48	1	12/0

Periodic behavioral variation between foraging and resting of ten most abundant species are shown in Figure 8. Generally, temporal patterns are also present in shorebird abundance since most of the shorebird species show many similarities with patterns observed within the Roggenplaat population. This pattern comprises lowest number of individuals during Period 1, which mainly use the Roggenplaat to rest (or wait) followed by numbers of foraging individuals observed during Period 2 and 3. The Shelduck however has striking low numbers of foraging individuals during Period 2. Three outliers during this period indicate there were counting days with larger numbers of individuals foraging during this period. There are differences between species in expression of resting behavior. Oystercatcher is the only species that rest with large number of individuals during Period 3. There are also differences in resting behavior during Period 1 since Eurasian Curlew, Sanderling, Redshank and Ringed Plover have relative low number of resting individuals during that period.

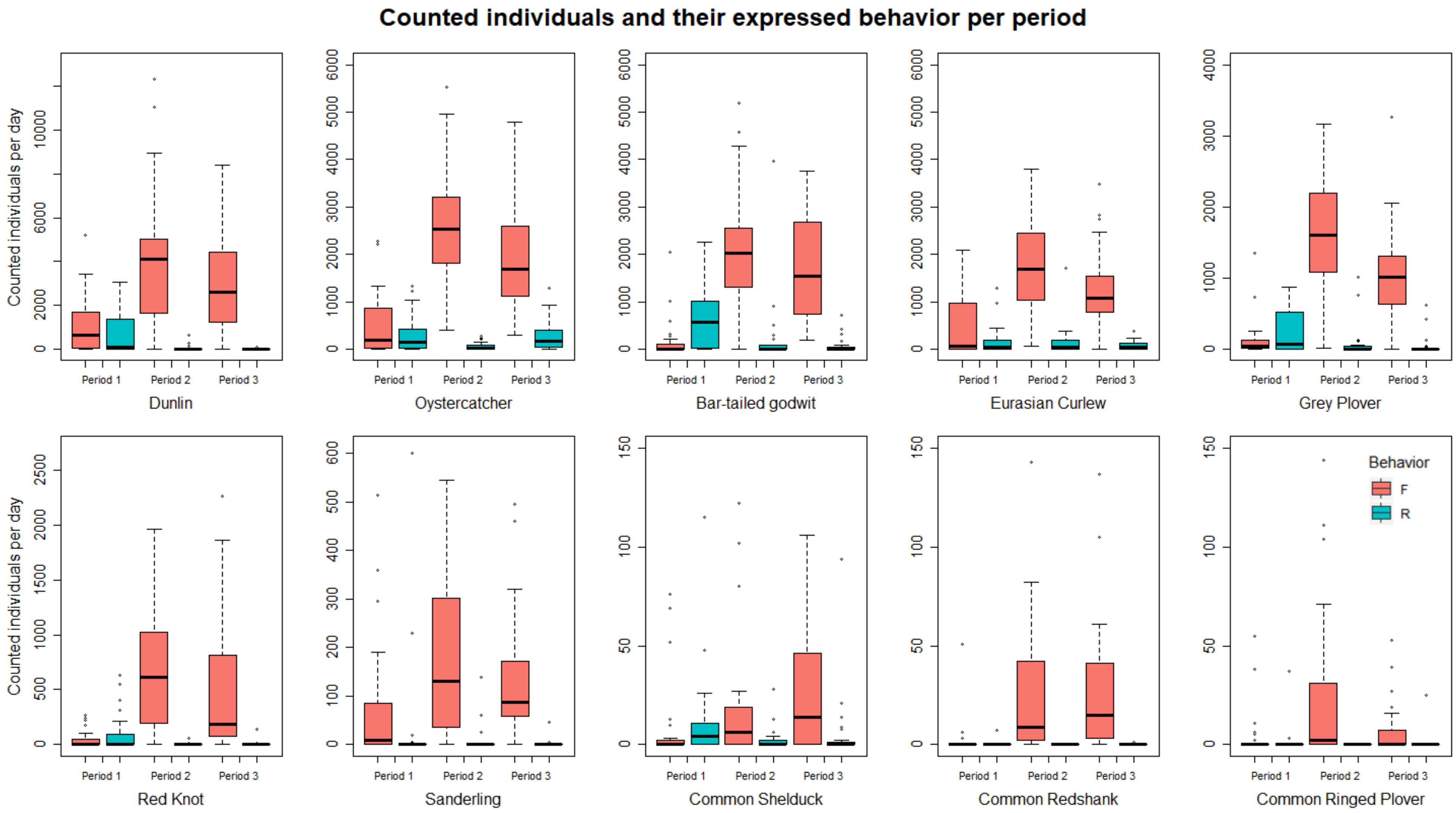


Figure 8: Observed number of individuals distinct for expressed behavior per period for ten most observed Nature2000 species. Foraging and Resting are shown by 'F' and 'R'. The y-axis values differ in each plot.

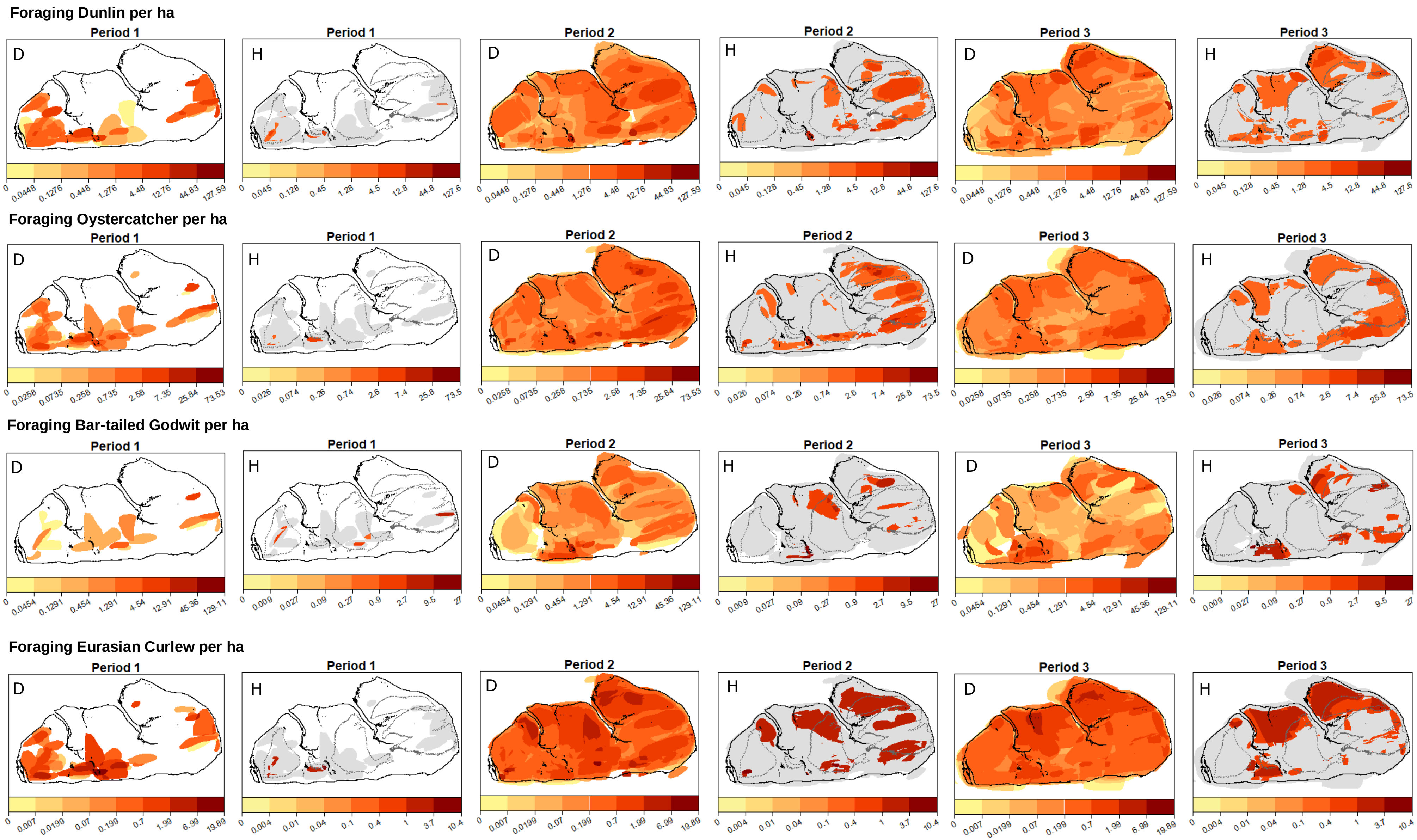
3.2 Spatial distribution of waders

We want to investigate how individual species use the Roggenplaat. To do so we created spatial density maps. Spatial distribution maps of birds that express resting behavior are presented in Appendix 2. For foraging behavior density maps of eight species that had the highest local daily presence over all counting days are shown in Figure 9. The density distribution maps of the remaining Nature2000 species are presented in Appendix 3. It can be observed that areas where foraging birds were counted expand between Period 1 and 3. Especially foraging area of Dunlin, Oystercatcher, Eurasian Curlew and Grey Plover cover the entire intertidal shoal during Period 2 and 3. All other species have either small or large areas where they are not observed at all during the 25 bird counts.

Hotspot maps were created to investigate which area are most frequently used by waders. Table 5 gives an overview of the local critical values for making hotspot maps of bird density distribution. Oystercatcher and Eurasian Curlew are the only species that are regularly present at the same location while expressing resting behavior since their maximum daily presence counts for resting behavior reach six days or more during Period 2 and 3. The remaining Nature2000 species did not show resting behavior at the same location on more than three counting days. Foraging behavior is more frequently observed at the same location because maximum daily presence counts of foraging behavior exceed counts of resting behavior for each Nature2000 species. Hotspot selection criteria for daily presence of Dunlin, Oystercatcher, Bar-tailed godwit, Eurasian Curlew, Grey Plover, Red Knot, Sanderling, and Common Redshank distinguish locations with at least four observations during Period 2 and 3 if >50% of the maximum local daily presence is used as critical value. Especially Oystercatcher and Eurasian Curlew are regularly observed foraging at the same location since they have a maximum local daily presence of at least 20 counting days during Period 3.

Density selection values show maximum local number of individuals per hectare are generally highest for foraging birds in Period 2. The seven most counted species have a minimum critical density (Q2) of 0.10 foraging individuals per hectare. Less frequently observed species have lower local critical densities or are absent.

The hotspot maps of the eight species which had the highest critical value for daily presence during Period 2 and 3 are presented in Figure 9. These are the periods with largest numbers of foraging individuals. The species density maps show that all species more or less use the same area during Period 1. These areas are located at the southwestern and eastern part of the intertidal shoal. Bird distribution covers a greater part of the Roggenplaat during Period 2 and 3. Dunlin, Oystercatcher, Bar-tailed Godwit, Eurasian Curlew, Grey Plover, Red Knot, and Common Redshank foraging hotspots are mainly located at the eastern or both the eastern and central part of the intertidal shoal during Period 2. Sanderling distribution deviates from the other species as their hotspots are located in the southwestern area. Dunlin, Oystercatcher, Bar-tailed godwit and Grey Plover also use a specific part of the southern area as foraging ground. Red knot, and Redshank distribution mainly focusses on the northern part of the intertidal shoal during Period 3. However, most other species like Dunlin, Oystercatcher, Bar-tailed Godwit, Eurasian Curlew, Grey Plover forage along the edges of the entire intertidal shoal. The southern edges are also preferred foraging ground for Sanderling individuals.


Foraging Dunlin per ha
Period 1 D
Period 1 H
Period 2 D
Period 2 H
Period 3 D
Period 3 H
0 0.0448 0.1276 0.448 1.276 4.48 12.76 44.83 127.59
0 0.045 0.128 0.45 1.28 4.5 12.8 44.8 127.6
Foraging Oystercatcher per ha
0 0.0258 0.0735 0.258 0.735 2.58 7.35 25.84 73.53
0 0.026 0.074 0.26 0.74 2.6 7.4 25.8 73.5
Foraging Bar-tailed Godwit per ha
0 0.0454 0.1291 0.454 1.291 4.54 12.91 45.36 129.11
0 0.009 0.027 0.09 0.27 0.9 2.7 9.5 27
Foraging Eurasian Curlew per ha
0 0.007 0.0199 0.07 0.199 0.7 1.99 6.99 19.89
0 0.004 0.01 0.04 0.1 0.4 1 3.7 10.4

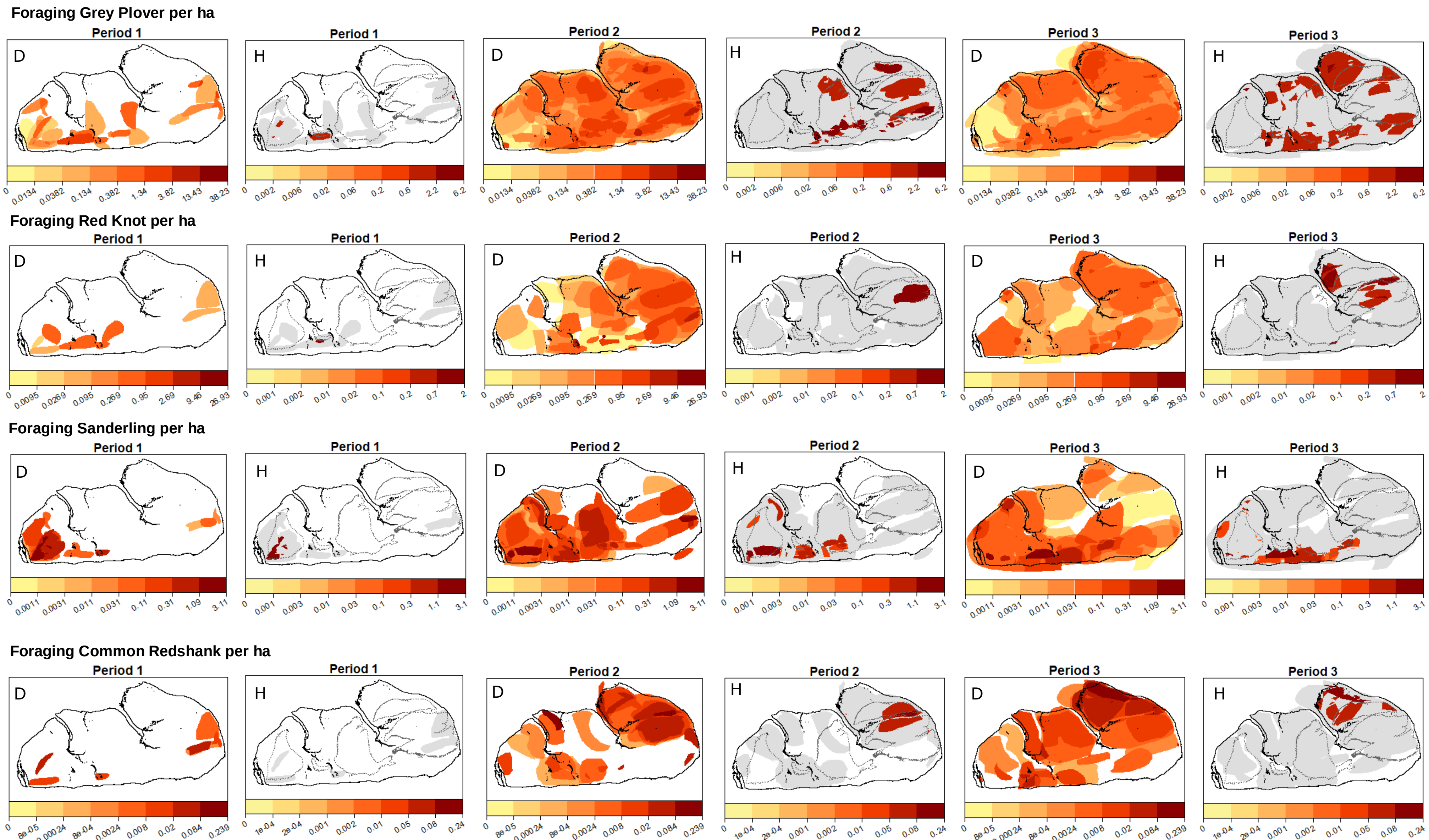


Figure 9: Daily mean density maps (D) (individuals/ha) of foraging bird species at the Roggenplaat (n=25). Hotspot maps (H) selected highest local daily presence and density. Hotspot maps show area that fulfill selection criteria in heatmap-colors, while grey area indicates area where birds were counted that not fulfill hotspots criteria. Grey lines show 50% exposure time.

Table 5: Critical value and maximum value for daily presence and density (ind/ha) of Nature2000 bottleneck species at the Roggenplaat. Periods and behavior are separated. Density values are based on maximum daily mean of all counting days (n=25) of all grid cells (2x2m). Q2 indicates the 2-quantile (or median) of the cells that pass the critical value selection by daily presence (>50% of max number of days at the same location).

		Days present						2-Quantile Density					
Common name	**Activity**	**Period 1**		**Period 2**		**Period 3**		**Period 1**		**Period 2**		**Period 3**	
		50%	**Max**	**50%**	**Max**	**50%**	**Max**	**Q2**	**Max**	**Q2**	**Max**	**Q2**	**Max**
Dunlin	Rest	3.5	7	1	2	0.5	1	10.5	61.4	0.58	2.06	0.03	0.03
	For	3.5	7	6.5	13	6.5	13	3.64	9.30	2.79	127	1.39	35.6
Oystercatcher	Rest	5.5	11	3	6	6.5	13	7.29	31.4	0.11	1.33	0.32	0.90
	For	5.5	11	9.5	19	10.5	21	2.07	4.75	1.57	73.5	1.04	8.21
Bar-tailed godwit	Rest	3.5	7	1.5	3	1.5	3	13.0	34.3	0.43	3.41	0.02	1.21
	For	1.5	3	7	14	6.5	13	0.59	3.15	1.31	27.0	1.16	9.60
Eurasian Curlew	Rest	4	8	4	8	4.5	9	2.72	4.82	0.24	0.56	0.21	0.78
	For	4.5	9	8.5	17	10	20	1.36	4.83	1.18	10.4	0.66	2.40
Grey Plover	Rest	3.5	7	1.5	3	1.5	3	6.02	13.3	0.22	2.19	0.05	0.48
	For	2.5	5	8	16	8.5	17	0.80	3.10	1.39	6.22	0.75	3.24
Red Knot	Rest	3.5	7	1	2	0.5	1	2.44	4.25	0.50	0.50	0.03	0.13
	For	1.5	3	7.5	15	5	10	0.83	1.01	1.33	1.98	0.52	1.10
Sanderling	Rest	1.5	3	0.5	1	0.5	1	0.07	4.95	0.01	0.28	.002	0.14
	For	3.5	7	4.5	9	5	10	1.05	2.96	0.17	2.67	0.10	3.11
Shelduck	Rest	2.5	5	1	2	1.5	3	0.06	0.11	.004	.004	.006	0.04
	For	1.5	3	3	6	3	6	0.03	0.28	.006	0.08	0.01	0.28
Redshank	Rest	0	0	0	0	0.5	1	0	0	0	0	0.01	0.01
	For	1	2	3.5	7	4.5	9	0.07	0.07	0.03	0.95	0.05	0.24
Ringed Plover	Rest	1	2	1	2	0.5	1	0.03	0.03	0.08	0.08	0.02	0.02
	For	1.5	3	3	6	2.5	5	0.19	0.21	0.09	2.55	.007	0.12
Ruddy Turnstone	Rest	0.5	1	0	0	0	0	.004	0.03	0	0	0	0
	For	1.5	3	2	4	2	4	0.05	0.91	.004	0.06	.004	0.03
Greenshank	Rest	0	0	0	0	0	0	0	0	0	0	0	0
	For	0	0	1.5	3	2.5	5	0	0	.008	.012	.022	.027
Spotted Redshank	Rest	0	0	0	0	0	0	0	0	0	0	0	0
	For	0	0	0.5	1	1	2	0	0	.001	.005	.001	.001

Oystercatcher and Eurasian Curlew are the only species that were regularly counted at the same location while expressing resting behavior. Figure 10 therefore shows the hotspots of their distribution over the Roggenplaat while resting. Both the Oystercatcher and Eurasian Curlew are most frequently resting at the western part of the intertidal shoal during Period 2 and 3. These locations differ from the hotspot of Period 1, in which largest densities are reached. Resting hotspots during Period 2 and 3 partly correspond to foraging hotspots of these species. The central and eastern area of the intertidal shoal however were hotspots for foraging behavior, but not for resting behavior.

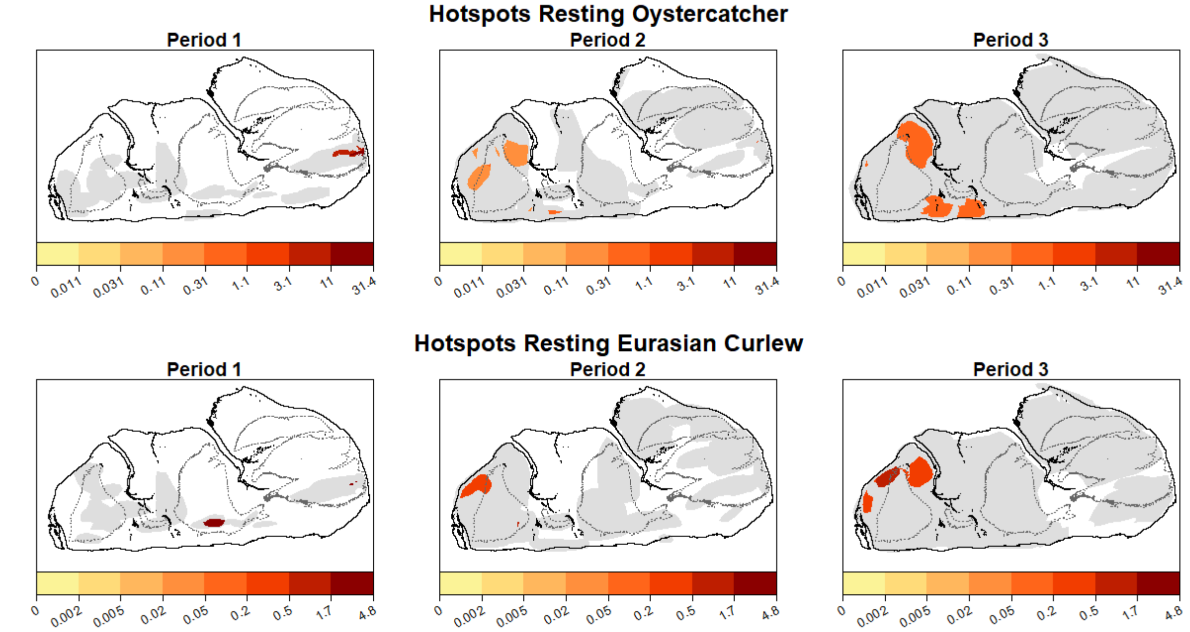


Figure 10: Hotspot maps of Resting Oystercatcher and Eurasian Curlew with daily mean number of individuals per hectare. Grey area indicates bird counts, but the area is excluded from the hotspot map based on criteria. Criteria are >50% maximum local daily presence and >2-Quantile local density. Dashed grey line shows 50% exposure line.

3.3 Bird distribution in relation to exposure time

The influences of exposure time on spatial distribution of foraging birds are shown by the position of hotspots regarding 50% exposure time in Figure 9. Period 1 hotspots are located within >50% zone, which are the locations exposed during this period in the tide. Most species' Period 2 hotspots are on both sides of the 50% exposure time line, while only Red Knot and Redshank hotspots are exclusively located in >50% exposure zones. This changes during Period 3, when the greater part of all species hotspots shift towards the <50% duration of exposure zone. Influences of exposure time are also observed for resting behavior. Resting behavior hotspots during Period 1 are located in an area with >50% exposure time. Hotspot of Period 2 and 3 are however primarily located in areas that are exposed for less than 50% of time.

Additional tests were done to investigate to which extend the observed spatial bird movement over periods towards locations with shorter exposure time occurs for all Nature2000 species combined. It is shown that the 40-60% exposed area has the highest number of individuals (Figure 11). Highest median number of individuals during all periods are observed at 50-60% exposure. Period 3 however has highest maximum range values at 40-50% exposure zone. Furthermore, no obvious changes in number of individuals within 0-40% exposed areas between Period 2 and 3 can be observed. Relative larger decrease in number of individuals is shown between 60-70% exposed zones of Period 2 and 3. Bird individuals per hectare of exposure zone are more gradually distributed due to differences in area of exposure zones. Highest bird densities are counted in 70-80% exposure time during Period 1, 50-70% exposure time during Period 2, and 20-50% exposure time during Period 3.

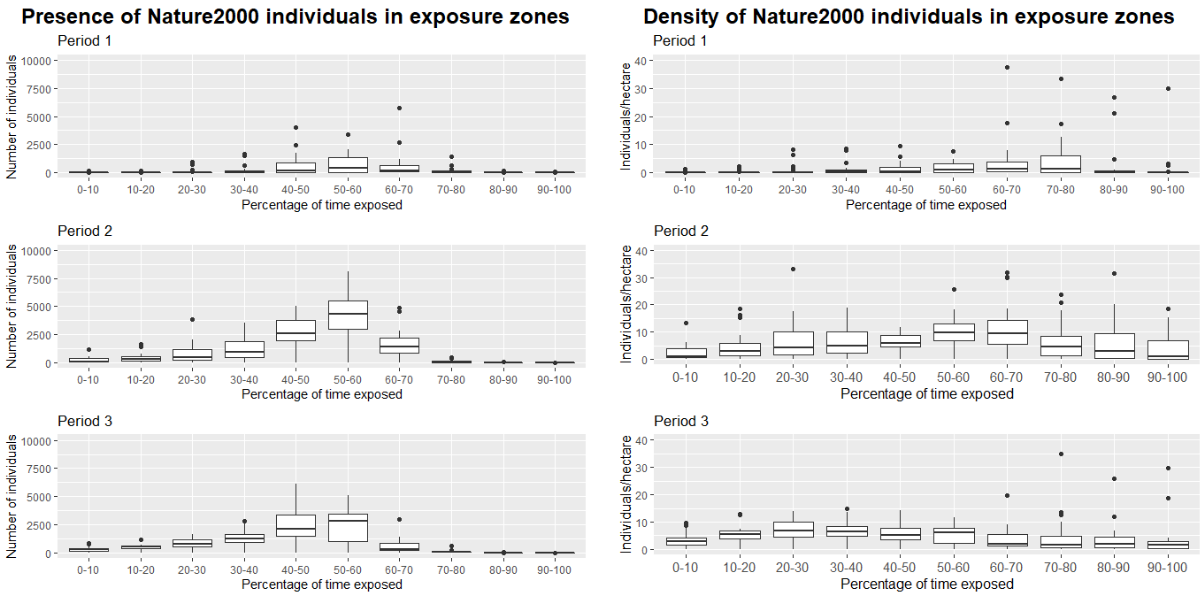


Figure 11: Daily mean number of individuals of 13 observed Nature2000 bottleneck species in exposure zones. The mean number of individuals are presented as the total number in a exposure zone (left) and the total number per hectare of an exposure zone (right).

For each species of which spatial distribution was mapped we investigate whether the highest densities of foraging individuals per hectare actually shift to lower exposure zones between Period 2 and 3 (Figure 12). A shift to lower exposure zones along the tide line indicates tide-following behavior of species. For almost all species a significant difference in density per exposure time was observed (Appendix 4), except for the Oystercatcher ($H(9) = 10.733$, $p = 0.29$). All species have highest median densities in 40-70% during Period 2, while highest median densities of Period 3 are observed in 20-40% exposed area.

In Period 2 significantly lower densities of Dunlin, Oystercatcher, Eurasian Curlew, Grey Plover and Red Knot were found in the area with an exposure time of 0-10% in comparison to the area with an exposure time of 50-60%. Densities of Bar-tailed godwit, Eurasian Curlew, Red Knot and Redshank were significantly lower at 80-90% exposure time compared to 40-60% exposure time. These four species, Grey Plover and Sanderling also show significant lower densities in 90-100% than in 50-60% exposure time during Period 2. Therefore, most of the significant differences that were observed during Period 2 are between 50-60% exposure and the minimum and maximum exposure time zones since zones with comparable exposure time as 50-60% exposure zone did not show significant differences.

In Period 3 significantly higher bird densities were observed in 20-60% than were found in 80-90% exposure zone for Dunlin, Bar-tailed godwit, Sanderling and Redshank. Moreover, the same species and the Grey Plover show significant lower densities in 90-100% than in 10-60% exposure zones, while the 0-10% exposure zone has significantly higher densities than 80-100% exposure zones for Bar-tailed godwit, Sanderling and Redshank. After a Kruskal-Wallis test found significant differences between Eurasian Curlew and Red Knot densities in exposure zones during Period 3, pair-wise testing showed these differences were not large enough to be significant ($p > 0.05$). Therefore, area with significant higher densities than bird density in maximum exposure time zones that were observed during Period 3 were always found in <60% exposure zones if differences were present.

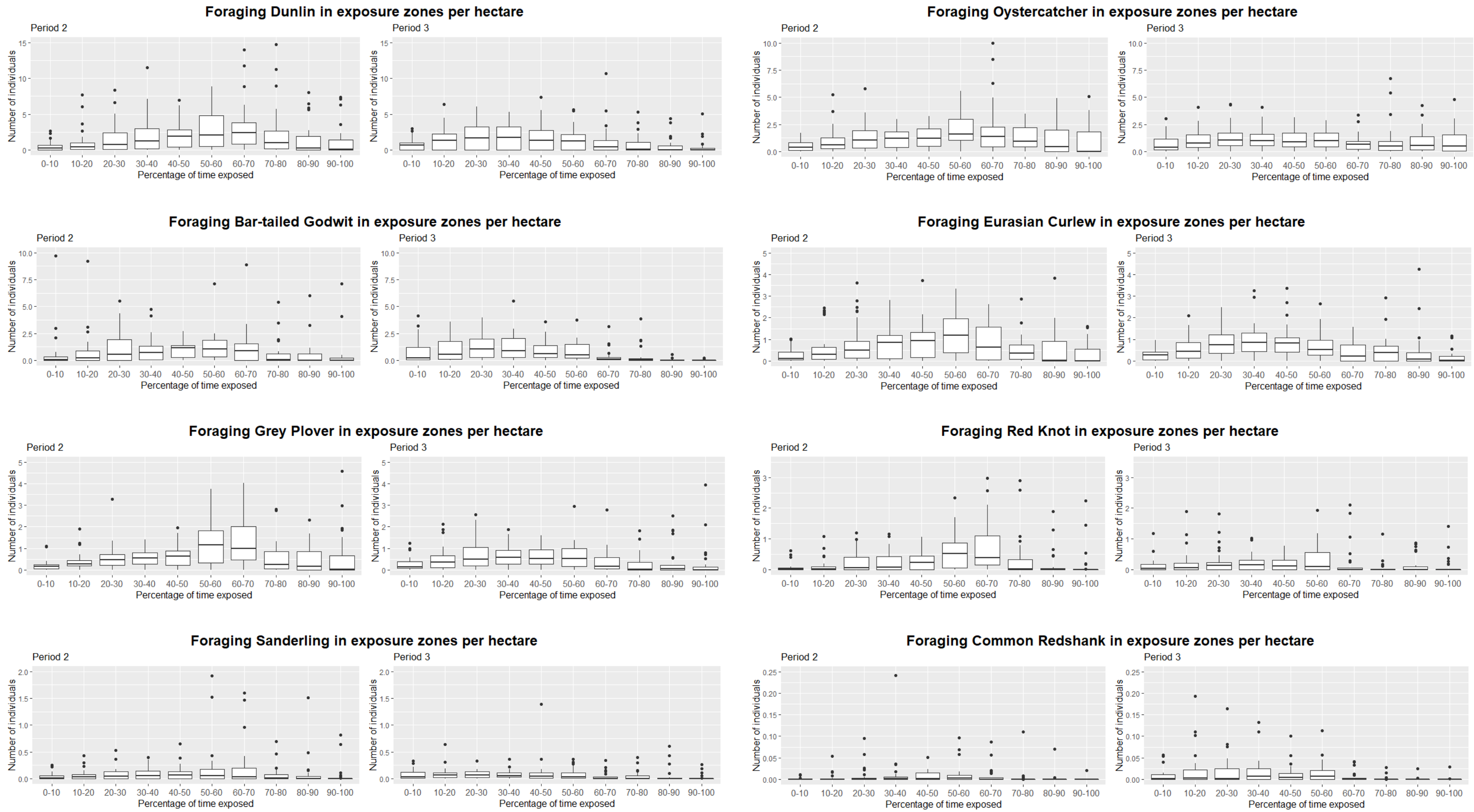


Figure 12: Number of individuals per hectare per exposure time (%) for the eight foraging species with the highest critical value for daily presence during Period 2 and 3.

3.4 Bird distribution in relation to food availability

Bird densities were compared to prey abundance to investigate if there is a relation between food availability and the spatial distribution of the birds on the intertidal shoal. For eight bird species foraging behavior characteristics were obtained from literature (Table 6). The oystercatcher, Bar-tailed godwit, Grey Plover, and Red Knot have a specific diet, while especially Eurasian Curlew and Redshank are more flexible. Polychaeta are the main prey of Dunlin, Bar-tailed godwit, Grey Plover and Sanderling. Bivalvia are primarily consumed by Oystercatcher and Red Knot. From literature the main prey of Sanderling is *Scolepsis squamata*. This prey is absent from the Roggenplaat. The small crustacea *Bathyporeia sp.* is also known to be a main prey of Sanderling. Per bird their preferred prey species were clustered for density and biomass to visualize where their preferred diet can be found and in which quantities. This was combined with hotspot maps to investigate whether there is an overlap between benthic infauna and foraging bird hotspots.

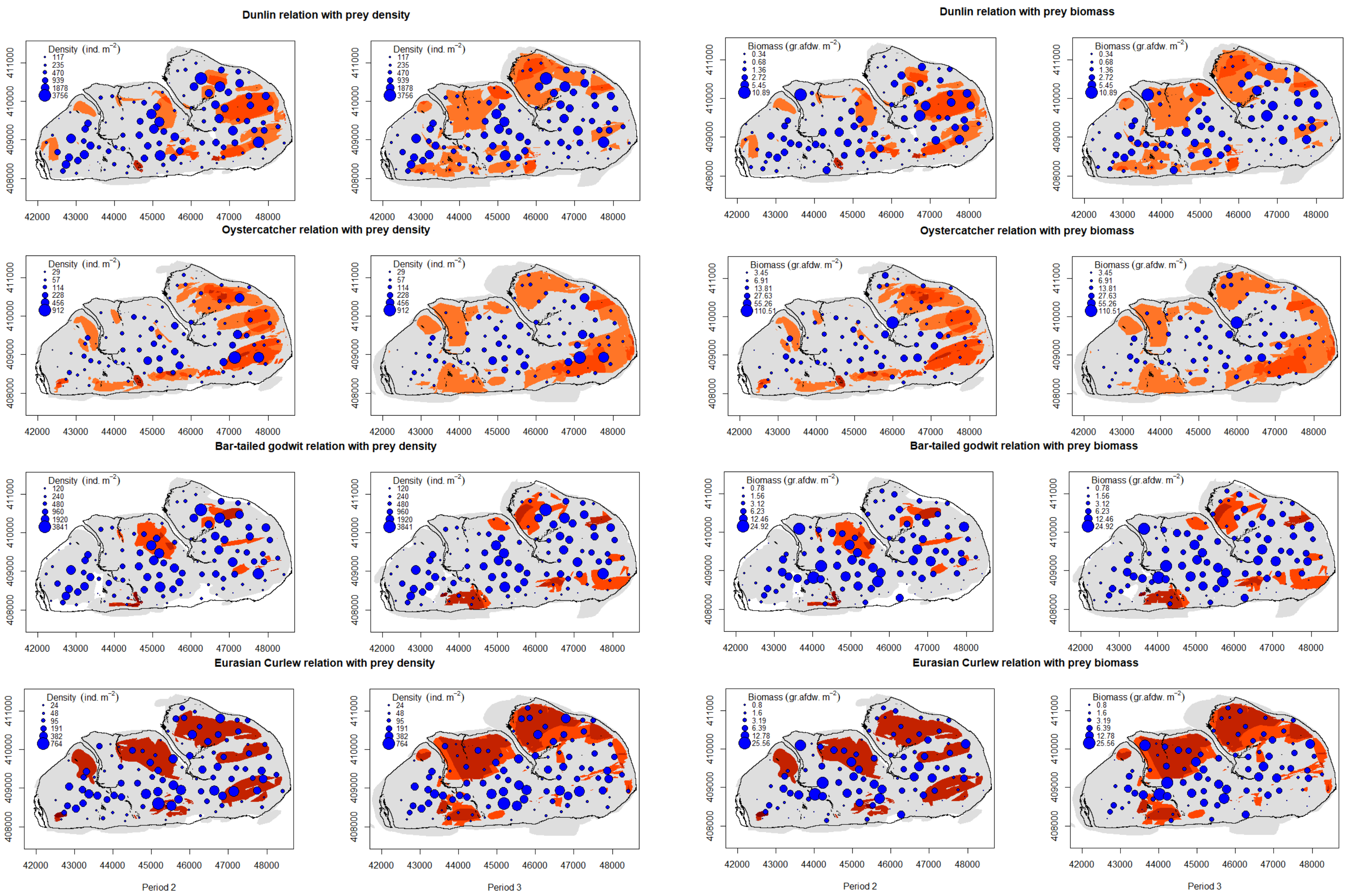
Table 6: Foraging method of eight species of which foraging density were visualized in figure 9. Bird diet is based on Leopold et al. (2004) and Lack (2010). Foraging strategies are derived from VanDusen et al. (2012) and Besterman et al. (2020).

Common name	Prey detection	Gregariousness	Diet	Main prey
Dunlin	Tactile (little visual)	High	Intermediate	**Focus: Polychaeta** Species: *Hediste diversicolor, Scoloplos armiger*
Oystercatcher	No bias / Tactile	Intermediate	Specialized	**Focus: Bivalvia** Species: *Cerastoderma edule, Mytilus edulis, Arenicola marina*
Bar-tailed godwit	No bias	High	Specialized	**Focus: Polychaeta** Species: *Arenicola marina, Hediste diversicolor, Nephtys sp., Scoloplos armiger*
Eurasian Curlew	Visual (little tactile)	Intermediate	Flexible	**Focus: Overall** Species: *Carcinus maenas, Mya sp., Arenicola marina, Hediste diversicolor*
Grey Plover	Visual	Intermediate	Specialized	**Focus: Polychaeta** Species: *Hediste diversicolor, Arenicola marina, Scoloplos armiger*
Red Knot	Tactile	High	Specialized	**Focus: Bivalvia** Species: *Limecola balthica, Cerastoderma edule*
Sanderling	Visual (little tactile)	High	Intermediate	**Focus: Polychaeta** Species: *Bathyporeia sp.*
Redshank	No bias	High	Flexible	**Focus: Overall** Species: *Crangon crangon, Corophium volutator, Limecola balthica*

The prey species of Dunlin, Bar-tailed godwit, Eurasian Curlew, and Grey Plover are present at most parts of the intertidal shoal. The relative amount of prey density and biomass per m^2 did not differ largely for these waders. Outer edges of the intertidal shoal generally have a lower density and biomass than the center part. Especially Period 2 bird hotspots overlap with high biomass zones, since hotspots move towards the intertidal shoal edges during Period 3. However, there are also areas with high biomass that did not overlap with bird hotspots. These areas were mainly located at the center and western part of the intertidal shoal.

Main prey of the Oystercatcher and Red Knot have a different distribution than the species discussed before. Moreover, prey density peak differed from prey biomass peak location. High prey density in the southeastern area overlaps with an Oystercatcher hotspot, but this location has a relatively low biomass. Red Knot hotspots are located near area with sufficient prey, but their hotspot is not located at the site where prey is most abundant. To investigate how biomass is related to density and why Oystercatchers are abundant at that spot we looked at data from the WOT-cockle survey which contains density per life-stage of *Cerastoderma edule* and *Limecola balthica* (Figure 14). *C. edule* is the main prey of the Oystercatcher. It can be observed that 1-year old *C. edule* are most abundant at the Oystercatcher hotspot. Older individuals that have higher individual biomass are most abundant in other areas. The northeastern part of the intertidal shoal houses large number of 1-year old *C. edule* individuals too. This area overlaps with the hotspot of Red Knot, which also has a Bivalvia-based diet. However, Red Knot are mainly foraging on *L. balthica.* Density of medium sized individuals of this bivalve are more abundant at the northeastern part of the Roggenplaat. This observation corresponds to the location of Red Knot density hotspots.

Most unique distribution of prey is shown for Sanderling species. Their density hotspot at the western part of the intertidal shoal overlaps with benthic infauna presence during Period 2. Sanderling hotspots however shift towards the southern shoal during Period 3, where no main prey were found. In general, Period 2 bird hotspots have the largest overlap with prey distribution. Birds are foraging at locations with presence of prey, but not necessarily highest density or biomass. Prey of most birds with a Polychaeta-based diet are well distributed over the entire intertidal shoal, while Bivalvia are more abundant at the eastern side. A hotspot at the southern part of the intertidal shoal that is observed for Dunlin, Oystercatcher, Bar-tailed godwit, Eurasian Curlew, Grey Plover, and Sanderling has both low density and biomass but provides regularly used foraging ground.


Dunlin relation with prey density
Dunlin relation with prey biomass
Oystercatcher relation with prey density
Oystercatcher relation with prey biomass
Bar-tailed godwit relation with prey density
Bar-tailed godwit relation with prey biomass
Eurasian Curlew relation with prey density
Eurasian Curlew relation with prey biomass
Density (ind. m^{-2})
117 235 470 939 1878 3756
29 57 114 228 456 912
120 240 480 960 1920 3841
24 48 95 191 382 764
Biomass (gr.afdw. m^{-2})
0.34 0.68 1.36 2.72 5.45 10.89
3.45 6.91 13.81 27.63 55.26 110.51
0.78 1.56 3.12 6.23 12.46 24.92
0.8 1.6 3.19 6.39 12.78 25.56
408000 409000 410000 411000
42000 43000 44000 45000 46000 47000 48000
Period 2
Period 3

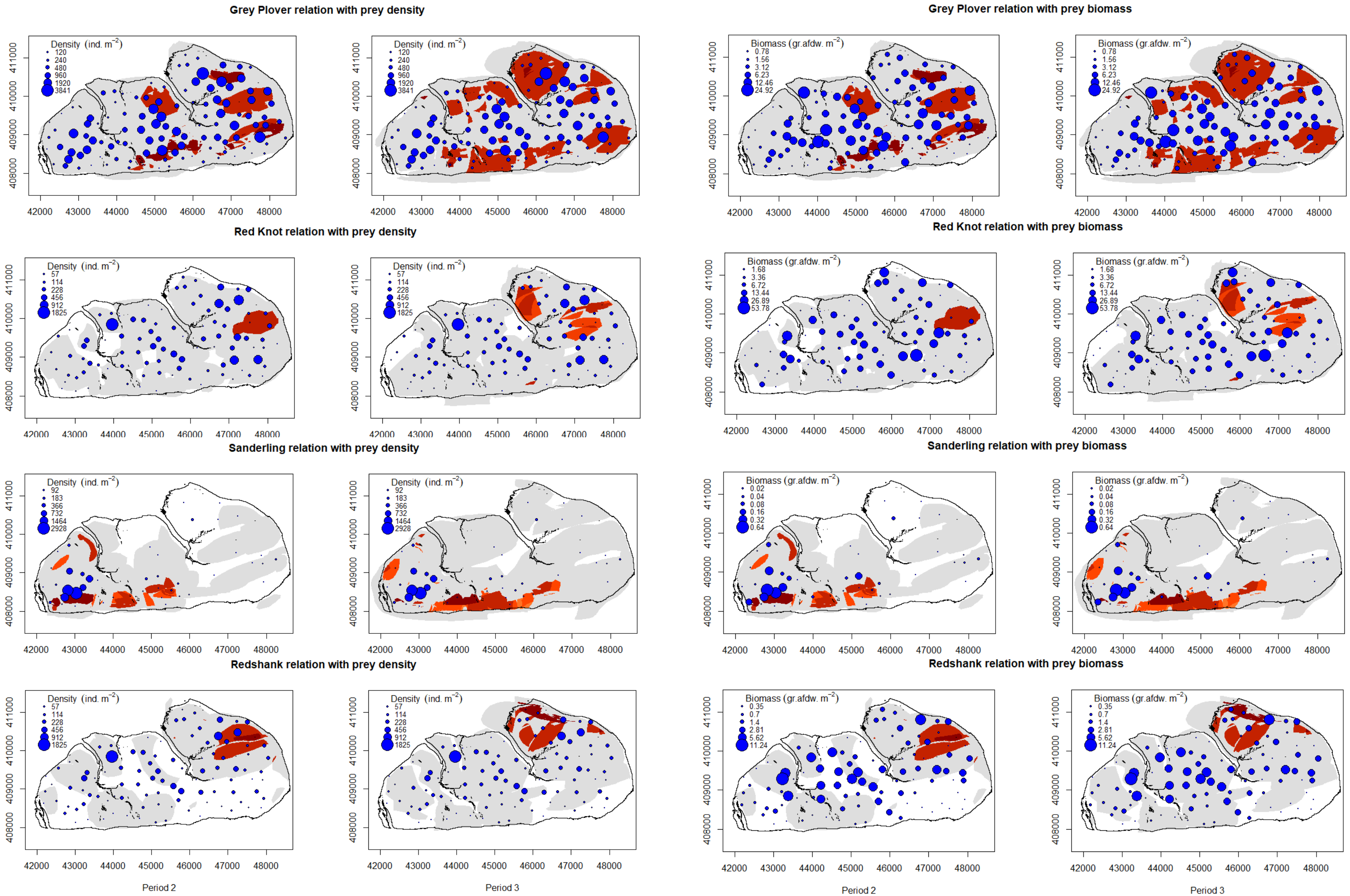


Figure 13: Bird density hotspots of Period 2 and 3 related to main prey density and biomass according to Table 6. Hotspot maps select highest local daily presence and density of birds. Hotspot maps show area that fulfill selection criteria in heatmap-colors, while grey area indicates area where birds were counted that not fulfill hotspot criteria. Prey density and biomass are averaged values of 2015 and 2019.

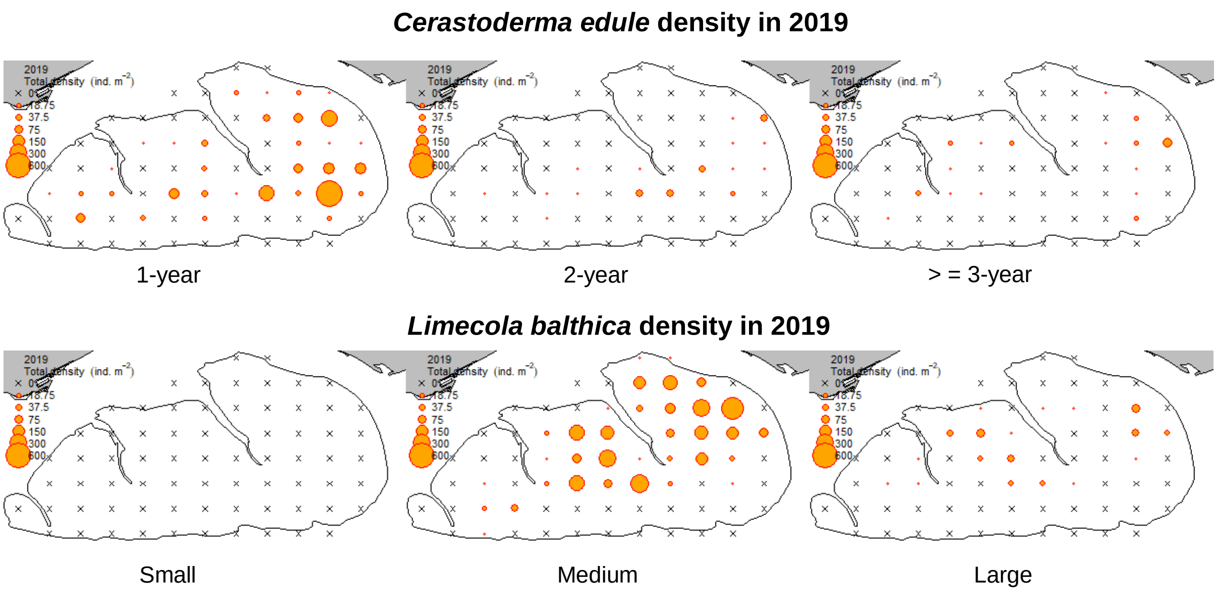


Figure 14: WOT-cockle survey data (van den Ende et al., 2020) with Cerastoderma edule and Limecola balthica density (ind/m²) in 2019. Bivalves are grouped by size- or age-class.

We investigate whether distribution of foraging birds is influenced by proportion of Polychaeta and Bivalvia rather than presence of the preferred prey only. Polychaeta are more dominant at the edges in the western and central part of the Roggenplaat (Figure 15). At these locations are Bivalvia more dominant at the center parts of the intertidal shoal than they are along the edges. This pattern is not observed at the eastern side of the intertidal shoal, where the dominant prey type varies spatially. Local benthic infauna composition ranges from a complete dominance by Polychaeta or Bivalvia to a Bivalvia dominated community. There are only three locations with a considerable amount of other types of benthic infauna, which are located at the western part of the intertidal shoal.

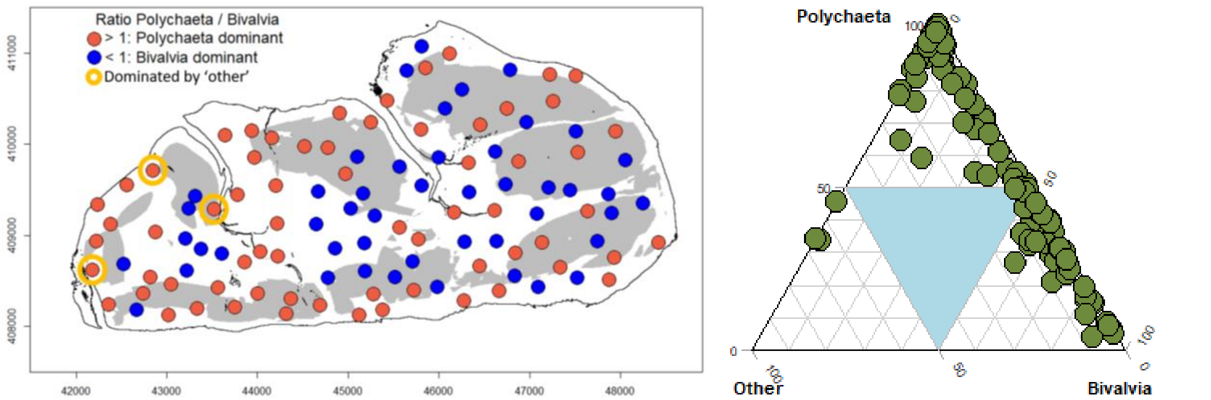


Figure 15: Polychaeta/Bivalvia ratio scores per sampling location (left) and the total biomass composition of Polychaeta, Bivalvia and other benthic infauna at each sampling location (right). All bird hotspots of Period 2 combined are plotted on the background (grey).

To investigate how total biomass and the locally dominant type of prey are related we looked at spatial differences in biomass on the Roggenplaat. Benthic sampling points were divided in an eastern, central or western group which were then further divided in a group dominated by Polychaeta or Bivalvia. The Polychaeta dominated points in the eastern and central were even further divided into a southern and northern group (Figure 16). The central and northeastern part of the Roggenplaat generally has >43 gr AFDW per m^2. South-western area however has relatively less biomass. Biomass ratio of Polychaeta, Bivalvia and other types of benthic infauna shows remarkable benthos composition at both locations with blue points. These areas are strongly dominated by Polychaeta. Observed benthos composition at these locations are similar to the preferred diet of Bar-tailed godwit and Grey Plover, which both have a density hotspot at the same areas. These bird hotspots are however positioned where total biomass is relatively low (blue points), which shows a relation of benthic infauna with bird distribution that is not primarily biomass or density-based. The area at the western part of the intertidal shoal (red points) contains proportionately most other types of benthic infauna, which overlaps with Sanderling hotspots. There are also five groups that have a larger proportion of Bivalvia (black, dark red, yellow, salmon, green points). These areas not directly corresponding with Oystercatcher or Red Knot density hotspots.

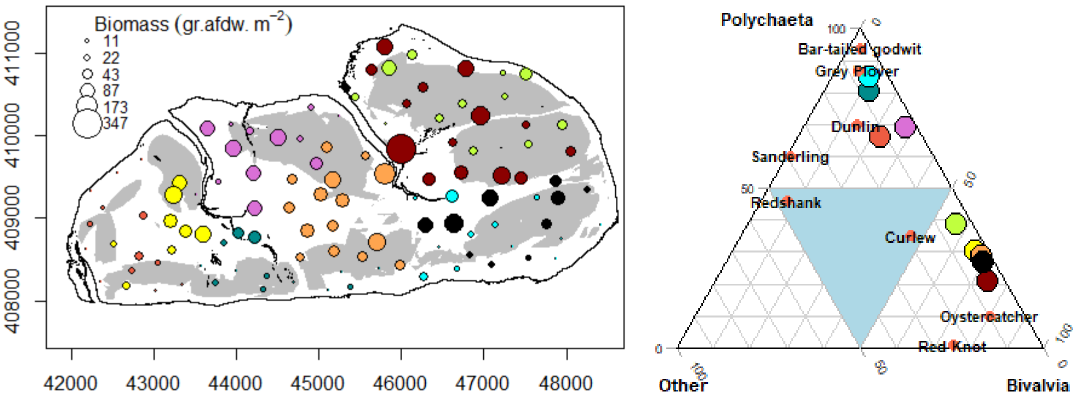


Figure 16: Total biomass and showed at the Roggenplaat (left). All bird density hotspots during Period 2 are combined in the background map. Areas with a specific dominant type of benthic infauna are grouped by colors that correspond to the dots in the triangle-plot (right). This plot shows the proportion of Polychaeta, Bivalvia and other types of benthic infauna. Also composition of bird diets is presented.

3.5 Bird distribution in relation to sediment composition

Sediment composition at the Roggenplaat was studied to analyze the relationship between bird distribution and site specific grain sizes. Figure 17 shows d50 sediment grain size in 2015 and combined bird hotspots during Period 2 and 3. Sanderling hotspots are excluded since they show a remarkably different distribution. It can be observed that sediment with higher d50 sediment grain size primarily covers the southwestern part of the Roggenplaat since the local d50 is between 170 - 282 µm. The western part did not comprise many selected bird hotspots during Period 2 and 3, so bird hotspots did generally not overlap with this area with high d50 sediment grain size. The few hotspots that are shown at the western side of the intertidal shoal are all Dunlin hotspots. Sanderling hotspots however are primarily located at this side of the intertidal shoal during Period 2, but shift towards area with smaller d50 grain sizes at the south during Period 3. The northeastern intertidal shoal has smaller d50 grain sizes that are ranging between 113 - 282 µm, but are dominated by 113 - 225 µm. Selected bird hotspots are well represented in this northeastern area. Figure 18 shows the mud fraction (< 64 µm particles) to investigate if bird distribution is influenced by this factor. Higher mud fractions up to 32% can be found at the northern part of the Roggenplaat, near the oyster reefs, which creates muddier conditions. Bird density hotspots mainly overlap with sampling locations with > 1% mud fraction. In general, there are sandy conditions at the Roggenplaat (> 64 µm grain size), with small mud fraction. The d50 grain size of the northwestern part also indicates presence of fine sand (64-250 µm), while the western area mainly comprises medium sized sand (250-500 µm). Bird hotspots overlap more frequently with locations with low d50 and high mud fraction than with high d50 and low mud fractions, especially during Period 3. Only fine sediment rich areas in the central part of the intertidal shoal near the Middle gully (most eastern gully) do not overlap with bird hotspots.

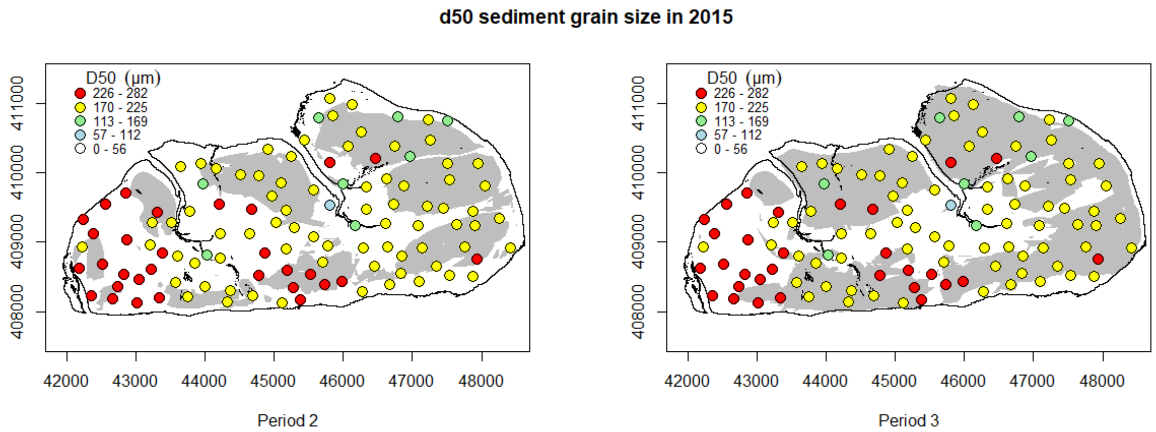


Figure 17: d50 sediment grain size in 2015 for each sample point. Background shows all bird density hotspots combined of species of which their hotspots were shown in Figure 9 for Period 2 and 3, except Sanderling.

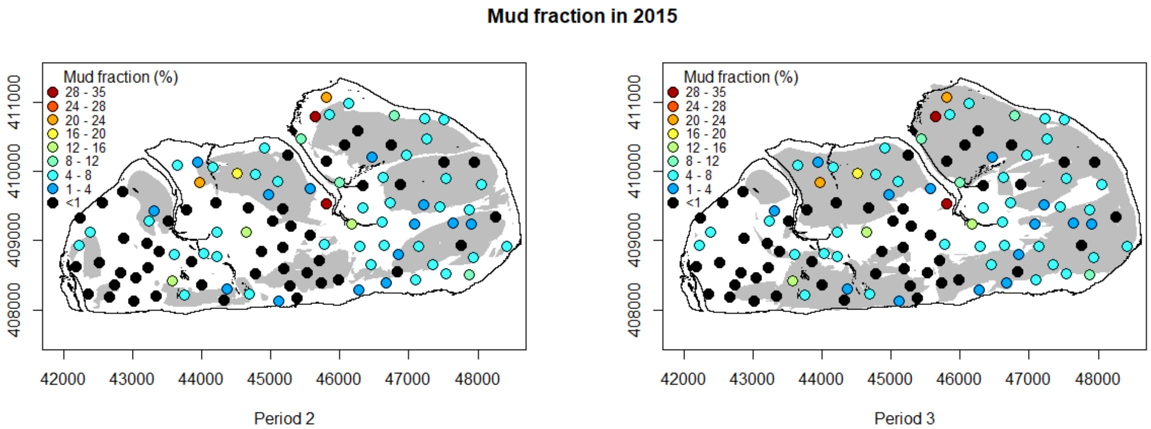


Figure 18: Fraction of sediment with a grain size <64 µm in October 2015 for each sampling location. Background map shows all bird density hotspots combined of eight species of which their hotspots were visualized in Figure 9 for Period 2 and 3, except Sanderling.

4. Discussion

4.1 Temporal wader abundance

The abundance and spatial and temporal distribution of waders on the Roggenplaat was studied in winter, spring and autumn for four consecutive years. No significant seasonal differences in population size were observed. Number of months in which species are present with high number of individuals however indicates that variation in bird abundance over the year does exist. Several Nature2000 species reach their highest number of individuals in the Oosterschelde estuary in divergent months (Troost & Ysebaert, 2011). Bar-tailed godwit (10 out of 12 months), Eurasian Curlew (9), Dunlin (8), Oystercatcher (7), and Grey Plover (7) are expected to approach their highest numbers in more than six months per year. This are also the species with highest daily mean number of individuals counted during our study. Shelduck (6), Ruddy Turnstone (6), Red Knot (5), Sanderling (5), Common Redshank (5), Ringed Plover (4), Spotted Redshank (4), and Greenshank (3) have less months in which they reach their highest number of individuals, which possibly explains lower averaged numbers. Monthly differences are especially shown by maximum daily numbers of Red Knot, which exceed many other species' numbers despite of being higher on average. Therefore, it can be useful to take bird counts during species peak-months into account while analyzing population dynamics instead of yearly averaged numbers. This way of analysis prevents underestimation of species abundance during their peak seasons, as we did for Red Knot. Highest species richness was observed in spring and autumn. During these seasons waders migrate and visit stopover sites like the Roggenplaat (Troost & Ysebaert, 2011).

Hotspot selection criteria that include number of days on which birds were present are not affected by interspecies variation in number of months with peak numbers. The applied hotspot-selection factor for daily presence at the same location was based on the grid-cell with maximum periodic number of counting days of a species. Therefore, the scenario specific critical value based on 50% of maximum days differed for each species. Lower critical values of a certain species could have been induced in two ways: (1) monthly variation in presence per species causes low number of days that a species was counted, or (2) the individuals of a species are less bounded to specific locations. Biologging can provide more insight in location-loyalty of individual foraging birds. However, biologging has not been used as a research-method for studying bird behavior in the Oosterschelde before.

As no clear seasonal differences in abundance were observed between species we studied the effect of the moment in the tide on wader abundance and distribution. There were temporal differences in bird abundance at the Roggenplaat with low number of individuals present 1 to 3 hours after high tide (period 1) and high number of individuals present 3 to 7 hours after high tide (period 2 and 3). These differences occurred in all seasons. Individual Nature2000 bird species shown a comparable pattern in relative to the timing in the tide. This is in line with Zwarts *et al.* (2011) who studied exploitation of intertidal area in the entire Oosterschelde. They observed that number of individuals for foraging Dunlin, Oystercatcher, Eurasian Curlew, Grey Plover, Red Knot, and Redshank are lower during Period 1 (HW +1-3 hours) than during Period 2 and 3 (HW +3-7 hours). They also observed seasonal occurrence of this pattern for the Bar-tailed godwit during summer and winter, while there were more individuals counted during Period 1 than during Period 2 and 3 in spring.

By investigating expressed behavior our study showed Nature2000 species mainly use the Roggenplaat in Period 1 for resting and Period 2 and 3 to forage. This observation partly agrees with Granadeiro *et al.* (2006) who showed that Bar-tailed godwit, Grey Plover and Redshank are more intensively foraging at low tide (± 2hr) than during passing tide. However, they did not observe significant differences in foraging intensity of Dunlin between these phases of the tidal cycle, while Dunlin at the Roggenplaat are less frequently expressing resting behavior during low tide than during previous periods. Passing tide in their study also included rising tide. Bird counts during ebbing tide, as we collected during our study, are not representative for bird behavior and spatial abundance during rising tide (Dias et al., 2006). Foraging birds can be found up to five hours after low tide at the intertidal area of the Oosterschelde (Zwarts et al., 2011). This suggests that foraging waders are not leaving the intertidal shoal shortly after Period 3 of our study, neither will they move on to resting behavior quickly.

4.2 Spatial wader distribution

Bird hotspots and number of individuals per period gave insight in bird movement during an ebbing tide. Hotspots obviously differ per period. Dunlin, Oystercatcher, Curlew, and Sanderling arrive during Period 1 at the western part of the intertidal shoal, where they immediately start foraging. Bar-tailed godwit and Grey Plover also arrive during Period 1, but they generally express resting behavior after arrival. Red Knot and Redshank don't use the Roggenplaat at all during Period 1. As birds are counted from a boat which moves in counterclockwise direction starting in the middle at the southern side less intertidal area is exposed in the east at the start of period 1 than in the west at the end of period 1. This could explain why foraging hotspots during Period 1 mainly were observed on the western side of the intertidal shoal and resting peak densities were observed at the eastern side (Appendix 2). This means that larger parts of the intertidal shoal can be exposed on the western side, while birds also have longer to relocate and start foraging after high tide. Future counting using a boat can be done by making cycles in different directions and with changing starting point to create an averaged image of bird hotspots during Period 1.

All species that were studied are primarily foraging during Period 2 and 3. Most individuals of each species were present at the Roggenplaat during Period 2. Every species except Sanderling has a hotspot at the eastern side. Therefore, birds that are counted for the first time during Period 2 arrive at this area, or individuals that arrived earlier relocate between Period 1 and 2. The transition between Period 2 and 3 seems to be a more gradual one since generally the same regions are colonized, although hotspots are generally moving further towards the edges of the intertidal shoal. Dunlin, Eurasian Curlew, and Redshank foraging at the northern part of the intertidal shoal, while Oystercatcher and Grey Plover are using the entire intertidal shoal except the western part. The overlap of multiple species foraging hotspots indicate that foraging individuals co-occur in the same area and share their foraging ground. Wader flocks are known for comprising multiple species. In British estuaries Dunlin with Curlew/Bar-tailed godwit/Oystercatcher and Bar-tailed godwit with Dunlin/Curlew/Oystercatcher show aggregated co-occurrence patterns, whereas Grey Plover, Red Knot, Sanderling, and Redshank did not show significant co-occurrence patterns (Mendez Aragon, 2012). Our study shows there is certainly overlap between hotspots of Dunlin, Oystercatcher, Bar-tailed godwit and Eurasian Curlew during Period 2 and 3, which agrees with the sightings in British estuaries. In the bay of Saint-Brieuc, Eurasian Curlew presence was positively related to Oystercatcher, while Bar-tailed godwit and Red Knot were positively related in both ways (Ponsero et al., 2016). Also at the Roggenplaat a relation between Eurasian Curlew and Oystercatcher seems to be present as their hotpots overlap to a large extend. Bar-tailed godwit and Red Knot are however not clearly related when looking at their distribution at the Roggenplaat.

Possibly, the observed overlap of the calculated density hotspots of different species is not present in reality because of a subdivision of species within the polygons that were drawn during bird counts. Subdivision of wader species within polygon area was observed by bird counters as shown in Appendix 5 (Deltamilieu Projecten, personal communication, July 6, 2020). Polygons are drawn by hand during field observations and the attached bird counts include all individuals of species present in the selected area, so larger area can be appointed to a number of birds if they are only partly using the area covered by a polygon. It is therefore expected that high bird density peaks in the field were smoothened in our density maps due to the used counting method.

The observed maximum bird densities at the Roggenplaat were compared to maximum densities at the intertidal area of the Oosterschelde obtained from Zwarts *et al.* (2011) who counted bird presence in a fixed grid of plots (Table 7). Comparing these numbers gives insight into dependence of each bird species on the foraging ground at the Roggenplaat. The maximum densities of Dunlin, Oystercatcher, and Bar-tailed godwit at the Roggenplaat exceed the average densities of the Oosterschelde, which indicates the Roggenplaat provides important foraging ground for these species. Grey Plover, Red Knot and Redshank maximum densities were however higher for the averaged Oosterschelde counts. Especially Red Knot use foraging ground on different intertidal area of the Oosterschelde since their densities represent a larger fraction of total Nature2000 wader density. Eurasian Curlew densities are comparable for both situations, which indicates they are widely distributed in equal numbers per hectare. Comparison of densities of the Roggenplaat and the Oosterschelde confirms that maximum density peaks resulting from our polygon-based bird counting method are probably not reduced immensely due to smoothening since both densities are in the same order of magnitude.

Table 7: Observed bird densities at the Roggenplaat, obtained during our study, compared to plot-based bird densities at the intertidal area of the Oosterschelde obtained from Zwarts et al. (2011). Ratios show the density fraction of the total density of the seven species included in the table that each species represents.

Common name	Max density Roggenplaat (ind/ha)	Ratio (%) Roggenplaat	Max density Oosterschelde (ind/ha)	Ratio (%) Oosterschelde
Dunlin	127	50	70	48
Oystercatcher	73.5	30	24	17
Bar-tailed Godwit	27	11	10	7
Eurasian Curlew	10.4	4	11	8
Grey Plover	6.22	3	9	6
Red Knot	1.98	0.8	20	14
Redshank	0.95	0.4	1.8	1

4.3 Wader distribution in relation to environmental factors

Environmental factors overall contribute to the spatial distribution of waders at the Roggenplaat. Table 8 shows which species are affected by duration of exposure, benthic infauna and sediment grain size as was shown in our results. No overlap between both spatial bird and prey hotspots is observed for most species. For these species however an overlap between general prey presence and bird hotspots is observed more frequently.

Table 8: Effect of environmental factors included in our study on eight Nature2000 waders based on visual and numerical data analysis. 'Tide-following behavior' shows whether waders show significant higher densities in the lower exposure zones that are exposed during a Period. 'Predator-Prey abundance overlap' shows whether species specific benthic infauna diet biomass or density could be related to bird density hotspots. 'Fine sediment preference' shows whether species ignore foraging ground with relatively large d50 grain sizes.

Common name	Tide-following behavior	Predator-Prey abundance overlap	Fine sediment preference
Dunlin	Yes	No	No
Oystercatcher	No	Yes	Yes
Bar-tailed godwit	Yes	No	Yes
Eurasian Curlew	No	No	Yes
Grey Plover	Yes	No	Yes
Red Knot	No	Yes	Yes
Sanderling	Yes	Yes	No
Common Redshank	Yes	No	Yes

4.3.1 Tide-following behavior

Tidal constraints are expected to prevent species feeding in their preferred habitat (Nehls & Tiedeman, 1993; Mu & Wilcove, 2020). Our study confirms existence of an effect of exposure time on bird distribution. Densities per exposure zone show highest numbers in < 70% exposure zones. The importance of 0-80% exposure zones was already mentioned by de Ronde *et al.* (2013) who therefore suggested measures to counter habitat surface decline of the 40-80% exposure zones at the Roggenplaat. The 70-80% exposure zone has lower densities in our study, but this zone is important to stretch availability time of foraging ground (Mu & Wilcove, 2020). The longest duration of exposure zone is more intensively used in the few hours before and after high tide when it is the only area accessible (Zwarts et al., 2011). This suggests birds don't prefer this area if foraging ground with shorter duration of exposure is available. Peak densities are observed in 20-40% exposed zones in Period 3, which partly overlap with presence of low tide peak densities of all bird species combined in 28-50% exposure zone of the Dutch Wadden Sea (Blomert, 2002).

Waders not necessarily move towards the areas with shortest exposure time. Variation per species is caused by intrinsic behavior that differs regarding movement with the tide line (Mu & Wilcove, 2020). Dunlin and Sanderling are tide-followers that reached densities up to five times higher near the tide line than elsewhere in the Tagus estuary (Dias, 2008). Tide-followers maximize their foraging efficiency since macrobenthic infauna are most easily accessible if they are near the surface (Schultz, 1998). Oystercatcher, Bar-tailed godwit, Eurasian Curlew, Grey Plover, Red Knot and Redshank are generalist or zone-specialists that are not primarily following the tide line (Granadeiro et al., 2006; Mu & Wilcove, 2020). In our study, non-tide-following behavior is expressed by Oystercatcher, Eurasian Curlew and Red Knot since their densities are not significantly higher in low lying areas when the intertidal shoal is fully exposed. However, significant differences between short and long exposed areas are found for Dunlin, Bar-tailed godwit, Grey Plover, Sanderling and Redshank during Period 3. Tide-following behavior explains foraging grounds of Dunlin and Sanderling are located in the shortly exposed zones, which is actually induced by improved food accessibility. More striking are Bar-tailed godwit, Grey Plover and Redshank behavior since they are not intrinsic driven to forage near the tide line as described by literature (Mu & Wilcove, 2020). These species are attracted to low lying area since they are related to food availability in another way.

4.3.2 Food availability

A spatial relation between waders and their prey has been observed in earlier studies (Nehls & Tiedemann, 1993; Folmer et al., 2010; VanDusen et al., 2012; Ponsero et al., 2016). However, the results show the relation between waders with flexible- or polychaeta-based diets (Dunlin, Bar-tailed godwit, Eurasian Curlew, Grey Plover, Sanderling, and Redshank) and their prey is not directly explaining movement of these species towards areas with short duration of exposure since low prey density and biomass are found over there. Only Sanderling are obviously attracted towards the western part of the intertidal shoal during Period 2 because of their predator-prey relation with *Bathyporeia sp*. Bird hotspots located at the northeastern Roggenplaat during Period 3 are also striking since both the benthic infauna density and biomass are not reaching maximum amounts over there. Polychaeta are however providing suitable foraging grounds over the entire Roggenplaat because of their wide distribution. This gives waders with a polychaeta-based diet the opportunity to choose their preferred foraging spot. Literature shows polychaeta are a substantial part of Bar-tailed godwit and Grey Plover diet (Leopold et al., 2004). Polychaeta-Bivalvia ratio can therefore be a reason for Bar-tailed godwit and Grey Plover to feed at the southern part of the intertidal shoal despite relatively little overall benthic infauna abundance. Both locations that are dominated by polychaeta comprise a density hotspot of these wader species. Tide-following behavior of Bar-tailed godwit and Grey Plover can be related to this local ratio since this area also has short exposure time. Redshank behavior of following the tide line without intrinsic tide-following behavior is explained by another relation with macrobenthic infauna. Preferred Redshank prey *C. volutator* leaves their burrows directly after the mudflat becomes exposed, which makes them vulnerable. Shortly after exposure *C. volutator* return to their burrows and become harder to catch (Zwarts et al., 2011). Therefore, all species that were observed with higher densities in short exposure zones prefer that area because it provides food-related advantages that are not directly related to total biomass or density of prey.

Different locations for density and biomass peaks of benthic infauna in the visualized diets of species that are mainly foraging on Bivalvia (Oystercatcher and Red Knot) are caused by negative density dependent growth of bivalves (Jensen, 2009). Research of Bijleveld *et al.* (2016) showed predicted energy intake of Red Knot decreased if cockle density increases. Red Knot therefore prefers foraging area with intermediate density of medium sized cockles over high density of small cockles to maximize energy intake rate. WOT-survey data presented in our study indeed shows high densities of medium sized *L. balthica* overlap with Red Knot hotspots. It is expected that predators are commonly foraging on intermediate sized prey, so high densities not necessarily determine predator distribution (Bijleveld et al., 2016). Our study shows Oystercatcher distribution doesn’t fulfil this expectation since their main density hotspot overlaps primarily with high densities of 1-year *C. edule*. Other studies found a positive relation between benthic infauna total biomass and Oystercatcher density (Ponsero et al., 2016), which is not visible in our results. Future analysis of the relationship between waders with a bivalve-based diet and distribution of their prey should therefore include WOT-survey data since age and size-classes could potentially affect bird distribution. The absence of a clear positive relation between bird distribution and our benthic infauna data is striking since it is present while comparing bird density with WOT-survey data. Differences between both types of data could have been caused by using multiple year averages (2015/2019) or diet-based benthic species combinations in our data. Moreover, total sampled surface per location is about five times larger for the WOT-survey, which probably increases the reliability of the sample. The age-class distinction of WOT-survey data adds an extra factor to macrobenthic infauna analysis that has potential consequences on bird density.

4.3.3 Grain size preference

A study of VanDusen *et al.* (2012) showed that sediment composition clarifies a large part of the variability in bird distribution that remains unexplained after analyzing duration of exposure and benthic infauna distribution. They found out that benthic infauna community is largely affected by sediment size and exposure time, but there is also an unknown direct effect that influences distribution of waders. Our results indeed show most bird hotspots overlap with relatively lower d50 sediment grain size and high mud fractions. Only Sanderling are primarily found at the western part of the intertidal shoal. Literature suggests that coarser particles interfere with prey detection of birds with tactile foraging method, which causes a decline in foraging success (Finn et al., 2008). This explains Sanderling density hotspots can overlap with large d50 sediment grain sizes since this species uses a visual foraging method (VanDusen et al., 2012). Moreover, Sanderling are known for foraging on sandy beaches, which may be even a preferred foraging ground (Leopold et al., 2004). On the other hand, bird hotspots that are located at the eastern side of the Roggenplaat are positioned in the muddiest conditions. Muddy areas are close to reef structures that are known for enriching their surroundings and providing valuable foraging area (Wijsman et al., 2007). It is therefore surprising that large oyster reefs at the center of the intertidal shoal don't interfere with bird hotspots. Bird counters experience a restricted view in this area because of variation in bed level height (DPM, personal communication, July 6, 2020). This can be an explanation for the low number of birds that were counted near these specific oyster reefs. Moreover, field experiences indicate that Common Redshank are more bounded to foraging ground near Oyster reefs than could be observed in their density hotspot maps (DPM, personal communication, July 6, 2020).

4.3.4 Additional factors

There are non-included environmental factors that possibly affected spatial bird distribution too. Overestimation of available biomass for short-billed bird species occurs when biomass lives too deep (Zwarts & Wanink, 1991). Moreover, intrinsic behavior could explain variability since foraging birds prefer to aggregate in large flocks. This causes neglection of suitable foraging ground that would normally fit their demands (Folmer et al., 2012). Especially Dunlin, Bar-tailed godwit, Red Knot, Sanderling, and Redshank are highly gregarious. Additionally, previous studies mention Bar-tailed godwit is attracted towards low lying areas because of their preference for high sediment water content (Ponsero et al., 2016). This can explain foraging of Bar-tailed godwit at the southern intertidal shoal since their hotspots are positioned in low-lying area. Disturbance is another factor that makes waders usually leave their foraging area to go to safe grounds (Colwell, 2010; Rolet et al., 2015). During our study disturbances were caused by presence of humans (two times) and Peregrine Falcon (17 individuals counted).

Further research is required to find out to which extend each environmental factor actually affected spatial bird distribution at the Roggenplaat. Analyzing relation between sediment grain size, benthic infauna distribution and bird density distribution can be done in a numerical way by comparing rasterized heatmaps instead of point-based data. General increase in understanding influencing factors of benthic infauna distribution and accessibility to waders are required to be able to explain effects of environmental factors on bird distribution. A multitrophic overview of all influencing factors will be a complex interlinking system since benthic infauna distribution and community composition are also determined by sediment composition and exposure time. Moreover, increased accessibility of prey due to tide-following behavior seems to compensate for lower local prey density or biomass to attract several foraging wader species, while also negative density dependent growth of bivalves influences energy intake rates of Red Knot. These factors make the relation between benthic infauna and bird distribution even more complex. It is also recommended to include benthic infauna variability throughout the year. Seasonal differences in bird density can be analyzed for predator-prey relations if benthic infauna data will be collected during multiple seasons.

4.4 Evaluation of the nourishment design approach

4.4.1 Overlap between nourished area and wader hotspots

This study contributes to the impact assessment of seven constructed nourishments at the Roggenplaat by identifying natural patterns in bird distribution. Figure 18 shows the nourishments and combined bird hotspots to assess if nourishment location interferes with important locations for the wader population. It can be observed that all nourishments to some extend will overlay foraging ground of waders during low tide. Nourishment 3 and 6 cover least bird hotspots, so they can be considered as well placed nourishments. Larger foraging area is covered by the remaining nourishments. Especially nourishment 2, 4, 5 and VOV will overlay valuable foraging ground since they are located at sites where at least five bird species are frequently foraging. Considerable overlap occurs mostly during Period 3. Nourishment 4 overlays an extended foraging area and has therefore the largest interference with wader hotspots.

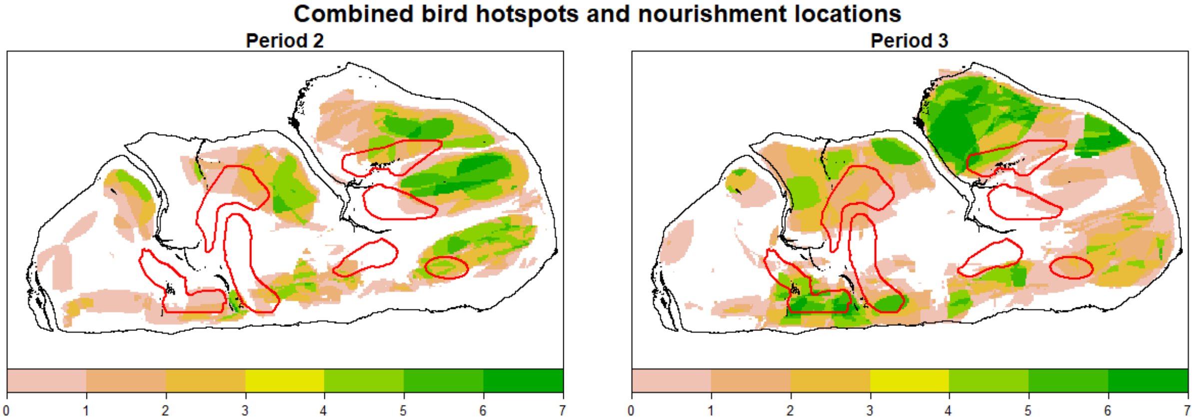


Figure 18: Combined bird hotspots per species during Period 2 and 3. Color bar shows the number of unique bird species that have a density hotspot on a specific location (max = 7). White indicates no bird hotspots were present. Nourishment 1-6 and VOV location are shown in red. Nourishment coding is presented in Figure 1.

Nourishments that will overlay bird hotspots probably affect local wader population in the long run, besides massive disturbance during construction. Site specific characteristics change largely after construction and it is therefore not assured that they still match with wader requirements. Environmental circumstances that are undesirable for ecology are created because of extreme burial induced by the Roggenplaat nourishments (Speybroeck et al., 2006; Baptist et al., 2009). Burial effects are negatively influenced by an increase in burial depth, burial time, sensitivity of benthic infauna, or different grain sizes (Baptist et al., 2009). As a result of burial, the underlying area becomes depleted foraging ground for waders for a certain period after construction since benthic infauna will die out locally. Benthic infauna recolonize the area after their arrival from unnourished areas or through the water column. Two pilot nourishments in the Oosterschelde at the Galgeplaat and Oesterdam showed that benthic infauna biomass fully recovered after 2-3 years (van der Werf et al., 2015; Boersema et al., 2018). Benthic community composition however differed from the original situation at both sites. Nourished foraging ground at the Galgeplaat was still used by Oystercatcher and Eurasian Curlew after benthic biomass restored. However, previously common waders such as Dunlin, Bar-tailed godwit, Grey Plover and Red Knot were hardly observed on the nourished area, while food was abundant and foraging area has enlarged duration of exposure (van der Werf et al., 2015). The return of Oystercatcher and Eurasian Curlew towards nourished foraging ground was also observed at the Oesterdam pilot nourishment. In addition, Shelduck kept using nourished area too.

Dunlin, Grey Plover and Redshank were only observed in unnourished area (Ysebaert et al., 2017). Changes in benthic infauna community were allocated to a significant increase in exposure time and sediment grain size (Ysebaert et al., 2017). The Roggenplaat nourishments however will be constructed using larger sediment grain size than was originally present (Vonhögen-Peeters et al., 2013). It is likely that benthic infauna community will differ from the original situation after recolonization (van der Werf et al., 2019). Based on both pilot studies Oystercatcher and Eurasian Curlew are expected to return to nourished area at the Roggenplaat after restoration of benthic biomass. Other wader species possibly abandon nourished locations. Dunlin and Grey Plover hotspots are widely spread over the intertidal shoal, so there is alternative foraging ground available that has proven to be valuable for them. Nourishments are conveniently located for Red Knot and Redshank since their hotspots will generally not be nourished. Density hotspots of Dunlin, Oystercatcher, Bar-tailed godwit, Eurasian Curlew, Grey Plover, Red Knot and Redshank are located adjacent to nourishment 2 and 3, which creates opportunities for stretching their foraging hotspots in the future. Less fortunately placed nourishment 4, 5 and VOV are constructed on valuable foraging ground of Sanderling and Bar-tailed godwit. Sanderling hotspots during low tide are buried by nourishments that makes their foraging ground inaccessible. Both Sanderling and Bar-tailed godwit have to find alternative foraging area until environmental characteristics fulfil their requirements again, which may possibly lead to large number of individuals abandoning the Roggenplaat. Field experiences during the first four months after nourishment construction as presented in Appendix 5 indicate that the nourished locations were not used by waders (DPM, personal communication, February 18, 2020).

Complete reduction of ecological impact during design of the Roggenplaat nourishment was complicated to achieve since a significant bed level elevation is required to maintain foraging ground for waders on the long term. Repeatedly disturbance of nourishment construction is avoided by large nourishments, which cause extreme burial on the other hand. Moreover, intertidal shoal nourishment requires usage of large sediment grain sizes to prevent fast erosion. As an alternative, a priming-layer can be used to enhance benthic infauna recolonization. Priming is implemented by removing the rich top 30cm of the sediment at the location that will be nourished and move the sediment on top of the nourishment after construction (Boersema et al., 2018). A pilot priming-layer has been added to nourishment 2 of the Roggenplaat (van der Werf et al., 2019).

4.4.2 Suitability criteria for nourishment location

Nourishment design approach can be improved by implementing bird foraging hotspots within location criteria. Roggenplaat nourishment design considered commercial mussel beds, haul-out area of seals, oyster reefs, tidal drainage channels, erosive area, and feasible construction locations in a suitability map that was used to determine most convenient nourishment locations (van der Werf et al., 2019). Figure 19 shows the original and updated suitability map that includes bird hotspots next to the originally used criteria. The map with all bird species hotspots combined shows the area that should ideally be avoided while selecting nourishment locations in grey. Obviously, insufficient amount of area remain to select appropriate nourishment locations. Therefore, criteria are relaxed in the third map, which only shows locations with more than two bird hotspots. This map shows nourishment 1, 3 and 6 meet requirements that takes prevention of disturbance of foraging waders into account. Nourishment 2, 4, 5 and VOV should have been designed in a different manner. Nourishment 2 should have been fitted within the green area on its eastern side, while the western part that overlays bird hotspots must be diminished. The 'tail' of nourishment 5 overlay an important foraging area for multiple species. This could have been avoided easily by locating the southern boundary slightly northward. Both other nourishments: 4 and VOV, were not optimal positioned regarding bird hotspots and cannot easily be adapted towards a design that meets requirements. The volume of sediment that was used could have been nourished adjacent to one of the nourishments that were placed more properly regarding bird hotspots. Moreover, notable amount of area that fulfils all requirements for convenient nourishment placement would have been available.

Overlay between important foraging ground and nourishments demonstrates future design approach of nourishments that are constructed to protect intertidal foraging ground should include spatial distribution of waders. More nourishments will be required in the future to preserve wader populations because of the global decrease of intertidal area. Our study showed that for some nourishments small adjustments to the design (nourishment 2 and 5) could reduce considerable disturbance during construction and possibly also in the long run. It was also shown that other nourishment designs (4 and VOV) could have been revised. Future research to the impact of the constructed nourishments at the Roggenplaat by studying bird distribution after construction can give a more substantiated answer regarding long term effects of each nourishment.

The other intertidal shoals in the Oosterschelde that provide valuable foraging ground for waders will also be preserved by constructing nourishments in the future. Holistic bird counts should therefore be planned ahead to be able to use spatial wader distribution as one of the suitability criteria for selecting nourishment locations. Moreover, an estuary overview of spatial use of intertidal area by waders can be used to identify barely used foraging ground in the Oosterschelde which might be improved to expand the overall foraging area in the estuary by strategic placement of nourishments.

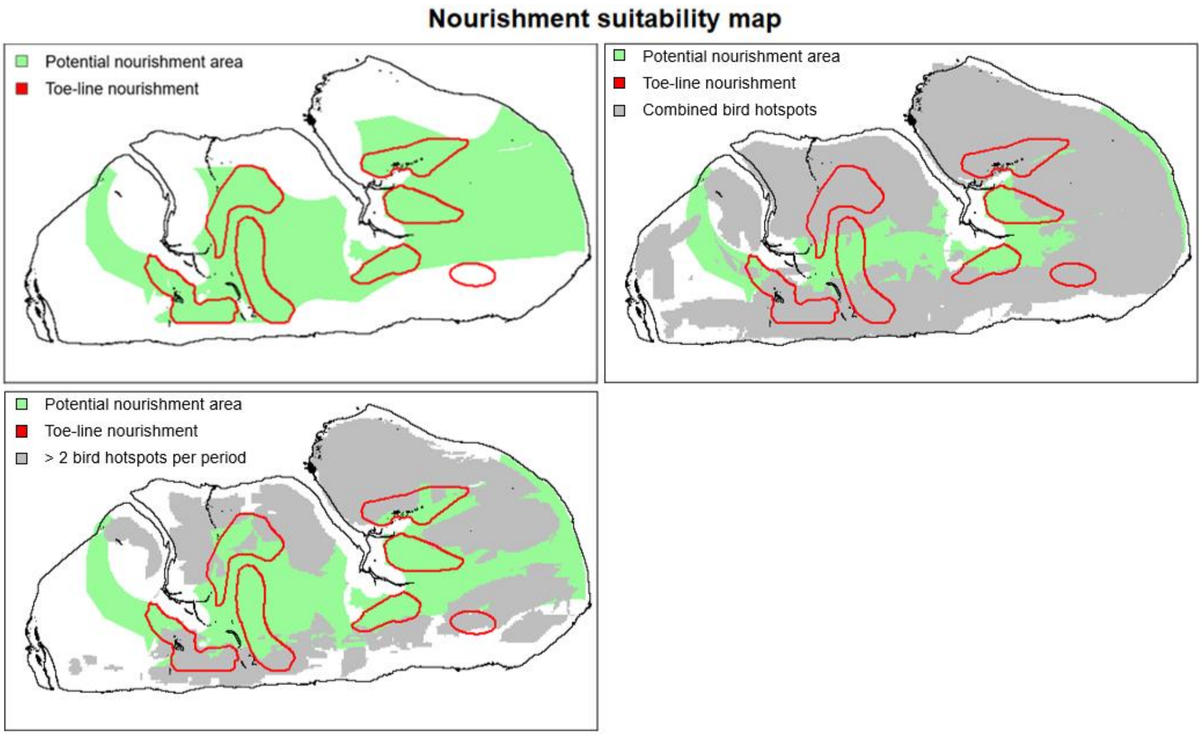


Figure 19: Suitability map of nourishments at the Roggenplaat. Green represents suitable nourishment area according to van der Werf et al. (2019). Suitability map without bird hotpots as was used for deciding nourishment locations is shown (top left). This suitability map is overlaid with bird hotspots of all species combined (right) and >2 bird species hotspots per period on a location (bottom left) in grey (hotspots period 2 and 3 are combined in each map). Nourishment (red) coding is according to figure 1. VOV nourishment serves foreshore protection purposes and is therefore located outside of the suitable area.

5. Conclusion

The main objective of this study was to identify natural presence of temporal and spatial patterns in wader distribution at the Roggenplaat and to look for existence of a relationship between these patterns and environmental factors: exposure time, benthic infauna distribution, and sediment grain size. Initially, an uniform pattern in temporal bird presence within a tidal cycle at the Roggenplaat was observed. Timeframe between three hours before low water and one hour after low water comprises most intensively utilized foraging time since significantly more foraging individuals were counted during Period 2 and 3 of our study than were counted during Period 1 (1-3 hours after high tide). General spatial patterns that were observed for foraging waders protected by Nature2000 are caused by the tidal cycle because waders mainly use areas positioned in > 50% exposure time in Period 1, ≈ 50% exposure time in Period 2, and < 50% exposure time in Period 3. Remaining interspecies variation in spatial distribution is caused by species specific preferences for environmental conditions.

Tidal constraints prohibited Dunlin, Bar-tailed godwit, Grey Plover, Sanderling, and Redshank from foraging in their preferred area or created favored conditions near the water line. This was shown by significantly higher wader densities in low exposure zones during low tide. Oystercatcher, Eurasian Curlew, and Red Knot do not favor foraging area in specific duration of exposure zones since their low tide densities were not divergent.

A positive relation between local wader densities and benthic infauna distribution are existent for Oystercatcher, Red Knot and Sanderling. Density hotspot of Oystercatchers correspond to density hotspot of small individuals of *C. edule*. Peak densities of Red Knot show overlap with medium sized *L. balthica* peak densities. Sanderling hotspots are related to both density and biomass peak of *Bathyporeia*. Dunlin, Bar-tailed godwit, Eurasian Curlew, Grey Plover and Redshank show no relation with benthic infauna in a way that bird hotspots overlap with highest prey biomass or density. Another type of relationship is existent because each species customized diet of benthic infauna covers the major part of the Roggenplaat, which causes overlap in presence of foraging waders and their prey. Furthermore, Bar-tailed godwit and Grey Plover are attracted to areas with unusually large proportion of polychaeta.

Sediment composition is also associated to wader distribution. Sanderling density hotspots are restricted to sediment with d50 grain size of 170 - 282 µm. Remaining species: Dunlin, Oystercatcher, Bar-tailed godwit, Eurasian Curlew, Grey Plover, Red Knot, and Redshank were less consistently observed while foraging on foraging ground with high d50 sediment size since their hotspots cover generally sediment grain sizes with d50 of 113 - 225 µm. All these species have their density hotspots at northeastern Roggenplaat where higher averaged mud fractions are present.

The relationship between spatial wader distribution and environmental factors demonstrate the importance of reducing overlay of wader hotspots with nourishments since exposure time, presence of benthic infauna, and sediment grain size are locally changed and therefore wader distribution will be affected. Studying wader distribution at the Roggenplaat after nourishment construction and comparing it to natural wader distribution will help understanding the impact of nourishments. It is recommended to include holistic spatial wader density hotspots to the suitability criteria of nourishment locations during the design process of human interventions in the future if they aim for protecting foraging ground. Understanding of wader distribution in a spatial and temporal manner and incorporate this knowledge effectively in management decisions that cope with challenges in the intertidal zone will help to preserve the valuable wader population in the Oosterschelde.

6. References

Arts, F.A., Hoekstein, M.S.J., Lilipaly, S.J., van Straalen, K.D., Sluijter, M., & Wolf, P.A. (2019). Kustbroedvogels in het Deltagebied in 2018. Rijkswaterstaat, Centrale informatievoorziening Rapport BM 19.07. Deltamilieu Projecten Rapportnr. 2019-05, Vlissingen.

Baker, A. J., Gonzalez, P. M., Piersma, T., Niles, L. J., de Lima Serrano do Nascimento, I., Atkinson, P. W., ... & Aarts, G. (2004). Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proceedings of the Royal Society of London. Series B: Biological Sciences, 271(1541), 875-882.

Baptist, M.J., Tamis, J.E., Borsje, B.W., & Van der Werf, J.J. (2009). Review of the geomorphological, benthic ecological and biogeomorphological effects of nourishments on the shoreface and surf zone of the Dutch coast. IMARES C113/08, Deltares Z4582.50.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B, 57, 289–300.

Besterman, A. F., Karpanty, S. M., & Pace, M. L. (2020). Impact of exotic macroalga on shorebirds varies with foraging specialization and spatial scale. *PloS one*, *15*(4), e0231337.

Blomert, A. M. (2002). De samenhang tussen bodemgesteldheid, droogligtijd en foerageerdichtheid van vogels binnen de intergetijdenzone. *A & W Rapport*.

Boersema, M. P., van der Werf, J., de Paiva, J. N. S., van den Brink, A. M., Soissons, L., Walles, B., ... & Bijleveld, M. (2018). Oesterdam sand nourishment: Ecological and morphological development of a local sand nourishment. Centre of Expertise Delta Technology.

Colwell, M. A. (2010). Shorebird ecology, conservation, and management. *Univ of California Press.*

Craeymeersch, J., & Escaravage, V. (2014). Perceel Benthos. PMR Monitoring natuurcompensatie Voordelta. Eindrapport 1e fase 2009-2013 deel B. . In: T. Prins and G. van der Kolff. Delft D (ed) Deltares rapport 1200672-ZKS-0043.

De Ronde, J.G., Mulder, J.P.M., Van Duren, L.A., & Ysebaert, T.J.W. (2013). Eindadvies ANT Oosterschelde, Deltares rapport 1207722-000-ZKS-0010.

Dias, M. A. F. P. (2008). Factors affecting the use of estuarine areas by waders: implications for their conservation (Doctoral dissertation, Universidade de Lisboa (Portugal)).

Dias, M. P., Granadeiro, J. P., Martins, R. C., & Palmeirim, J. M. (2006). Estimating the use of tidal flats by waders: inaccuracies due to the response of birds to the tidal cycle. *Bird Study*, *53*(1), 32-38.

Finn, P. G., Catterall, C. P., & Driscoll, P. V. (2008). Prey versus substrate as determinants of habitat choice in a feeding shorebird. *Estuarine, Coastal and Shelf Science*, *80*(3), 381-390.

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*(4), 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*(4), 551-561.

Fretwell, S. D. (1969). On territorial behavior and other factors influencing habitat distribution in birds. Acta biotheoretica, 19(1), 45-52.

Galbraith, H., Jones, R., Park, R., Clough, J., Herrod-Julius, S., Harrington, B., & Page, G. (2002). Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. Waterbirds, 25(2), 173-183.

Granadeiro, J. P., Dias, M. P., Martins, R. C., & Palmeirim, J. M. (2006). Variation in numbers and behaviour of waders during the tidal cycle: implications for the use of estuarine sediment flats. Acta oecologica, 29(3), 293-300.

Hesselink, A. W., van Maldegem, D. C., van der Male, K., & Schouwenaar, B. (2003). Verandering van de morfologie van de Oosterschelde door de aanleg van de Deltawerken. Evaluatie van de ontwikkeling in de periode 1985-2002. Werkdocument RIKZ/OS/2003.810 x. RIKZ, Middelburg.

Jensen, K. T. (1993). Density-dependent growth in cockles (Cerastoderma edule): evidence from interannual comparisons. *Journal of the Marine Biological Association of the United Kingdom*, *73*(2), 333-342.

Kruskal, W. (1952). Use of ranks in one-criterion variance analysis. Journal of the American Statistical Association. 47 (260): 583–621. doi:10.1080/01621459.1952.10483441.

Lack, P. (2010). The atlas of wintering birds in Britain and Ireland. A&C Black.

Leopold, M. F., Smit, C. J., Goedhart, P. W., Van Roomen, M. W. J., Van Winden, A. J., & Van Turnhout, C. (2004). 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 (No. 2004/07). Alterra.

Mann, H. B., & Whitney, D. R. (1947). On a Test of Whether one of Two Random Variables is Stochastically Larger than the Other. Annals of Mathematical Statistics. 18 (1): 50–60. doi:10.1214/aoms/1177730491. MR 0022058. Zbl 0041.26103.

Mendez Aragon, V. (2012). Spatial and temporal variation in the functional diversity of non-breeding wader communities across British estuaries (Doctoral dissertation, University of East Anglia).

Mu, T., & Wilcove, D. S. (2020). Upper tidal flats are disproportionately important for the conservation of migratory shorebirds. *Proceedings of the Royal Society B*, *287*(1928), 20200278.

Mulder, J. P., & Louters, T. (1994). Changes in basin geomorphology after implementation of the Oosterschelde estuary project. In The Oosterschelde Estuary (The Netherlands): a Case-Study of a Changing Ecosystem (pp. 29-39). Springer, Dordrecht.

Nehls, G., & Tiedemann, R. (1993). What determines the densities of feeding birds on tidal flats? A case study on Dunlin, Calidris alpina, in the Wadden Sea. Netherlands Journal of Sea Research, 31(4), 375-384.

Nienhuis, P.H. & Smaal, A.D. (1994). The Oosterschelde Estuary (The Netherlands): A case-study of a changing ecosystem. Kluwer Academic Publishers, 1994. ISSN 07923288175 Dfl. 475, 00. Internationale Revue der gesamten Hydrobiologie und Hydrographie, 82(1), 14-14.

Pitelka, F. A. (1979). Shorebirds in marine environments (No. 598.8 SHO). Cooper Ornithological Society.

Ponsero, A., Sturbois, A., Desroy, N., Le Mao, P., Jones, A., & Fournier, J. (2016). How do macrobenthic resources concentrate foraging waders in large megatidal sandflats?. Estuarine, Coastal and Shelf Science, 178, 120-128.

R Core Team (2019). R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rijkswaterstaat (2016). Natura 2000 Deltawateren Beheerplan Deltawateren 2016-2022 Oosterschelde, Ministerie van Infrastructuur en Milieu| Rijkswaterstaat.

Rolet, C., Spilmont, N., Davoult, D., Goberville, E., & Luczak, C. (2015). Anthropogenic impact on macrobenthic communities and consequences for shorebirds in Northern France: A complex response. *Biological Conservation*, *184*, 396-404.

Santinelli, G., & De Ronde, J. G. (2012). Volume analysis on RTK profiles of the Eastern Scheldt. Deltares, The Netherlands.

Schekkerman, H., Meininger, P.L.M., & Meire, P.M. (1994). Changes in the waterbird populations of the Oosterschelde 5SW Netherlands) as a result of large-scale coastal engineering works, in: Nienhuis, P.H. et al. (Ed.) The Oosterschelde Estuary (The Netherlands): a case-study of a changing ecosystem. Hydrobiologia, 97: pp. 509-524

Schellekens, T., Ens, B. J., & Ysebaert, T. (2013). Energiehuishouding van steltlopers en de effecten van verandering in foerageer-oppervlak op populaties: Studie uitgevoerd in het kader van ANT-Oosterschelde & LTV-Natuurlijkheid (No. C 067/13). IMARES.

Schultz, S. T. (1998). The Northwest coast: a natural history. Timber Press.

Shapiro, S. S., & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). Biometrika. 52 (3–4): 591–611. doi:10.1093/biomet/52.3-4.591. JSTOR 2333709. MR 0205384. p. 593

Speybroeck, J., Bonte, D., Courtens, W., Gheskiere, T., Grootaert, P., Maelfait, J. P., ... & Lancker, V. V. (2006). Beach nourishment: an ecologically sound coastal defence alternative? A review. *Aquatic conservation: Marine and Freshwater ecosystems*, *16*(4), 419-435.

Studds, C. E., Kendall, B. E., Murray, N. J., Wilson, H. B., Rogers, D. I., Clemens, R. S., ... & Milton, D. A. (2017). Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. Nature communications, 8(1), 1-7.

Troost, K., & Ysebaert, T. (2011). ANT Oosterschelde: Long-term trends of waders and their dependence on intertidal foraging grounds (No. C063/11). Imares.

Troost., K., van Asch., M., Brummelhuis., E. B. M., van den Ende., D., Perdon., J., van Zweeden., C., van Zwol, J. & v. d. Pool, J. (2019). Handboek bestandsopnames schelpdieren WOT Versie 3, december 2019. CVO rapport: 18.013.

Tukey, J. (1949). Comparing Individual Means in the Analysis of Variance. Biometrics. 5 (2): 99–114. JSTOR 3001913.

Van Asch, M., van den Ende, D., van der Pool, J., Brummelhuis, E.B., van Zweeden, C., van Es, Y., & Troost, K., (2019). Het kokkelbestand in de Nederlandse kustwateren in 2019.

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 (No. 19.022). Stichting Wageningen Research, Centrum voor Visserijonderzoek (CVO).

Van der Werf, J. J., De Vet, P., Boersema, M. P., Bouma, T. J., Nolte, A. J., Schrijvershof, R. A., ... & Ysebaert, T. (2019). An integral approach to design the Roggenplaat intertidal shoal nourishment. *Ocean & coastal management*, *172*, 30-40.

Van der Werf, J., Reinders, J., Van Rooijen, A., Holzhauer, H., & Ysebaert, T. (2015). Evaluation of a tidal flat sediment nourishment as estuarine management measure. Ocean & coastal management, 114, 77-87.

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. Eds.: Kloepper S. et al., Common Wadden Sea Secretariat, Wilhelmshaven, Germany. Last updated 21.12.2017.

Van Zanten, E., & Adriaanse, L. A. (2008). Verminderd getij. Verkenning naar mogelijke maatregelen om het verlies van platen, slikken en schorren in de Oosterschelde te beperken. Rijkswaterstaat Zeeland, Middelburg, The Netherlands.

VanDusen, B. M., Fegley, S. R., & Peterson, C. H. (2012). Prey distribution, physical habitat features, and guild traits interact to produce contrasting shorebird assemblages among foraging patches. PloS one, 7(12).

Vonhögen-Peeters, L., De Kleine, M., Rutten, R., Marges, V., & Mesdag, C., (2013). Verkenning Zandwinning Oosterschelde. Report 1205505-000. Deltares, The Netherlands (in Dutch).

Walles, W., Slager, A., Wijsman, J., & Ysebaert, T. (2019). Procesmonitoring en risicomonitoring realisatie suppletie Roggenplaat 2018-2020: Tweemaandelijks voortgangsrapport 11: 1 september – 31 oktober 2019. Rapport Wageningen Marine Research Wageningen UR (University & Research centre), Yerseke.

Ysebaert, T., Brummelhuis, E., van den Ende, D., van Ijzerloo, L., van Dalen, J., & Walles, B. (2017). The conservation of eroding intertidal flats through nourishments: Ecological development on the Oesterdam tidal flat (Oosterschelde, the Netherlands). Wageningen Marine Research Report.

Ysebaert, Y., van der Werf, J., de Vet, L., Bouma, T. (2016). Monitoringsplan Roggenplaat Suppletie. Definitief.1. Centre of Expertise Delta Technology.

Zwarts, L., & Wanink, J. H. (1991). The macrobenthos fraction accessible to waders may represent marginal prey. *Oecologia*, *87*(4), 581-587.

Zwarts, L., Blomert, A.M., Bos, D., & Sikkema, M. (2011). Exploitation of intertidal flats in the Oosterschelde by estuarine birds, A&W rapport 1657 Altenburg & Wymenga ecologisch onderzoek, Feanwâlden

7. Appendices

7.1 Appendix 1: Overview of all bird counts

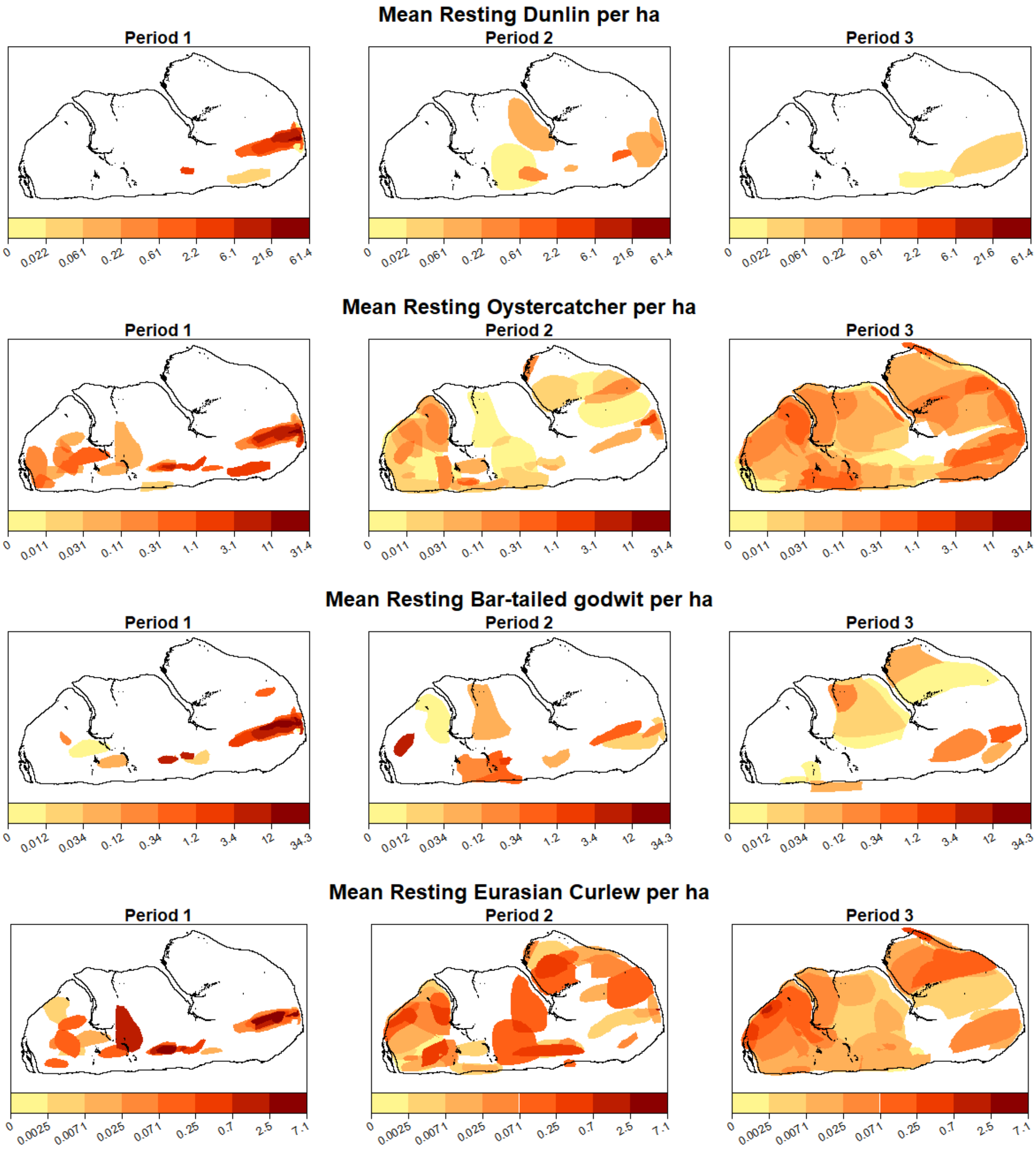
Table 7.1.1: All bird species counted over all 25 counting days combined. Number of individuals counted shows the largest periodic number of birds of each day summed for all counting days. Daily mean shows the daily average of the maximum periodic number of individuals counted on each counting day. Nature2000 bottleneck yes/no indicates whether a species is classified as a bottleneck species for intertidal area in the Oosterschelde (Rijkswaterstaat, 2016).

English name	Taxa	Individuals counted	Daily mean	Range daily numbers Min	Max	Nature2000 bottleneck
Dunlin	*Calidris alpina*	120949	4838	100	12341	Yes
Bar-tailed Godwit	*Limosa lapponica*	67245	2690	510	5417	Yes
Oystercatcher	*Haematopus ostralegus*	67209	2688	426	5811	Yes
Eurasian Curlew	*Numenius arquata*	48887	1995	114	5216	Yes
Grey Plover	*Pluvialis squatarola*	44679	1787	26	3309	Yes
Black-headed Gull	*Larus ridibundus*	33451	1338	0	8668	No
Red Knot	*Calidris canutus*	26399	1056	10	8705	Yes
European Herring Gull	*Larus argentatus*	18226	729	0	2661	No
Sanderling	*Calidris alba*	9276	371	21	1581	Yes
Brant	*Branta bernicla*	5783	231	0	1418	No
Common Gull	*Larus canus*	3330	133	0	511	No
Common Eider	*Somateria mollissima*	3268	131	0	530	No
Common Shelduck	*Tadorna tadorna*	1701	68	0	815	Yes
Great Cormorant	*Phalacrocorax carbo*	1511	60	0	542	No
Common Redshank	*Tringa totanus*	1081	43.2	0	174	Yes
Common Tern	*Sterna hirundo*	947	37.9	0	230	No
Common Ringed Plover	*Charadrius hiaticula*	709	28.0	0	144	Yes
Eurasian Spoonbill	*Platalea leucorodia*	476	19.0	0	144	No
Ruddy Duck	*Oxyura jamaicensis*	470	18.8	0	470	No
Great Black-backed Gull	*Larus marinus*	463	18.5	0	72	No
Sandwich Tern	*Sterna sandvicensis*	361	14.4	0	120	No
Barnacle Goose	*Branta leucopsis*	332	13.0	0	330	No
Greylag Goose	*Anser anser*	268	10.7	0	130	No
Lesser Black-backed Gull	*Larus fuscus*	268	10.7	0	130	No
Eurasian Wigeon	*Anas penelope*	214	8.6	0	89	No
Ruddy Turnstone	*Arenaria interpres*	208	8.0	0	40	Yes
Mallard	*Anas platyrhynchos*	186	7.4	0	74	No
Eurasian Magpie	*Pica pica*	130	5.2	0	130	No
Eurasian Whimbrel	*Numenius phaeopus*	109	4.4	0	54	No
Common Greenshank	*Tringa nebularia*	95	3.8	0	31	Yes
Northern Pintail	*Anas acuta*	91	4.0	0	60	No
Red-breasted Merganser	*Mergus serrator*	87	3.0	0	34	No
Little Egret	*Egretta garzetta*	57	2.3	0	14	No
Black-tailed Godwit	*Limosa limosa*	51	2.0	0	39	No
Peregrine Falcon	*Falco peregrinus*	17	0.68	0	3	No
Common Goldeneye	*Bucephala clangula*	15	0.60	0	15	No
Spotted Redshank	*Tringa erythropus*	15	0.60	0	3	Yes
Horned Grebe	*Podiceps auritus*	13	0.52	0	12	No
Great Crested Grebe	*Podiceps cristatus*	12	0.48	0	11	No
Mediterranean Gull	*Larus melanocephalus*	12	0.48	0	11	No
Little Tern	*Sterna albifrons*	9	0.36	0	4	No
Black Brant	*Branta bernicla nigricans*	7	0.28	0	1	No
European Golden Plover	*Pluvialis apricaria*	6	0.24	0	5	No
Tundra Swan	*Cygnus columbianus*	6	0.24	0	6	No
Little Stint	*Calidris minuta*	5	0.20	0	4	No
Eurasian Teal	*Anas crecca*	5	0.20	0	4	No
Common Scoter	*Melanitta nigra*	5	0.20	0	5	No

Northern Lapwing	*Vanellus vanellus*	3	0.12	0	2	No
Arctic Tern	*Sterna paradisaea*	3	0.12	0	3	No
Common Snipe	*Gallinago gallinago*	3	0.12	0	3	No
Pied Avocet	*Recurvirostra avosetta*	2	0.08	0	1	No
Caspian Gull	*Larus cachinnans cachinnans*	2	0.08	0	1	No
Black Tern	*Chlidonias niger*	2	0.08	0	2	No
Yellow-legged Gull	*Larus cachinnans michahellis*	1	0.04	0	1	No
Curlew Sandpiper	*Calidris ferruginea*	1	0.04	0	1	No
European Shag	*Phalacrocorax aristotelis*	1	0.04	0	1	No
Broad-billed Sandpiper	*Limicola falcinellus*	1	0.04	0	1	No
Egyptian Goose	*Alopochen aegyptiacus*	1	0.04	0	1	No
Red Phalarope	*Phalaropus fulicaria*	1	0.04	0	1	No
Red-necked Grebe	*Podiceps griseigena*	1	0.04	0	1	No
Northern Shoveler	*Anas clypeata*	1	0.04	0	1	No
Eurasian Sparrowhawk	*Accipiter nisus*	1	0.04	0	1	No
Common Starling	*Sturnus vulgaris*	1	0.04	0	1	No
Osprey	*Pandion haliaetus*	1	0.04	0	1	No
Common Loon	*Gavia immer*	1	0.04	0	1	No

7.2 Appendix 2: Resting Nature2000 species distribution

Spatial distribution of resting individuals shows where on the Roggenplaat species express resting behavior. Density maps of all resting Nature2000 species, excluding Common Redshank, Ruddy Turnstone, Common Greenshank, and Spotted Redshank, are shown in Figure 7.2.1. Common Redshank, Ruddy Turnstone, Common Greenshank, and Spotted Redshank were not frequently counted while expressing resting behavior. Resting individuals of these species were absent during one or more periods. The density maps show that all species use the same area during Period 1 since all species except Sanderling use the eastern part of intertidal shoal where also highest densities are reached. In Period 2 and 3 are Oystercatcher and Eurasian Curlew the only species that were counted on many parts of the intertidal shoal while resting. Moreover, Bar-tailed godwit, Grey Plover and Common Shelduck distribution cover a notable part of the Roggenplaat. The remaining species are barely observed while resting during Period 2 or 3, so they do not cover large area.



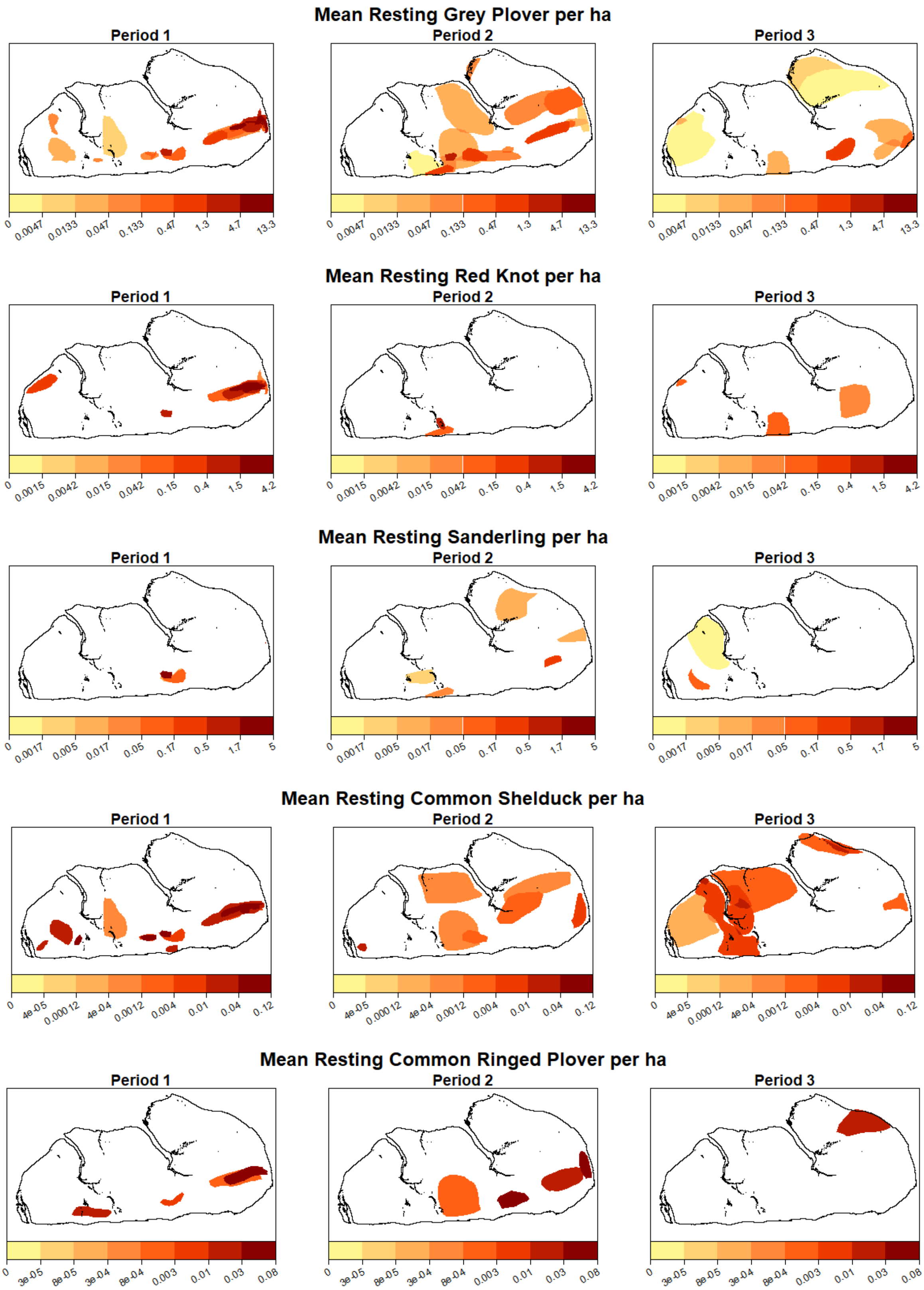


Figure 7.2.1: Daily averaged (n=25) density maps of Nature2000 species while expressing resting behavior during Period 1, 2, and 3. Color bar shows number of individuals per hectare.

7.3 Appendix 3: Foraging Nature2000 species distribution

The spatial distribution of Nature2000 species that were not presented in Figure 9 are shown in Figure 7.3.1. Common Shelduck primarily uses the western part of the Roggenplaat for foraging during Period 1. The other species are less frequently observed or completely absent during Period 1. In Period 3 the Common Shelduck is the only species that uses large parts of the intertidal shoal. The Common Ringed Plover, Ruddy Turnstone, and Common Greenshank primarily use the eastern or northeastern side of the Roggenplaat during Period 3. Spotted Redshank counts did not overlap, so its distribution seems to be more random.

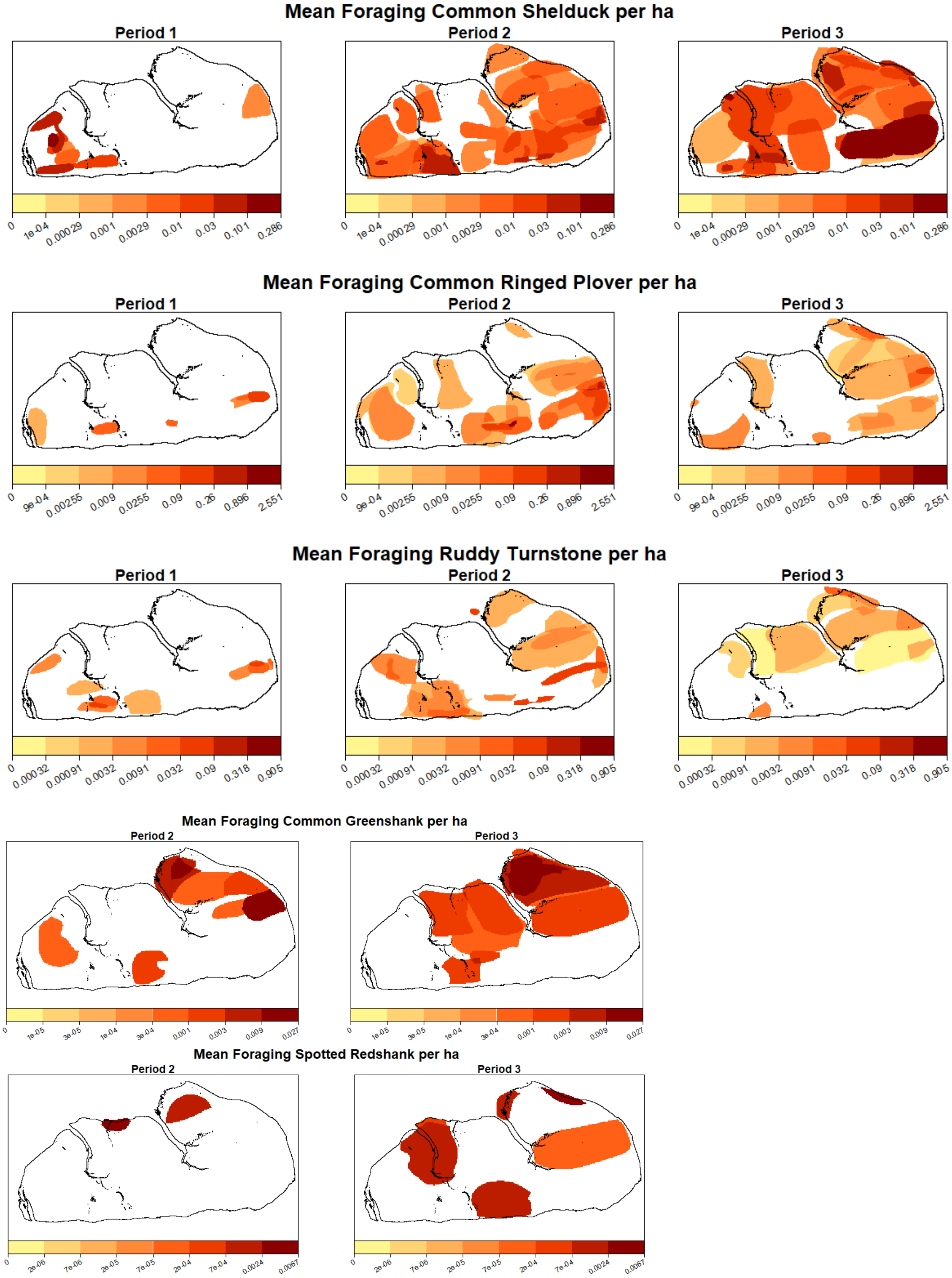


Figure 7.3.1: Daily averaged (n=25) density maps (ind/ha) of Nature2000 species while expressing foraging behavior during Period 1, 2, and 3. Common Greenshank and Spotted Redshank had no counts during Period 1.

7.4 Appendix 4: Statistical tests of bird density in exposure zones

Bird densities in different exposure time zones were statistically compared to find significant differences (*p* < 0.05). Outcome of the statistical tests are shown for eight studied Nature2000 species.

7.4.1 Foraging Dunlin

Period 2

Kruskal-Wallis test by ranks: chi-squared = 20.436, df = 9, p-value = 0.0154

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.496	-	-	-	-	-	-	-	-
20-30	0.271	0.484	-	-	-	-	-	-	-
30-40	0.254	0.442	0.959	-	-	-	-	-	-
40-50	0.116	0.364	0.746	0.834	-	-	-	-	-
50-60	**0.032**	0.123	0.411	0.460	0.449	-	-	-	-
60-70	**0.032**	0.116	0.364	0.442	0.442	0.959	-	-	-
70-80	0.291	0.449	0.959	0.959	0.775	0.442	0.419	-	-
80-90	0.746	0.969	0.702	0.595	0.465	0.388	0.364	0.655	-
90-100	0.801	0.607	0.406	0.364	0.364	0.137	0.123	0.364	0.746

Period 3

Kruskal-Wallis test by ranks: chi-squared = 31.77, df = 9, p-value = 0.0002182

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.203	-	-	-	-	-	-	-	-
20-30	0.094	0.556	-	-	-	-	-	-	-
30-40	0.096	0.624	0.931	-	-	-	-	-	-
40-50	0.203	0.967	0.623	0.697	-	-	-	-	-
50-60	0.254	0.977	0.556	0.637	0.931	-	-	-	-
60-70	0.957	0.347	0.203	0.203	0.325	0.370	-	-	-
70-80	0.580	0.231	0.157	0.179	0.214	0.254	0.623	-	-
80-90	0.150	**0.032**	**0.019**	**0.019**	**0.032**	**0.037**	0.179	0.484	-
90-100	**0.037**	**0.018**	**0.018**	**0.018**	**0.018**	**0.018**	**0.038**	0.179	0.624

7.4.2 Foraging Oystercatcher

Period 2

Kruskal-Wallis test by ranks: chi-squared = 24.424, df = 9, p-value = 0.00368

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.2808	-	-	-	-	-	-	-	-
20-30	0.0725	0.3765	-	-	-	-	-	-	-
30-40	0.0638	0.3765	0.9768	-	-	-	-	-	-
40-50	**0.0459**	0.3256	0.9436	0.8756	-	-	-	-	-
50-60	**0.0048**	0.0638	0.2520	0.2520	0.2520	-	-	-	-
60-70	**0.0459**	0.2520	0.7012	0.7012	0.7968	0.5321	-	-	-
70-80	0.0948	0.4826	0.9436	0.9436	0.9436	0.2808	0.7012	-	-
80-90	0.7012	0.7012	0.4378	0.4817	0.3765	0.1286	0.2810	0.4817	-
90-100	0.7012	0.3765	0.2520	0.2520	0.2520	0.0638	0.1650	0.2520	0.6758

Period 3

Kruskal-Wallis test by ranks: chi-squared = 10.733, df = 9, p-value = 0.2945 (not significant)

7.4.3 Foraging Bar-tailed godwit

Period 2

Kruskal-Wallis test by ranks: chi-squared = 32.256, df = 9, p-value = 0.0001798

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.485	-	-	-	-	-	-	-	-
20-30	0.148	0.559	-	-	-	-	-	-	-
30-40	0.088	0.461	0.894	-	-	-	-	-	-
40-50	0.051	0.217	0.629	0.666	-	-	-	-	-
50-60	**0.042**	0.148	0.559	0.541	0.559	-	-	-	-
60-70	0.148	0.441	0.934	0.922	0.953	0.559	-	-	-
70-80	0.934	0.559	0.217	0.141	0.088	0.051	0.217	-	-
80-90	0.559	0.235	0.090	**0.047**	**0.024**	**0.018**	0.051	0.577	-
90-100	0.235	0.078	**0.024**	**0.017**	**0.012**	**0.012**	**0.024**	0.254	0.595

Period 3

Kruskal-Wallis test by ranks: chi-squared = 79.153, df = 9, p-value = 2.38e-13

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.39741	-	-	-	-	-	-	-	-
20-30	0.16141	0.39659	-	-	-	-	-	-	-
30-40	0.18964	0.44712	0.94581	-	-	-	-	-	-
40-50	0.24044	0.72268	0.57947	0.57947	-	-	-	-	-
50-60	0.29761	0.90430	0.35044	0.43405	0.70946	-	-	-	-
60-70	0.20663	**0.01169**	**0.00299**	**0.00350**	**0.00536**	**0.00899**	-	-	-
70-80	**0.03476**	**0.00514**	**0.00088**	**0.00120**	**0.00216**	**0.00350**	0.28679	-	-
80-90	**0.00088**	**0.00021**	**4.4e-05**	**4.4e-05**	**6.8e-05**	**8.0e-05**	**0.01169**	0.21867	-
90-100	**2.4e-05**	**7.5e-06**	**6.8e-06**	**6.8e-06**	**6.8e-06**	**6.8e-06**	**0.00021**	**0.01169**	0.20663

7.4.4 Foraging Eurasian Curlew

Period 2

Kruskal-Wallis test by ranks: chi-squared = 33.268, df = 9, p-value = 0.00012

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.326	-	-	-	-	-	-	-	-
20-30	0.102	0.395	-	-	-	-	-	-	-
30-40	**0.040**	0.326	0.638	-	-	-	-	-	-
40-50	**0.028**	0.322	0.638	0.758	-	-	-	-	-
50-60	**0.017**	0.138	0.372	0.337	0.445	-	-	-	-
60-70	0.057	0.395	0.786	0.799	0.904	0.610	-	-	-
70-80	0.322	0.938	0.464	0.202	0.180	0.067	0.244	-	-
80-90	0.454	0.159	0.083	0.056	**0.046**	**0.028**	0.056	0.296	-
90-100	0.244	0.075	**0.028**	**0.017**	**0.017**	**0.017**	**0.017**	0.121	0.511

Period 3

Kruskal-Wallis test by ranks: chi-squared = 27.132, df = 9, p-value = 0.00133

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.220	-	-	-	-	-	-	-	-
20-30	0.062	0.361	-	-	-	-	-	-	-
30-40	0.062	0.220	0.637	-	-	-	-	-	-
40-50	0.062	0.279	0.857	0.725	-	-	-	-	-
50-60	0.079	0.499	0.637	0.396	0.539	-	-	-	-
60-70	0.830	0.466	0.159	0.107	0.138	0.220	-	-	-
70-80	0.573	0.573	0.207	0.124	0.138	0.279	0.923	-	-
80-90	0.466	0.220	0.138	0.098	0.124	0.138	0.479	0.545	-
90-100	0.220	0.098	0.062	0.062	0.069	0.079	0.237	0.273	0.499

7.4.5 Foraging Grey Plover

Period 2

Kruskal-Wallis test by ranks: 33.694, df = 9, p-value = 0.000101

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.0900	-	-	-	-	-	-	-	-
20-30	**0.0216**	0.1610	-	-	-	-	-	-	-
30-40	**0.0216**	0.1358	0.7072	-	-	-	-	-	-
40-50	**0.0211**	0.0900	0.4870	0.6459	-	-	-	-	-
50-60	**0.0063**	**0.0216**	0.0634	0.0634	0.1143	-	-	-	-
60-70	**0.0063**	**0.0211**	0.0634	0.0774	0.1358	0.9923	-	-	-
70-80	0.3309	0.8955	0.7072	0.5642	0.4010	0.0634	0.0731	-	-
80-90	0.6172	0.8955	0.7953	0.6459	0.4757	0.0731	0.0900	0.8546	-
90-100	0.7473	0.3460	0.1380	0.1380	0.1107	**0.0313**	**0.0216**	0.3994	0.6158

Period 3

Kruskal-Wallis test by ranks: chi-squared = 34.209, df = 9, p-value = 8.21e-05

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.256	-	-	-	-	-	-	-	-
20-30	0.066	0.433	-	-	-	-	-	-	-
30-40	0.061	0.338	0.885	-	-	-	-	-	-
40-50	0.091	0.554	0.859	0.719	-	-	-	-	-
50-60	0.083	0.582	0.871	0.732	0.952	-	-	-	-
60-70	0.885	0.352	0.138	0.093	0.177	0.177	-	-	-
70-80	0.177	0.061	**0.040**	**0.040**	0.058	**0.047**	0.177	-	-
80-90	0.177	0.067	0.059	0.061	0.067	0.066	0.177	0.992	-
90-100	0.061	**0.031**	**0.020**	**0.020**	**0.020**	**0.020**	0.061	0.327	0.352

7.4.6 Foraging Red Knot

Period 2

Kruskal-Wallis test by ranks: chi-squared = 44.028, df = 9, p-value = 1.395e-06

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.6647	-	-	-	-	-	-	-	-
20-30	0.1587	0.4467	-	-	-	-	-	-	-
30-40	0.0883	0.1984	0.7908	-	-	-	-	-	-
40-50	**0.0493**	0.1023	0.5448	0.6742	-	-	-	-	-
50-60	**0.0036**	**0.0136**	0.0921	0.1023	0.1466	-	-	-	-
60-70	**0.0036**	**0.0072**	**0.0534**	0.0662	0.1466	0.8458	-	-	-
70-80	0.6448	0.8379	0.7758	0.6448	0.3814	0.0919	0.0534	-	-
80-90	0.1466	0.1093	**0.0493**	**0.0265**	**0.0161**	**0.0036**	**0.0036**	0.1482	-
90-100	0.0662	0.0508	**0.0206**	**0.0117**	**0.0036**	**0.0033**	**0.0033**	0.0919	0.7908

Period 3

Kruskal-Wallis test by ranks: chi-squared = 25.944, df = 9, p-value = 0.002087

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.730	-	-	-	-	-	-	-	-
20-30	0.454	0.708	-	-	-	-	-	-	-
30-40	0.415	0.631	0.938	-	-	-	-	-	-
40-50	0.631	0.773	0.928	0.916	-	-	-	-	-
50-60	0.605	0.760	1.000	1.000	0.888	-	-	-	-
60-70	0.656	0.415	0.321	0.321	0.401	0.364	-	-	-
70-80	0.102	0.078	0.062	0.062	0.062	0.062	0.321	-	-
80-90	0.134	0.102	0.072	0.078	0.102	0.074	0.364	1.000	-
90-100	0.065	0.062	0.062	0.062	0.062	0.062	0.106	0.717	0.717

7.4.7 Foraging Sanderling

Period 2

Kruskal-Wallis test by ranks: chi-squared = 20.901, df = 9, p-value = 0.0131

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.713	-	-	-	-	-	-	-	-
20-30	0.626	0.811	-	-	-	-	-	-	-
30-40	0.503	0.669	0.809	-	-	-	-	-	-
40-50	0.503	0.713	0.811	0.951	-	-	-	-	-
50-60	0.246	0.503	0.669	0.795	0.781	-	-	-	-
60-70	0.503	0.724	0.795	0.899	0.899	0.811	-	-	-
70-80	1.000	0.811	0.781	0.669	0.669	0.489	0.604	-	-
80-90	0.489	0.390	0.274	0.174	0.174	0.106	0.174	0.503	-
90-100	0.086	0.055	**0.042**	**0.032**	**0.032**	**0.032**	**0.032**	0.163	0.669

Period 3
Kruskal-Wallis test by ranks: chi-squared = 44.277, df = 9, p-value = 1.255e-06

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.7438	-	-	-	-	-	-	-	-
20-30	0.5204	0.7230	-	-	-	-	-	-	-
30-40	0.5330	0.9978	0.8295	-	-	-	-	-	-
40-50	1.0000	0.6938	0.4821	0.5764	-	-	-	-	-
50-60	0.9553	0.6803	0.4699	0.5204	1.0000	-	-	-	-
60-70	0.1397	0.0771	**0.0356**	**0.0272**	0.1115	0.0790	-	-	-
70-80	0.1361	0.0787	**0.0419**	**0.0490**	0.1290	0.1115	0.6803	-	-
80-90	**0.0104**	**0.0053**	**0.0034**	**0.0034**	**0.0053**	**0.0053**	0.0787	0.4165	-
90-100	**0.0020**	**0.0017**	**0.0016**	**0.0016**	**0.0017**	**0.0016**	**0.0122**	0.1115	0.5204

7.4.8 Foraging Common Redshank

Period 2
Kruskal-Wallis test by ranks: chi-squared = 34.795, df = 9, p-value = 6.474e-05

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.688	-	-	-	-	-	-	-	-
20-30	0.362	0.650	-	-	-	-	-	-	-
30-40	0.182	0.368	0.687	-	-	-	-	-	-
40-50	0.053	0.182	0.496	0.688	-	-	-	-	-
50-60	0.062	0.178	0.414	0.662	0.923	-	-	-	-
60-70	0.662	0.923	0.714	0.480	0.343	0.331	-	-	-
70-80	0.304	0.182	0.083	**0.045**	**0.017**	**0.017**	0.258	-	-
80-90	0.083	0.053	**0.036**	**0.017**	**0.011**	**0.011**	0.094	0.480	-
90-100	**0.041**	**0.024**	**0.016**	**0.011**	**0.006**	**0.006**	0.053	0.304	0.714

Period 3
Kruskal-Wallis test by ranks: chi-squared = 72.265, df = 9, p-value = 5.466e-12

Mann-Whitney U test:

	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
10-20	0.45633	-	-	-	-	-	-	-	-
20-30	0.39187	0.84891	-	-	-	-	-	-	-
30-40	0.29933	0.79440	0.97493	-	-	-	-	-	-
40-50	0.45633	0.97493	0.95488	0.84891	-	-	-	-	-
50-60	0.16249	0.69724	0.87751	0.84891	0.61951	-	-	-	-
60-70	0.52734	0.15351	0.06365	0.07063	0.08205	**0.03219**	-	-	-
70-80	**0.00563**	**0.00025**	**0.00019**	**0.00017**	**0.00021**	**0.00014**	**0.01823**	-	-
80-90	**0.00062**	**2.5e-05**	**2.5e-05**	**2.5e-05**	**2.5e-05**	**2.5e-05**	**0.00154**	0.54503	-
90-100	**0.00046**	**2.5e-05**	**2.5e-05**	**2.5e-05**	**2.5e-05**	**2.5e-05**	**0.00149**	0.55483	1.00000

7.5 Appendix 5: Personal communication with bird counters

On July 6, 2020 bird counters of Deltamilieu Projecten gave their opinion about topics that were discussed in our study to check whether our findings agree with field observations (Table 7.5.1).

Table 7.5.1: Field experiences of bird counters at the Roggenplaat of Deltamilieu Projecten (July 6, 2020).

Topic	Deltamilieu projecten
Margin of Error bird counts	• Based on experiences an error margin of ±10% is estimated. It primarily depends on group size and species.
Resting bird hotspots selected by this study	• Factors that birds prefer for resting: (1) Exposed area, (2) Close to foraging ground, (3) No disturbance, and (4) Close to high water residence. • Period 1 resting distribution: These areas are probably exposed during high water, so birds could stay at the Roggenplaat during high water. • Period 2 resting distribution: These birds are waiting for their preferred foraging ground to become exposed. • Period 3 resting distribution: These birds finished foraging and look for a place where no disturbance occurs. They will continue foraging when water level rises again.
Foraging bird hotspots selected by this study	• Bird hotspots selected in this study agree with field observations. • There is an area with restricted view at the center of the intertidal shoal at the end of the Middle gully (most eastern gully). It seems that birds are not foraging in large numbers at this location (also in the field), but these low numbers that were counted are probably also caused by a restricted view. • Bird movement towards the edges of the intertidal shoal is also observed in the field. This is caused by accessibility of prey. Prey are close to the surface as long as water is on top of it, as soon as their location becomes exposed they move deeper into the sediment. The moment of exposure is therefore the best moment for short-billed birds to catch their prey.
Uniform bird distribution within drawn polygons	• Birds are not uniformly distributed in the polygons that are drawn in the field. There are area where individuals of a certain species are more or less abundant. It is however not possible to separate this by drawing multiple polygons due to time restrictions and reduced accuracy of long-distance counting.
Unique bird species distributions	• The unique distribution of the Sanderling is clearly shown in the hotspots, this is also observed in the field. • The Redshank distribution is generally more bounded to the oyster reefs as can be observed in the figures.
External bird density affecting factors	• No consequent substantial sources of disturbance are present, so there is probably no additional reason to abandon specific area. • It is expected that accessibility of prey is crucial in explaining foraging wader distribution (as described by foraging bird hotspot-topic). Therefore, total biomass and density are not the only important characteristics of food availability, but also the depth of prey in the sediment.
Impact of disturbance by nourishments	• The first counting days after nourishment construction showed wader distribution differed from the original situation since almost no waders were observed at the nourished locations. Birds probably forage on the adjacent Neeltje Jansplaat or Galgeplaat intertidal shoals if they abandon the Roggenplaat.