Studie over de impact van zandsuppleties op het ecosysteem – fase 5

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1 Summary

1.1 Nederlandse samenvatting

De Vlaamse stranden hebben een hoge toeristische waarde maar aangezien het ultra-disseptieve stranden zijn, zijn ze aan sterke erosie onderhevig. Die erosie wordt op veel plaatsen langs onze kust enigszins in toom gehouden door middel van harde kustverdediging zoals dijken, pieren en strekdammen. Tegenwoordig wordt meer en meer geopteerd voor bijkomende zachte maatregelen zoals strandsuppletie om te compenseren voor het verlies aan zand. Deze studie betreft de vijfde fase van een brede ecologische studie naar de effecten van strandsuppletie op het kustecosysteem en behelst de effecten op de avifauna die van onze zandstranden gebruikt maakt. Reeds in een aantal eerdere studies werd het belang van de Vlaamse stranden voor vogels beschreven. Het zijn vooral meeuwen (*Larus argentatus* and *Chroicocephalus ridibundus*), bonte strandlopers (*Calidris alpina*), scholeksters (*Haematopus ostralegus*) en steenlopers (*Arenaria interpres*) die het strand soms gebruiken om te foerageren, maar vooral ook om er te rusten. Alleen de drieteenstrandloper (*Calidris alba)* gebruikt het strand vrijwel uitsluitend om er te foerageren. Vandaar dat deze laatste soort in deze studie wordt gebruikt als voorbeeldsoort om de effecten van strandsuppletie in een volgende fase te kunnen modelleren. Om het toekomstige model te kunnen voeden wordt in deze studie aanvullende basisinformatie verzameld over de voedselbehoeften van drieteenstrandlopers. Het aantal drieteenstrandlopers langs onze kust is laatste decennia afgenomen, maar nog altijd worden er in de winter geregeld meer dan 500 exemplaren aangetroffen.

In een recente studie van Vanermen et al. (2009) werd duidelijk gemaakt dat drieteenstrandlopers vooral op aangespoelde prooien foerageren en hoog in het intergetijdegebied ook op gemshoornworm *Scolelepis*. De studie van Vanermen et al. (20090 toonde tegelijkertijd aan dat het nuttigen van uitsluitend gemshoornworm geenszins voldoende is voor een drieteenstrandloper om in haar dagelijkse energiebehoefte te voorzien. Naast occasioneel beschikbare prooien, zoals insecten en schelpdieren die met een onvoorspelbare frequentie aanspoelen, zouden kleine kreeftachtigen, zoals amphipoden, wel eens belangrijk kunnen zijn als een meer voorspelbare bron van voedsel. Om dat te onderzoeken werd in deze studie gebruik gemaakt van een videorecorder (mini DV SONY Handycam DCR-HC51, 40x optische zoom) waarmee foeragerende drieteenstrandlopers gedurende enkele minuten werden gevolgd (1-5 min.). De volledige studie vond plaats in de periode 6 januari 2010 – 3 maart 2010 op het strand van Oostduinkerke ter hoogte van de Schipgatduinen. In tegenstelling tot de eerdere studie van Vanermen et al (2009) concentreerde deze studie zich vooral op het laag intertidaal.

In totaal werd 4 uur videomateriaal van foeragerende drieteenstrandlopers geanalyseerd. Het foerageergedrag werd tot op de seconde nauwkeurig opgemeten en opgeslagen in een databestand. Vooral de frequentie van de foerageeractiviteit (uitgedrukt in aantal bewegingen per minuut), de opnamesnelheid van de prooien (aantal succesvolle bewegingen per minuut) het foerageersucces (percentage succesvolle pogingen ten opzichte van het totaal aantal pogingen) en de prooikeuze kregen speciale aandacht.

Uit de videobeelden bleek dat een drieteenstrandloper gemiddeld 30 foerageerbewegingen per minuut maakte, waarvan er 12 succesvol waren (i.e. prooi of duidelijke slikbeweging te zien op de video). Het foerageersucces bedroeg dus bijna 40%. Van de 2418 prooien die werden geconsumeerd door drieteenstrandlopers kon 54% niet worden gedetermineerd (niet goed zichtbaar op het videobeeld of te klein). Van de wel determineerbare prooien was de tweekleppige *Ensis spp*. verreweg de meest dominante prooisoort (N = 960). Daarnaast werden ook wel kleine mariene wormen (N = 14) gegeten. Ook werd veel gepikt in aangespoeld materiaal (N = 132) of in eipakketten van wulken (*Buccinum undatum*) (N = 3), waar waarschijnlijk werd gezocht naar insecten en kleine kreeftachtigen.

Heel typisch werden er twee verschillende groottes van Ensis spp. geconsumeerd door de drieteenstrandlopers. In de eerste plaats waren er de kleinere, jonge exemplaren van gemiddeld 2,7 cm (SD ± 0,6 cm, N = 183), welke overeenkomen met een leeftijd van minder dan 1 jaar oud. Deze jonge exemplaren zaten ofwel levend in het sediment en werden dan door middel van borende bewegingen (waarbij de snavel tenminste deels in het zand verdween) levend en wel uit het sediment getrokken (67% van alle *Ensis spp.*). Foerageren op deze kleinere *Ensis spp*. werd bijna uitsluitend gezien tijdens laag water, waarbij de drieteenstrandlopers zich dicht tegen de waterlijn ophielden. Iets minder belangrijk waren de aangespoelde exemplaren van deze kleinere *Ensis spp*. (20% van alle *Ensis spp.*). Die werden bovendien meestal niet helemaal opgegeten, maar er werden delen uit de vlezige binnenkant gepikt. Hetzelfde werd overigens gedaan met de grotere exemplaren van *Ensis spp.* (> 2,7 cm), die nooit ingegraven in het intertidaal zaten maar altijd waren aangespoeld. De korte pikkende bewegingen waarmee de aangespoelde prooien werden geconsumeerd waren meestal zeer succesvol en de opnamesnelheid was vergelijkbaar met die van ingegraven kleinere Ensis spp. (3,6 tot 3,9 succesvolle bewegingen per minuut). Echter, er werd op die manier tekens slechts een klein deel van de energie-inhoud van de gekozen prooien benut terwijl de levend uitgegraven kleinere exemplaren in hun geheel werden opgegeten.

Om te onderzoeken in hoeverre het foerageergedrag van de drieteenstrandlopers indicatief was voor de werkelijke beschikbaarheid van benthische prooien, werden ter plaatse stalen genomen met een box core. Daartoe werd het laag intertidaal (waar de meerderheid van de gedragswaarnemingen was uitgevoerd) opgedeeld in 25 vierkante gridcellen van 20x20 m. In elke gridcel werden twee stalen genomen van de aanwezige prooidieren die later door de sectie Mariene Biologie van de Universiteit Gent werden gedetermineerd. Tevens werden hoger in het intertidaal langs een transect stalen genomen maar met een lagere dichtheid dan in het grid (zie figuur 2).

Inderdaad werden langs de laagwaterlijn, waar de drieteenstrandlopers veel kleine *Ensis spp.* vonden, hoge densiteiten van deze prooidieren aangetroffen (546 individuen/m^2). Dit kwam dus overeen met het feit dat de drieteenstrandlopers tijdens laagwater vrijwel uitsluitend en zeer geconcentreerd in deze zone foerageerden, hoewel dan een maximaal deel van het intertidaal beschikbaar was als foerageergebied. Hoger op het intertidaal ontbrak *Ensis spp.*, waardoor de drieteenstrandlopers zich al snel na laagwater en enige tijd voor laagwater meer over het gehele intergetijdegebied verspreidden waar volgens de videobeelden werd overgegaan op het eten van aangespoelde prooidieren.

Op 5 februari werd tijdens een volledige cyclus van opkomend en afgaand tij elke 2 minuten het aantal drieteenstrandlopers per gridcel geregistreerd. Door deze gegevens te projecteren over de staalnames van het aanwezige benthos kwam iets zeer opmerkelijks aan het licht. In de periodes voor en na laag water, wanneer de kleinere exemplaren van *Ensis spp.* niet meer beschikbaar waren omdat de laagste getijde zone reeds was overspoeld met water, volgde de verspreiding van de vogels redelijk goed de verspreiding van de aanwezige vlokreeftjes (amphipoden). Deze prooidieren kenden blijkbaar een redelijke 'patchy' verspreiding en werden lokaal in hoge dichtheden gevonden (maximum of 2734 ind/m²) in de benthos stalen. Met opkomend water verkozen de drieteenstrandlopers vooral patches met hoge dichtheden aan vlokreeftjes die op dat moment in de getijcyclus vlak aan waterlijn waren gelegen. Op de videobeelden werden deze kleine prooien niet herkend, maar ze zijn wel bekend vanuit de literatuur (maagonderzoek, onderzoek van faeces, ..). Het gaat bij ons dan waarschijnlijk om soorten als *Bathyporeia spp.* en *Talitrus saltator.*

Om eens na te gaan in hoeverre amphipoden belangrijk kunnen zijn voor drieteenstrandlopers werd uitgerekend hoeveel exemplaren er nodig zouden zijn om aan de dagelijkse energiebehoefte van een drieteenstrandloper te voldoen. Voor het gemak werd aangenomen dat het uitsluitend om *Bathyporeia* zou gaan. De energie-inhoud van *Bathyporeia* die werd gevonden in de literatuur varieerde sterk waardoor de schattingen van het aantal individuen dat een drieteenstrandloper nodig heeft ook nogal uiteenlopen. Op een dag moet een drieteenstrandloper maar liefst 23661 tot 132300 exemplaren eten, hetgeen overeenkomt met het volledig leegeten van bijna 9 m² intertidaal ofwel meer dan 11 uur foerageren. Een schier onmogelijke taak. Amphipoden kunnen dus in geen geval het hoofdvoedsel vormen voor drieteenstrandlopers langs de Belgische kust, maar zouden wel een belangrijke bijkomende en voorspelbare bron van voedsel kunnen zijn. Daar staat tegenover dat *Ensis spp.* wel een zeer lucratieve prooisoort lijkt waarmee in theorie binnen enkele uren (57-138 minuten) in de dagelijkse energiebehoefte kan worden voorzien.

Het lijkt dus perfect in het energetische plaatje te passen dat de drieteenstrandlopers zich veel ophielden langs de laagwaterlijn waar zich deze winter zeer veel jonge *Ensis spp.* had ingegraven. Men moet echter wel beseffen dat dit een uitzonderlijke situatie was welke in het verleden nog nooit is geconstateerd. Het betreft een invasieve soort die zich in goede jaren snel weet te verspreiden en dan een goede voedselbron vormt voor veel vogelsoorten, vooral voor opportunistische soorten als de drieteenstrandloper. Bij gebrek daaraan is de drieteenstrandloper echter veel meer aangewezen op laag-energetische prooisoorten zoals amphipoden en polychaeten en daarnaast op het aanspoelen van allerlei prooidieren.

Strandsuppletie zal vooral een effect hebben op de aanwezigheid van de voorspelbare voedselbronnen van drieteenstrandlopers. Het aanspoelen van prooidieren zal ook na de suppletie plaatsvinden, maar hun zekere bron van inkomsten zal tijdelijk niet beschikbaar zijn. Laag in het intertidaal is het de aanwezigheid van bivalven, halverwege zijn het vooral amphipoden en hoog in het intertidaal polychaete wormen die door suppletie tenminste tijdelijk wordt aangetast.

Wanneer door suppletie substantiële zones intertidaal verloren gaan als foerageergebied, zou dat belangrijke consequenties kunnen hebben voor het voorkomen van drieteenstrandlopers langs onze kust. Anderzijds is uit onze studies gebleken dat de soort enorm opportunistisch is en gemakkelijk kan uitwijken naar alternatieve voedselbronnen of alternatieve locaties. De soort zal daarom vooral gebaat zijn bij gefaseerde suppletie (in ruimte of tijd), waarbij altijd stukken intertidaal beschikbaar zullen blijven als foerageergebied.

1.2 English summary

The Belgian beaches have a high touristic value but are ultra-dissipative with strong tidal currents responsible for quick erosion. Soft measures like beach nourishment are now preferred over hard measures (construction of breakwaters, groins or piers) to counter the loss of beach surface. This study is the fifth phase of a broader study on the impact of sand suppletion on the beach ecosystem financed by the Agency for Maritime and Coastal Services – Coastal division. Already in the third phase the importance for the avifauna (birds) was pointed out. Out of the species using the beach ecosystem during winter, mainly gulls (*Larus argentatus* and *Chroicocephalus ridibundus*), dunlins (*Calidris alpina*), oystercatchers (*Haematopus ostralegus*) and turnstones (*Arenaria interpres*), the sanderlings (*Calidris alba)* is the only species that almost exclusively depends on the sandy beaches to forage. The number of sanderlings is declining since the 1970s but still their wintering numbers often exceed 500 individuals along the Belgian coast.

The recent study Vanermen et al. (2009) pointed out that the benthic polychaete worm *Scolelepis* could not fulfil the daily energy demand of the overwintering sanderlings and it is hypothesised that organic wreck washed ashore is the most important food source. Additionally crustaceans, more precisely amphipods, might be consumed to complete their needs. In this study, the foraging behaviour and diet of the sanderlings were video taped and samples of the benthic fauna available to the birds were collected in order to gather more information about the use of the beach surface. This took place in the intertidal zone at the western part of the Oostduinkerke beach in front of the Schipgatduinen between the 6th of January and the 3rd of March 2010.

Four hours of movie were analysed and the duration of each behaviour as well as each foraging attempt was registered to the second and stored in a database. Special attention was given to foraging events. It showed that sanderlings made around 30 foraging attempts per minute (i.e. foraging rate being the total number of foraging events per minute of movie) but only were successful 12 times per minute (i.e. success rate being the total number of successful food intakes per minute of movie). Compiling these two rates, a foraging efficiency (percentage of successful prey/food intakes to the total number of foraging events) of almost 40% can be calculated. Out of the 2418 prey items eaten, 54% could not be identified (N = 1286). Among the identifiable food items, the main prey was the bivalve *Ensis spp.* (N = 960). Sometimes small marine worms were extracted from the intertidal zone (N = 14). Debris (N = 132) and egg balls of whelk (*Buccinum undatum*) (N = 3) were not directly eaten but the sanderlings foraged on small insects and crustaceans that find shelter and food in these structures.

Two sizes of *Ensis spp*. could be distinguished. Smaller specimens measuring on average 2.7 cm (SD ± 0,6 cm, N = 183) corresponding to an age of less than one year and the bigger ones measuring > 7cm. The small *Ensis spp.* were either found by probing (partly or totally intruding the bill in the sediment) and removed from the sediment alive (67% of all *Ensis spp.*) or by pecking, removing parts of the body meat was removed from beached individuals (20%) by pecking. Pecking on beached *Ensis* *spp.* concerned both smaller and larger specimens. Pecking was the most successful foraging behaviour (foraging efficiency of 35%) and had the highest success rate.

Probing on small *Ensis spp.* mainly took place around low tide and always close to the waterline. This corresponded to highest densities of *Ensis spp*. in our samples (546 individuals/m²). The beached *Ensis spp.* and feeding on debris gained importance while getting closer to high tide when the birds were using the entire surface of the available beach. The success rate (between 3.6 and 3.9 successful events per minute) was similarly high for the *Ensis spp.* that were extracted from the sediment as for the beached ones (but for beached items we considered the number of successful pecks per minute, whereas the number of preys captured per minute was used for prey that were removed from the sediment).

During this winter high numbers of *Ensis spp*. were washed at the Belgian beaches. But this is not the case every year. *Ensis spp.* is an invasive species with outstanding dispersal capabilities. During years of high production this species seems able to quickly colonise the intertidal zone and similarly it might colonize new space created by the beach nourishment.

Surprisingly the results of this study suggest, although it was not directly observed in the video images, that when the tide came in and the smaller Ensis were no longer available, the birds started feeding on amphipods, probably *Bathyporeia spp.* or *Talitrus saltator.* These prey were found living in high density patches (maximum of 2734 ind/m² in the benthos samples) mainly in the high intertidal zone. As the feeding activity of the sanderlings closely followed the patches of high amphipod density as the tide came in, the birds were either directly feeding on amphipods or on something that was related to these patches. It is, however, questionable if amphipod prey can provide sufficient energy for sanderlings. Compiling literature data, the observed pecking rate of sanderlings and the density of amphipods in our samples, we calculated that a sanderling should eat between 23,661 and 132,300 *Bathyporeia spp.* to fulfil its daily energy need. This would take at least 11 hours of foraging. On the contrary, they should only eat between 271 and 656 *Ensis spp*. which would take between 57 minutes and 2 hours 18 minutes. The lower part of the beach with the high densities of *Ensis spp*. was available to the birds longer than the maximum time needed to gain enough energy from this type of prey.

It should not be omitted to point out that sanderlings are opportunistic feeders and that they take advantage of every kind of prey type available. In this study it was mainly *Ensis spp.*, but the importance of amphipods, polychaete worms and debris should not be neglected in further studies.

Beach nourishment will mainly affect the availability of the predictable food resources of sanderlings, their certain sources of energy income. Low in the intertidal beach nourishment will at least temporarily affect the availability of bivalves, somewhat higher that of amphipods and in the highest part it will lead to a decreased availability of polychaete worms. This means that when large parts of the coastline will be suppleted in a short period of time, it may have serious consequences for the occurrence of sanderlings in front of our coast. On the other hand, our study shows that sanderlings are truly opportunistic species which can easily switch to alternative prey species and alternative locations. This means that beach nourishment will have least effects on sanderlings when it is carried out in phases. Organising the nourishment (either spatially or temporally) in a way that only short stretches are affected, will ensure the presence of alternative feeding zones for sanderlings.

2 Introduction

Belgium has about 65 km of coastline, of which 35 km is protected by beaches in combination with seawalls, 3 km by breakwaters (harbours) and the remaining part by beaches and dunes (Hanson et al. 2002). The beaches are ultra-dissipative (Degraer et al. 1999, Degraer et al. 2003 and Short 1996) with strong tidal currents responsible for beach erosion (Degraer et al. 2003) and a flat and relatively featureless beach profile. In order to maintain the beaches, which have a high touristic value, two types of measures are in use. In the first place, ‘hard’ measures are applied such as the construction of breakwaters, groins or piers, and secondly, ‘soft’ measures like beach nourishment. The latter is considered as a more environmentally sound method (Hanson et al. 2002), and in many countries coastal management evolves towards more recurrent use of ‘soft’ measure. This study is the fifth phase in a broader study on the impact of sand suppletion on the beach ecosystem financed by the Agency for Maritime and Coastal Services - Coastal Division. In a previous phase (phase 3) of the study, the importance of the Belgian beach ecosystem for the avifauna was studied (Speybroeck et al. 2007). During winter, high numbers of foraging gulls (*Larus argentatus* and *Chroicocephalus ridibundus*), dunlins (*Calidris alpina*), sanderlings (*Calidris alba)*, oystercatchers (*Haematopus ostralegus*) and turnstones (*Arenaria interpres*) are present on Belgian beaches. Of these species, the sanderling is the only one that depends almost exclusively on sandy beaches for foraging and has therefore been chosen as a model species to study the effects of beach nourishment on birds. Sanderlings are opportunistic feeders that depend both on benthic species and organic wreck (Cramp 1983, Glutz von Blotzhein et al. 1984, Nuka et al. 2005 and Vanermen et al. 2009). On the Belgian coast, there is an autumn passage from the end of July until the beginning of November, the wintering population occurs during the period November-March and spring passage mainly takes place from March until the first decade of May (Devos pers. communications). Wintering numbers often exceed 500 individuals with a maximum of 939 in 1979 (Devos et al. 1998 and Devos 2008) but since the 1970s the number declines (-46%).

In the recent study made by Vanermen et al. (2009), it was pointed out that the benthic polychaete worm *Scolelepis* couldn’t fulfil the daily energy demand of the overwintering sanderlings and it is hypothesized that organic wreck washed ashore is the most important food source. Unfortunately, in that study, the actual densities and distribution of benthic prey species were not measured or correlated with the distribution and behaviour of the foraging sanderlings. Therefore in this study we will examine how sanderlings make use of the intertidal flat, how this is related to densities of preys and whether or not the birds make use of the patchy occurrence of their food in order to obtain enough energy.

3 Materials and methods

3.1 Study area

We conducted this study on the the intertidal zone of the western part of Oostduinkerke Bad beach in front of the Schipgat dunes. During the study this beach was used by herring gulls (*Larus argentatus*), oystercatchers (*Haematopus ostralegus*), dunlins (*Calidris alpine*) and sanderlings (*Calidris alba*) for feeding and resting. Approximatively 500 sanderlings spend the winter on the Belgian Coasts (520 in January 1975, 312 in January 1990 and 480 in January 2000 Devos 2005). Flocks of a few to 50 birds were regularly observed foraging at the study site.

3.2 Movies

In order to obtain information about the foraging behaviour and the diet of the birds, foraging sanderlings were filmed with a mini DV SONY Handycam DCR-HC51 (Carl Zeiss lense, 40x optical zoom, 2000x digital zoom). We filmed as close as possible when the birds were actively foraging along the waterline and used the zoom to get even closer to enhance the chance of determining the prey to the species level. The filming took place around low tide on the 6th, 7th, 20th, 21st and 22nd of January 2010. The movies lasted at least one minute and a maximum duration of five minutes was fixed.

Different types of foraging behaviours were distinguished:

- Pecking (P) when the bird was removing a prey from the surface of the sand in fast movement.

- The bird was probing (B) when it intruded its bill partly or entirely in the sand. We distinguished three types of probing:
    - surface probing (B1) when the bill was penetrating the sediment up to half the size of the bill (approximately 1.5 cm),
    - entire bill probing (B2) when it intruded its bill up to the beginning of the feathers in the sediment
    - and deep probing (B3) when even a part of the head penetrated the sediment.

  When the bird was feeding in the water it was sometimes impossible to determine the penetration depth of the bill and as a consequence the probing was not qualified by a number and simply called B.

- Spooning (S) when the bird was feeding with the bill constantly in the water in a walking action and moving the head from one side to the other.

- Tactile walking (T) looked a little like spooning but the bird had no head movement and this action often finishes with a probing to pull out the prey. It will then be called TB, TB1, TB2 or TB3 depending on the penetration depth of the bill at the end of the action.

These actions were put in an Excel file with their start time, the number of actions realised at one spot, the success of the action and finally, if possible, the prey type and its length. The condition of the sediment the bird was also indicated, if it was on wet sand at the waterline (WW), on dry sand at the waterline (DW) or if it was on the intertidal more dry part of the beach.

We defined:

- **foraging rate** as the total number of foraging events per minute of movie,
- **success rate** as the total number of successful prey intakes per minute of movie
- and finally **foraging efficiency** as the percentage successful prey intakes to the total number of foraging events.

3.3 Grid and transect

A grid of 100mx100m was put up (Figure 1 and Figure 2) at the lowest part of the beach parallel to the waterline. It was divided in 25 squares of 20mx20m and each corner was marked with a pole. Two parallel transects were traced from the grid till the beginning of the dunes (Figure 2). The grid was used to count the density of the sanderlings on the beach. The grid and the transect were used to take samples of the possible preys available to the sanderlings (Figure 1 and Figure 2).

3.3.1 Sanderlings

Sitting on the highest dune in front of the grid, with a telescope (Swarowski ATM-65 25-50x wide angle) the numbers of sanderlings present in each square were counted every second minute during ebbing and incoming tide. The way of counting the birds was always the same beginning with the zone without water the furthest away from the left to the right (Figure 1). The birds were counted the 5th of February 2010.

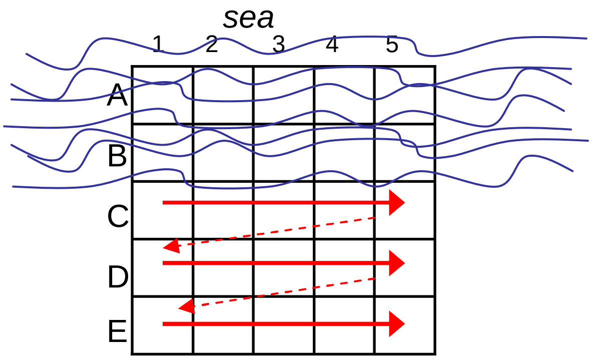


Figure 1: Counting sanderlings in the grid. The birds were counted in each square beginning from the zone de furthest away without water from the left to the right following the red arrows. In this case C1-C2-C3-C4-C5-D1-D2-D3…E4-E5

3.3.2 Benthos

The prey available to the sanderlings could either be beached or living individuals which were buried in the sediment. The preys living in or on the sediment of the beach are defined as benthos. The benthos was sampled the 9th February, 19th February and the 3rd March with a box core that collected 0.1026 m² of sediment. The box core was put in the sediment to a depth of little more than 15 cm and the upper 15 cm were removed with a shovel and filtered through a sieve with a mesh size of 1mm.

Two types of benthos samples were taken: transect samples and grid samples.

- Inside the 100mx100m grid, 50 samples were collected. Samples were taken at 10m distance from each other in each square. Between rows (A,B,C,D or E) the samples were located at 20 m distance from each other. Two replicates in each square were taken. The duplicates were called for example A1L and A1R for the 2 samples collected in square A1 (Figure 2).

- 20 samples were collected in two transects every 50m in the prolongation of column 1L and 5R. These samples were collected to compare food availability along the entire tidal cycle. The choice of 2 parallel transect was to verify if there was any differences in prey composition at this 90m interval (Figure 2).

The sieved benthos samples were put in jars containing a 35% formaldehyde solution and brought to the laboratory of the Marine Biology Section at the University of Ghent for identification. The preys were determined to group level, only the bivalve *Ensis spp.* was determined to species level.

Next prey densities were computed in order to allow statistical analysis for differences in prey availability. A Shanon-Wiener diversity index was calculated to allow comparison of the species composition between the grids. The density and the diversity were put into total transect (grid+transect) (Table 1) graphs to explain the evolution of these two measures on the beach.

Table 1: Total transect description. Grid and transect samples with their distances from the beginning of the grid (Figure 2)

Sample name	A	B	C	D	E	1	2	3	4	5	6	7	8	9	10
Grid (G) or transect (T) sample	G	G	G	G	G	T	T	T	T	T	T	T	T	T	T
Distance from the beginning of the grid (m)	10	30	50	70	90	150	200	250	300	350	400	450	500	550	600

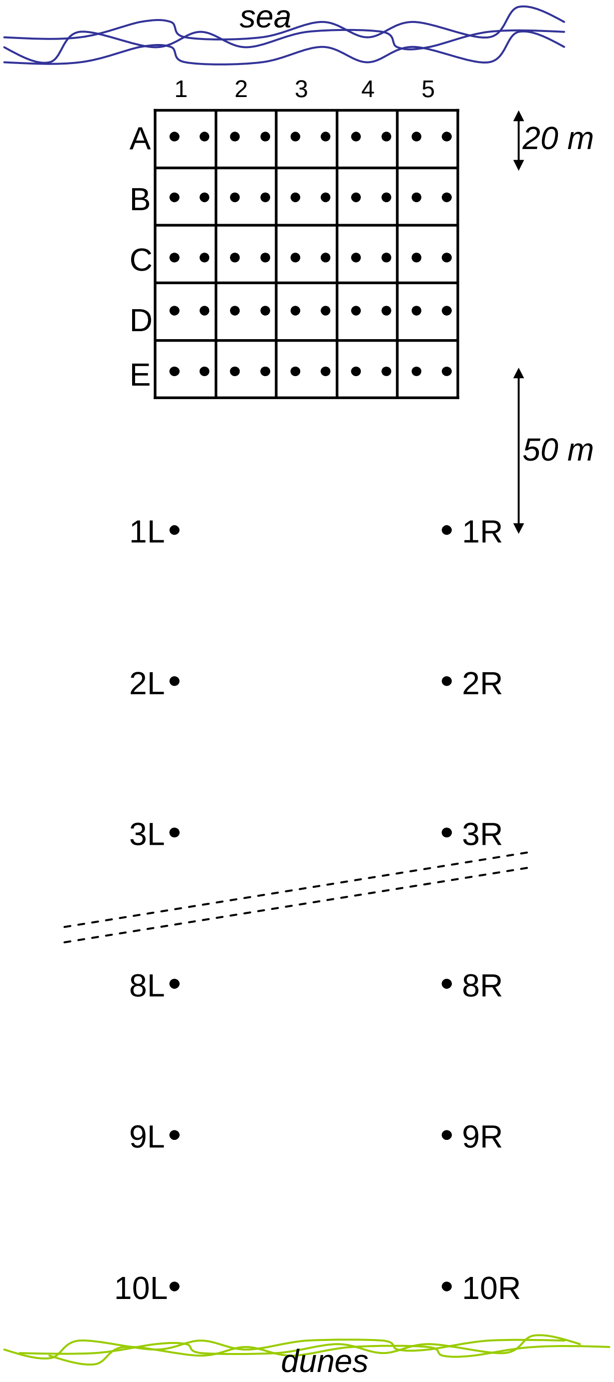


Figure 2: Grid and transect set up for benthos sampling (dots). Two benthos samples were taken by square in the grid, on a line in the middle of the zone (A, B, C, D and E) every 10m. In total 50 samples were taken in the grid. The transect samples were collected in two parallel lines, 20 in total.

3.4 Statistical analysis

Analysis of variance was used to compare the prey densities, the diversity and the number of birds inside the grid and the transect. If the data were not normally distributed they were log transformed before being analysed.

4 Results

4.1 Movies analysis

Hundred movies of foraging sanderlings were analyzed, containing a total of 3 hours 52 minutes and 49 seconds of protocols. The movies were on average 2’20” long with a minimum of 1’00” and a maximum 4’03”. The movies were recorded from 88 minutes (1h28min) before low tide to 244 minutes (4h04min) after (Figure 3)

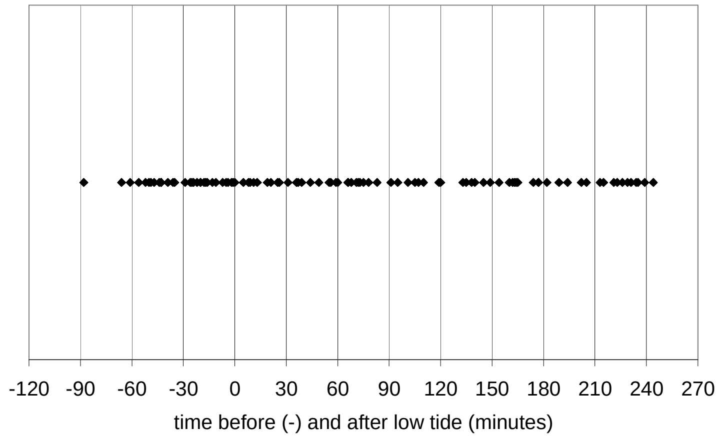


Figure 3: Distribution of the movies along the tidal cycle, 0 corresponds to low tide, - numbers: time before low tide and + numbers: time after low tide in minutes.

4.1.1 Foraging efficiency, foraging rate and success rate

The hundred individuals attempted to feed 7151 times and had success in 2768 cases, which gives a foraging efficiency of 39.4%. The foraging rate was on average 30.3 attempts per minute (SD ± 9.0 times per minute) and the success rate 11.8 per minute (SD ± 5.9 times per minute) (Table 2).

Table 2: Foraging efficiency (percentage of successful foraging events), foraging rate (total number of foraging events per minute) and success rate (total number of successful foraging events per minute) during the tidal cycle (minutes).

Time before (-) and after low tide (minutes)	Number of movies	Foraging efficiency (%)		Foraging rate (attempts per minute)		Success rate (successful events per minute)	
		mean	SD	mean	SD	mean	SD
-120 to -61	3	41.5	8.5	28.3	8.0	11.4	1.9
-60 to -1	29	43.2	15.6	29.3	7.3	12.4	4.9
0 to 59	19	31.9	9.0	29.7	8.4	9.1	2.5
60 to119	17	38.5	16.2	34.6	8.2	13.9	9.2
120 to179	16	33.0	21.7	27.0	11.8	8.4	3.8
180 to 239	15	47.5	15.6	31.6	10.2	14.8	5.8
240 to 300	1	62.6		33.5		21.1	
Total	100	39.4	16.5	30.3	9.0	11.8	5.9

4.1.2 Preys eaten

Out of the 2418 prey items that were eaten by the sanderlings, 1286 could not be determined (53.5%). Unidentified prey items were present in almost all movies (98) and in 99% of the movies the sanderlings had successful foraging attempts. Despite the difficulty to determine smaller prey from a video, seven different prey types could be determined being bivalves, debris, whelk (*Buccinum* undatum) egg balls, jackknives *Ensis spp.)* (Figure 4), blue mussels (*Mytilus edulis*) (Figure 4), sea urchins (*Psammechinus miliaris*) and worms.

In this study **two size classes of the bivalve *Ensis spp.*** could be distinguished:

- The bigger specimens (further called big *Ensis spp.*) corresponding to *Ensis spp.* at least 3 times longer (often more) than the sanderling's bill length (24.2-26.2 mm Cramp 1983) (Figure 4). This prey type was only present as beached specimens and eaten through pecking.

- The second type of *Ensis spp.* taken by the sanderlings was much smaller, less than three times the bird's bill length. These smaller *Ensis spp.* were either beached specimens (small *Ensis spp.* dead: SED) or living individuals buried in the sediment (small *Ensis spp.* alive: SEA) (Figure 5) or impossible to determine whether beached/living in the sediment (small *Ensis spp.* unknown:SEU).

Those prey items could be classified into the categories removed alive from the sediment or beached:

- 59.7% of the prey items (N=661) were **removed from the sediment** being bivalves, small *Ensis spp.* alive (SEA) (Figure 5c+d) or worms (Figure 5b)

- and 40.3% (N=446) were **beached** being bivalves, debris, whelk egg balls, big *Ensis spp.* (Figure 4a+b), small *Ensis spp.* dead (SED), blue mussels (Figure 4c) or sea urchins.

4.1.2.1 Beached prey items

The beached items could be classified in two categories:

- the first category contained the prey items upon which the sanderlings actually fed: mussels, small *Ensis spp.* dead, big *Ensis spp.* and sea urchins (59.7% of the beached items). Pecking on bivalves other than *Ensis spp.* was scarce (<0.1% for both undetermined bivalves and mussels), but beached *Ensis spp*. were pecked upon frequently (see Table 3 for more details). With rapid pecks the birds took small parts of the fleshy content of the bivalves or the sea urchins. Approximately four times per minute the sanderlings removed pieces of flesh from the 195 SED or the 110 big *Ensis* (Table 3 and 4). A single sanderling pecked with flesh-removal on a SED every second (34.6 successful pecks per minute) but less than two *Ensis spp.* (SED or big ones) were "attacked" per minute (Table 4). More birds foraged on SED (N=45) than on big *Ensis spp.* (N=29) (Table 3).

- the second category contained debris + whelk egg ball (Figure 4). The sanderlings do not forage directly on those, but on the small insects and crustaceans that find shelter and food in these structures. They pecked with success 135 (132+3) times on the small insects/crustaceans (Table 3). Debris was foraged on by 11 birds and egg ball by a single one.

Table 3: Number and occurrence of the different prey species eaten. 2418 prey items could be determined and occurred in 99% of the movies. Different behaviours were used to catch different types: the big *Ensis spp.* and the small *Ensis spp.* dead were foraged by pecking, the small *Ensis spp.* alive were caught by probing (P) preceded or not by tactile walking (TB), worms were caught by the same techniques as the small *Ensis spp.* alive. Unknown prey items were the most abundant and most occurent. Small *Ensis spp.* alive seemed to be the main prey because it constituted 27% of the total number of preys and occurred in 75% of the movies.

Prey	Type of behaviour used	Number of preys N=2418		Occurrence N=99	
		N	%	N	%
Big *Ensis spp.*	P	110	4.6	29	29.3
Bivalve	P, TB3	3	0.1	3	3.0
Debris	P	132	5.5	11	11.1
Egg ball	P	3	0.1	1	1.0
Ensis spp. alive	TB, TB1,TB2, TB3, B, B1, B2 and B3	646	26.9	74	74.7
Ensis spp. dead	P	195	8.1	45	45.5
Ensis spp. unknown	T, U	9	0.4	9	9.1
Mussel	P	1	<0.1	1	1.0
Unknown	All behaviours	1286	53.5	98	99.0
Sea urchin	P	3	0.1	2	2.0
Worm	B1, B2, B3, P, T, TB2, TB3 and U	14	0.6	8	8.1

Figure 4: Sanderlings foraging on beached prey items: big *Ensis spp.* (4a+4b), blue mussel (4c) and on debris (4d).

Table 4: Number of *Ensis spp.* foraged on per minute per bird for all the different *Ensis spp.* types: big, small alive, small dead and small unknown. And number of pecks removing flesh per minute for the two beached *Ensis spp.* kinds: big ones and SED. The SEA were foraged on by most of the birds (74 out of 99), followed by the SED (N=45) and the big *Ensis spp.* (N=29). 3.6 SEA were eaten per minute but less than 2 beached *Ensis spp.* (big ones and SED) were foraged on per minute per bird. The number of pecks removing flesh from the big *Ensis spp.* or the SED were equivalent to the number of SEA eaten.

		Big *Ensis spp.*	Small *Ensis spp.* alive (SEA)	Small *Ensis spp.* dead (SED)	Small *Ensis spp.* unknown
	Occurrence	29	74	45	9
Number of *Ensis spp.* foraged on per minute per bird	Mean	1.7	3.6	1.8	0.4
	±SD	1.7	2.3	2.5	0.2
	Maximum	6.3	8.9	9.7	0.8
Number of pecks removing flesh per minute per bird	Mean	3.8	-	3.9	-
	±SD	4.5	-	6.8	-
	Maximum	20.5	-	34.6	-

4.1.2.2 Benthic prey items

Three benthic prey types were removed from the sediment and could be classified a follows:

- **non-Ensis bivalves** - only a single undetermined bivalve representing less than 0.1% of the total number of prey items eaten (Table 3).
- **small Ensis SEA** (Figure 5c+d). This prey type was taken by 74 birds and on average each bird was removing 3.6 SEA per minute (Table 3). The SEA were removed from the sediment by using different techniques: probing (B) and tactile walking often followed by probing (TB) (Table 3 and Figure 5).
- The third and last type of benthic prey removed from the sediment were **worms** (Figure 5b). In our study worms represent less than 1% of all determined prey

Figure 5: Sanderlings probing (5a), pulling a worm out of the sediment (5b), pulling out a small *Ensis spp.* (5c) and handling a small *Ensis spp.* (5d).

4.1.2.3 Size estimation of the small *Ensis spp.* alive

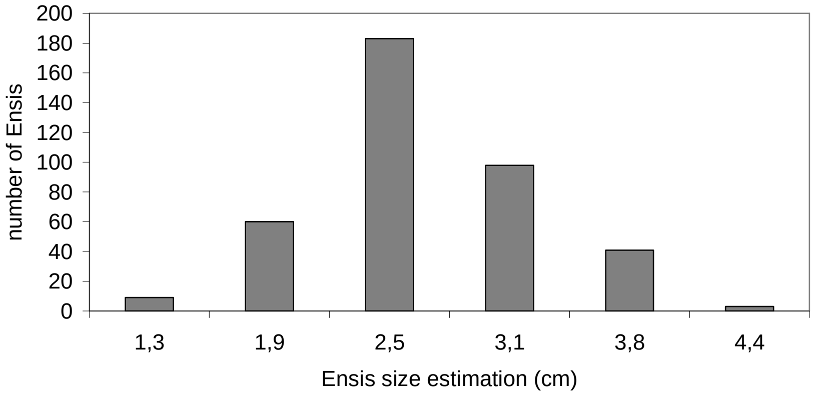


Figure 6: Size estimation the *Ensis spp.* alive eaten by the sanderlings (N=394). The average size was 2.7 ± SD: 0.6 cm.

The size of 394 *Ensis spp.* could be estimated by comparing their size to the bill of the bird (2.5 cm on average) (Figure 6). The *Ensis spp.* measured on average 2.7 ± SD: 0.6 cm with a maximum of 4.4 cm (N=3) and a minimum of 1.3 cm (N=9). Half of the *Ensis spp.* were as long as one bill length (N=183), equivalent to 2.5 cm in length.

4.1.2.4 Removed *Ensis spp.*, beached ones and debris

There was a clear tidal pattern in foraging activities, with the small *Ensis spp.* (SEA) captured around low tide and with a maximum of 4.7 specimens per minute (±SD: 1.7) the first hour after low tide (Figure 7). Beached big *Ensis spp.* and debris feeding increased during incoming tide (Figure 7). Small beached Ensis (SED) were foraged on around low tide (Figure 7).

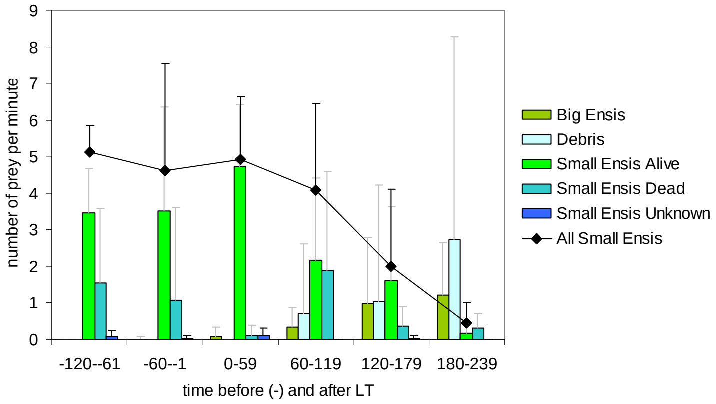


Figure 7: Number of prey items eaten per minute. The SEA were mainly eaten around low tide. The big *Ensis spp.* and SED, both beached, were gaining importance with incoming tide as well as debris.

4.1.3 Foraging mode

The type, frequency and efficiency of the foraging behaviour varied throughout the tidal cycle. This also accounts for the way in which the two different categories of prey (beached / removed from the sediment) were exploited.

4.1.3.1 Foraging mode used and their efficiency

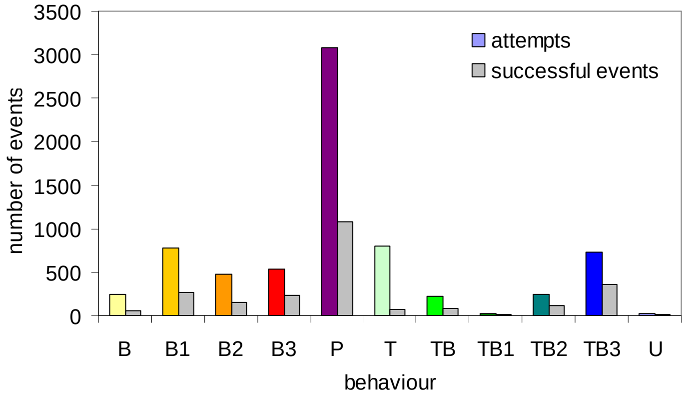


Figure 8: Number of events depending on the behaviour used. The behaviour used the most was pecking (P) but it wasn't the most efficient (35% of the attempts resulted in a food intake). The deeper the sanderlings probed, preceded or not by tactile walking, the more success they had (B1: 33.9% Nattempts=778; B3: 43.2% Nattempts=532; TB1: 46.2% Nattempts=26 TB3:48.4% Nattempts=732).

The behaviour used most was pecking (3080 attempts) out of which 35% were successful (Figure 8). Probing alone (B+B1+B2+B3=2020) was used twice as much as the tactile walking-probing (T+TB+TB1+TB2+TB3= 1223). When the birds encountered a prey while probing they inserted their bill deep to catch it, the deeper the bill penetrated the sediment the more success the bird had. For probing the foraging efficiency (percentage of successful foraging events) ranged from 33.9 % (B1 N attempts: 778) to 43.2% (B3 N attempts: 532) (Figure 9). If the probing events were preceded by tactile walking the foraging efficiency ranged from 46.2% (TB1 N attempts: 26) to 48.4% (TB3 N attempts: 732) (Figure 9). The least efficient behaviour was tactile walking (T) (8% foraging efficiency, N attempts: 800).

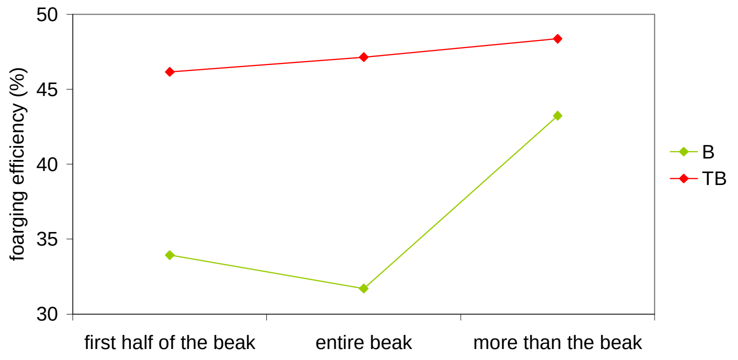


Figure 9: Foraging efficiency (%) depending on the penetration depth of the beak: first half of the beak (B1 and TB1), entire beak (B2 and TB2) and more than the beak (B3 and TB3). The deeper the birds probe the higher the efficiency was (B1:33.9%; B2:31.7%; B3:43.2%; TB1:46.2%; TB2:47.1%; TB3:48.4%)

Looking more into detail, the different foraging behaviours did not have the same success rate along the tidal cycle.

4.1.3.2 Foraging modes during the tidal cycle

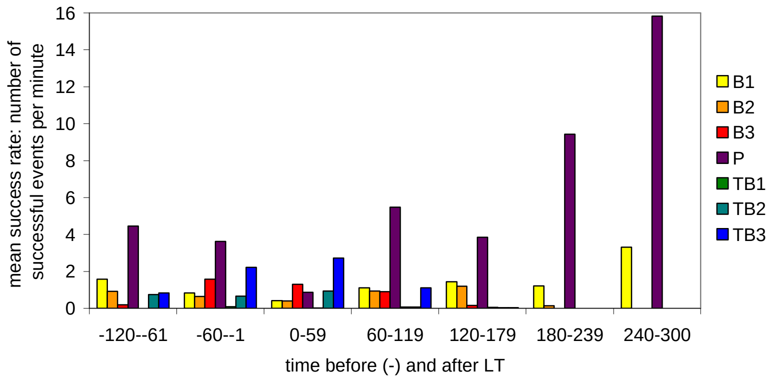


Figure 10: Mean success rate: number of successful events per minute during the tidal cycle. Pecking had the highest success rate during the tidal cycle except at low tide. The deep probing behaviours (TB3 and B3) were mainly occurring during low tide.

Not surprisingly, pecking had the highest success rate, although there was some variation during tide (Figure 10). The mean success rate of deep probing (B3 and TB3) was highest one hour before low tide and decreased to almost zero three hours after low tide. More superficial probing (only the first half of the beak - B1) had a quite constant success rate during the tidal cycle. These tidal patterns become even more obvious when looking at the consumption rates of the different prey types (Figure 11 and Figure 12). Here, we are going to focus on the small *Ensis spp.* eaten alive (Figure 11) and than on the beached *Ensis spp.* (small and big ones) (Figure 12).

4.1.3.3 Behaviours used to eat small *Ensis spp.* alive during the tidal cycle

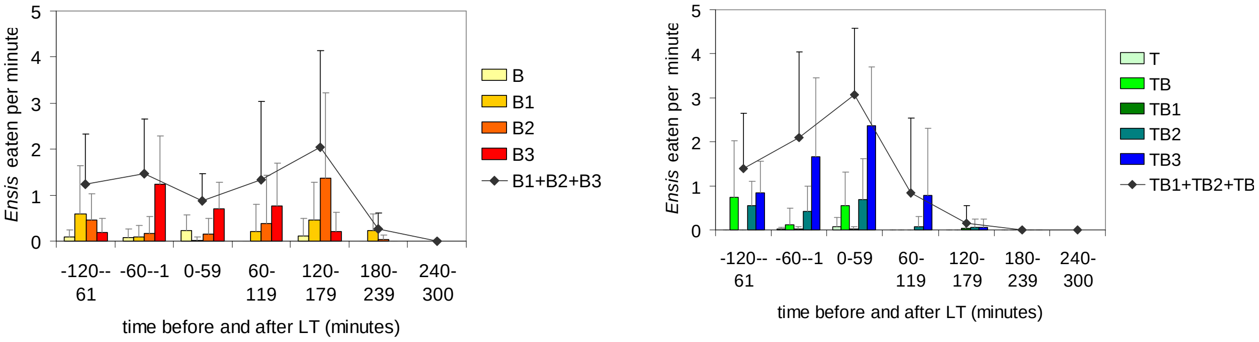


Figure 11: Mean number of *Ensis spp.* alive taken by probing alone (B) (left figure) or preceded by tactile walking (TB) (right figure) per minute during the tidal cycle (colour bars with grey SD) and the sum of the behaviours with a known probing depth (black line with black SD). The deepest behaviours (B3 and TB3) occurred around low tide.

In order to eat the small *Ensis spp.* alive, sanderlings had to remove them from the sediment and a probing action was therefore needed. Both for direct probing (B) and probing preceded by tactile walking (TB), the deepest events were occurring around low tide (Figure 11). The mean number of *Ensis spp.* eaten per minute by probing was highest the third hour after low tide due to a intake of *Ensis spp.* by probing at intermediate depth (B2) and no longer at maximum depth (B3, Figure 11). This was probably related to the softness of the sediment where the sanderling couldn’t penetrate as deep anymore during incoming tide. The highest number of *Ensis spp.* taken by deep probing (B3) occurred one hour before low tide. The gap in the first hour after low tide in line summing up B1+B2+B3 is compensated by the peak in the mean number of *Ensis spp.* eaten per minute by TB3. The number of *Ensis spp.* taken by TB3 was above 1.6 individuals per minute just before and after low tide (Figure 11).

4.1.3.4 Beached *Ensis spp.*: small dead and big *Ensis spp.*

Small dead *Ensis spp.* (SED) were consumed during the entire tidal cycle but the number of pecks removing flesh were highest just after low tide (Figure 12). The number of pecks with success used per SED did not show a clear tidal pattern (Figure 12). The pecks removing flesh from big beached *Ensis spp.* increased from less than 1.5 per minute just before low tide to more than 5 pecks per minute towards high water. The small *Ensis spp.* dead were mainly preyed upon around low tide and the big *Ensis spp.* were mainly pecked on during the late incoming tide. More pecks were used on the big *Ensis spp.* than on the SED (Figure 12).

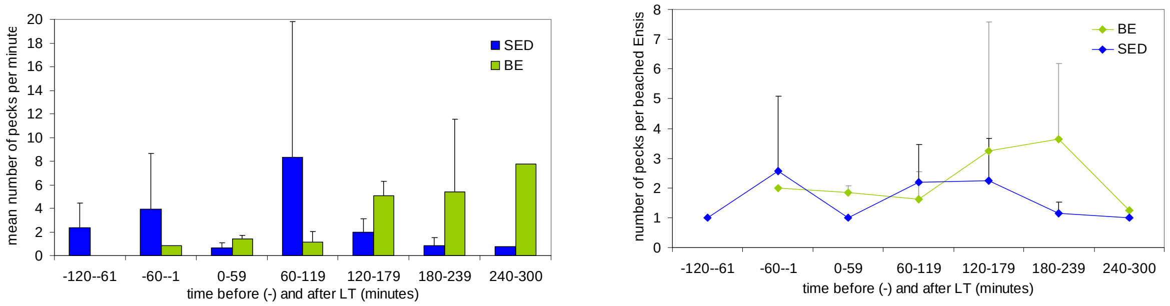


Figure 12: Mean number of pecks per minute (left figure) and per individual (right figure) for the beached big *Ensis spp.* and small *Ensis spp.* dead during the tidal cycle. The SED were pecked on with flesh-removal during the entire tidal cycle with highest number of pecks per minute during incoming tide. The number of pecks per SED did not show a pattern during the tidal cycle in opposition to the big *Ensis spp.* where the number of pecks per prey items clearly increased with the incoming tide. The number of pecks with success per minute also increased for the big *Ensis spp.* with the incoming tide.

4.1.4 Wet and dry waterline

The birds spent most of the time along the wet part of the waterline, with time spent in the dry part increasing towards high tide. From two hours after low tide on, the birds even began to spend time in the intertidal zone (Figure 13).

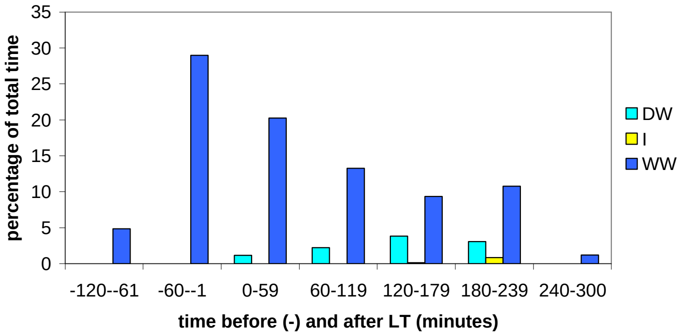


Figure 13: Percentage of total time spent in the different zones: dry waterline (DW), intertidal (I) and wet waterline (WW) during the tidal cycle. The birds were clearly sticking to the wet waterline during low tide and with rising water the importance of the dryer parts, waterline and intertidal, increased.

4.2 Grid and transect analysis

Detailed information on the relationship between sanderling numbers and their possible prey were collected in a grid. Furthermore an extended transect stretching from the grid situated on the lower part of the beach to the dunes was sampled to get more data on the prey types available to the sanderlings in the higher parts of the beach.

4.2.1 Benthos

4.2.1.1 Possible prey types

The different families found in the benthos samples (Table) were:

- Crustaceans: undetermined, Amphipods, Copepods and Isopods
- Bivalves: undetermined and *Ensis spp.*
- Echinodermata (phylum which contains star fishes or sea urchins)
- Hydrozoa (class which contains the jellyfish)
- Juvenile Pleuronectidae (family) or commonly called flat fish
- Polychaete worms

Not every prey type occurred in all the grid and the transect (Table 5). In the grid all the types occurred except the Echinodermata. In the transect samples copepods, crustaceans, Hydrozoa and juvenile Pleuronectidae did not occur, which seems logical because those species are exclusively living in water and do not tolerate to be in the open air (Table 5).

Table 5: Possible prey types available to the sanderlings in the grid and the transect.(see text for the description of the different benthic species)

Prey type	Transect	Grid
Amphipods	X	X
Bivalves	X	X
Copepods		X
Crustaceans		X
Echinodermata	X	
Ensis spp. spp.	X	X
Hydrozoa		X
Isopods	X	X
Juvenile Pleuronectidae		X
Polychaete worms	X	X

4.2.1.2 The diversity of the samples

The Shanon-Wiener index was used to compare the species diversity of the different samples (Table 1 and Figure 2). In the grid, there was a statistical difference between the lines (A, B, C, D or E) (DF=4, F=12.70 and P<0.001) but not between the columns (1. 2, 3 ,4 or 5) (Figure 15). For the transects there was a statistical difference between the different samples along the transect (DF=9, F=7.68 and P=0.0028). In general the diversity was higher in the grid than in the transect samples, the mean diversity index for the grid was 0.91 (±SD: ± 0.30) and for the transect 0.41 (±SD: ± 0.35) (Figure 14).

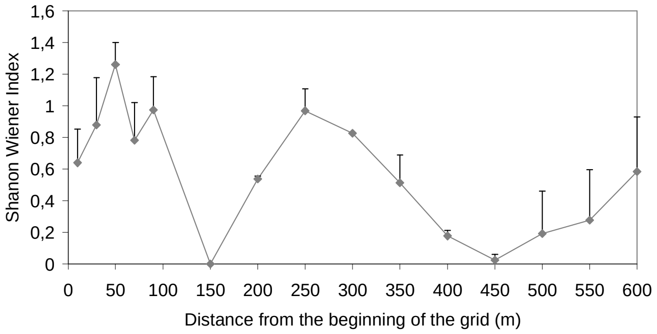


Figure 14: Mean Shanon Wiener diversity index (± SD) along the total transect (grid+transect) (Table 1 and Figure 2). The diversity was higher in the grid (from 10 to 90 m) than in the transect samples (from 150 to 600 m). Two peaks of maximum diversity occurred in the total transect: the first at 50m and the second at 250m.

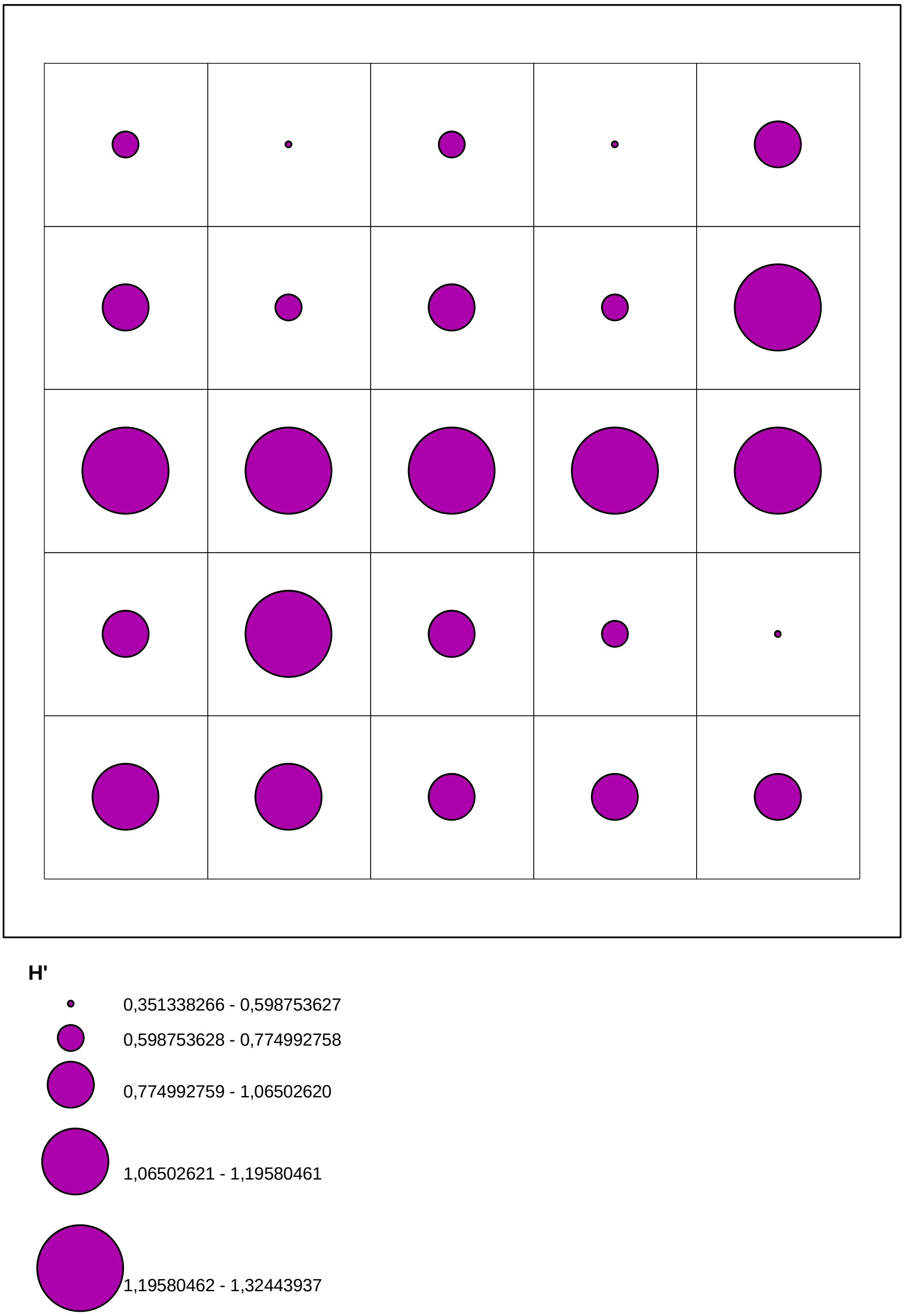


Figure 15: The Shanon-Wiener diversity index (H') in the grid. There was a statistical difference in the diversity between the lines (DF=4, F=12.70 and P<0.001). It seems to be higher in the middle of the grid (C-line).

4.2.1.3 Density in the grid

Two species groups dominated the benthic samples. Both Amphipods and *Ensis spp.* spp. were found in densities above 80 individuals per m² (Table 6). A maximum of 409 ind/m² for Amphipods was recorded in square D5 and a maximum of 546 ind/m² of *Ensis spp.* in square A2 . Polychaete worms were also present in rather high densities. All species groups together made out a total density of 212 ind/m² (Table 6) and a maximum of 497 ind/m² was found in square A2 (Figure 16).

Table 6: Mean density (individuals per m²) (± SD) for the different benthic groups. The groups standing out were the Amphipods and the *Ensis spp.* followed by the worms. A maximum of Amphipods were recorded in D5 (409ind/m²) and a maximum for the *Ensis spp.* in A2 (546 ind/m²) (Figure 1 and Figure 2). The total density was 212.3 individuals per m² on average per square.

Species in the grid	Mean density (ind/m²)	± SD
Amphipods	86.4	76.1
Bivalves	1.8	4.3
Copepods	0.4	1.9
Crustaceans	9.6	21.1
Ensis spp. spp.	83.2	127.3
Hydrozoa	1.4	5.2
Isopods	1.6	4.1
Juvenile Pleuronectidae	0.2	1.4
Polychaete worms	27.7	19.6
Total density	212.3	131.0

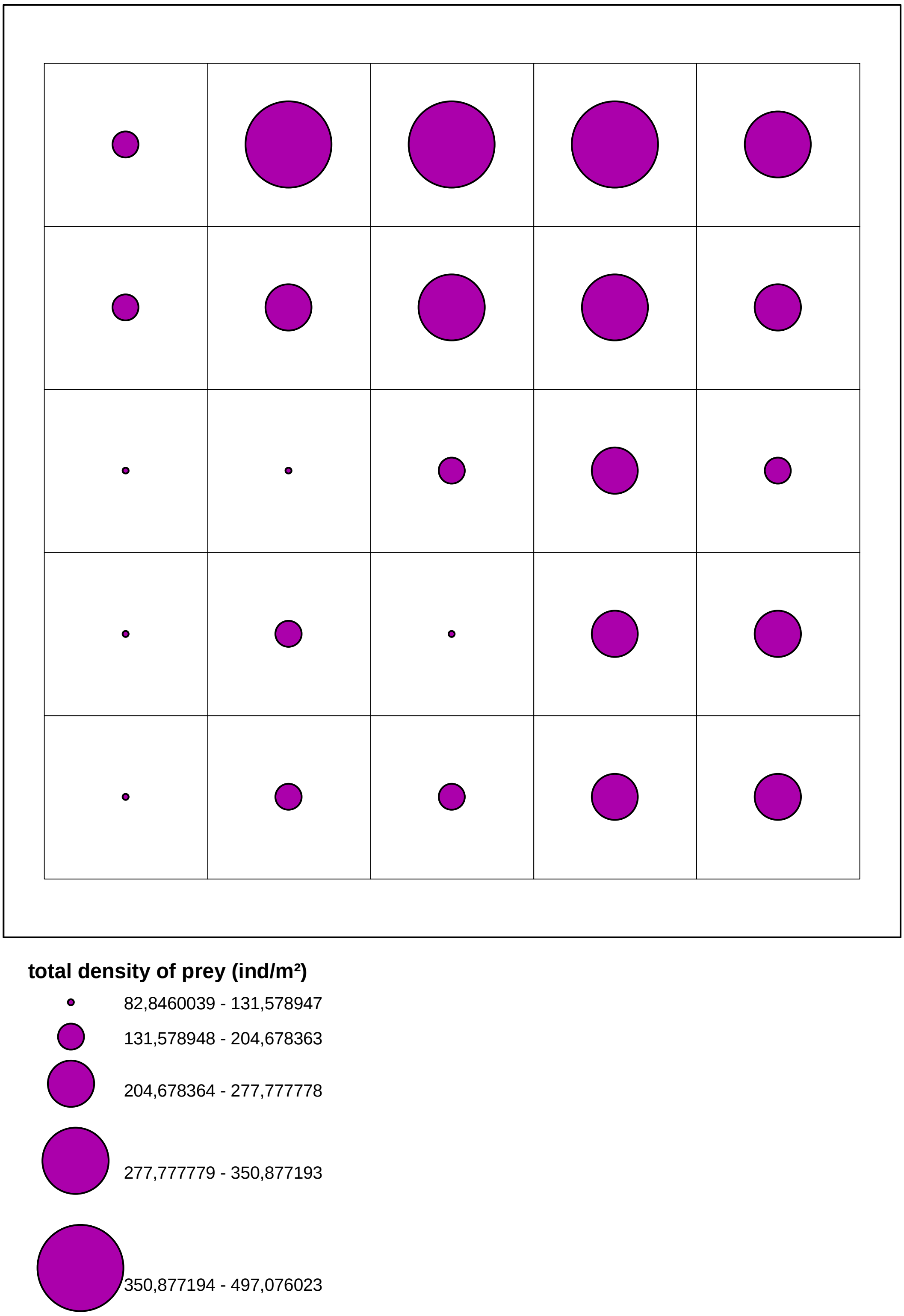


Figure 16: Density of the possible prey items in the grid, the maximum of 497 ind/m² was found in A2 mainly due to *Ensis spp.* 458 ind/m² (Figure 17).

For the Amphipods and the *Ensis spp.* there was a clear pattern in their distribution. The density of *Ensis spp.* was related to the distance from the low water line (ANOVA shows significant of the parameter “line”, DF=4, F=48.07, P<0.0001). When looking at Figure 17, the *Ensis spp.* densities were the highest in the lowest part of the intertidal (line A). For amphipods densities (Figure 18) was both “line” and “column” had significant effects (line: DF=4, F=3.26 and P=0.028; column: DF=4, F=4.90 and P=0.005). There even was a significant effect of the interaction term “line*column” (DF=16, F=2.35 and P=0.027), suggesting a certain amount of patchiness. This is also illustrated in figure 18 where it can be observed that the Amphipods are more numerous on the right side of the grid (line 4 and 5) and more in the middle of it (zone C and D).

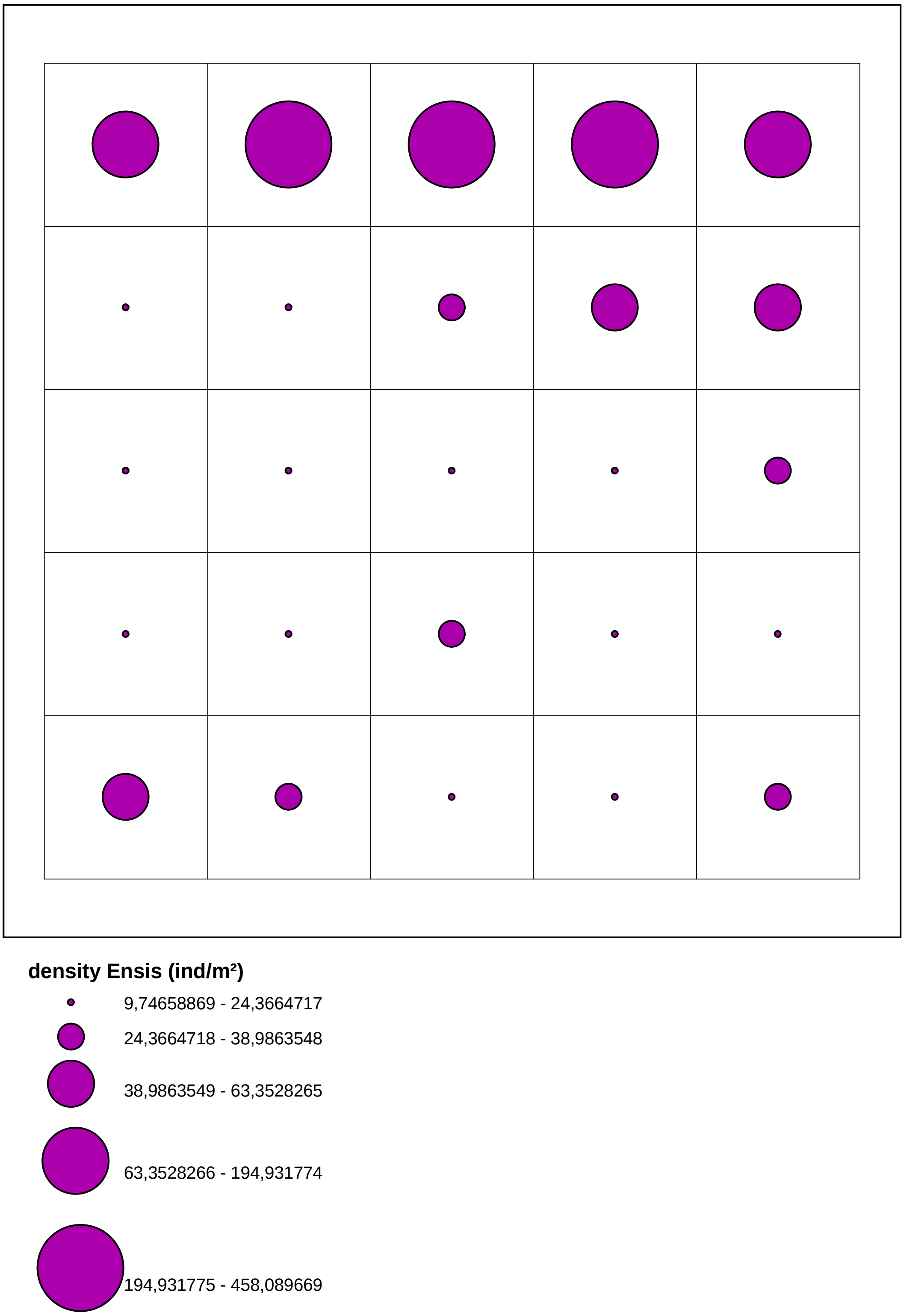


Figure 17: Density of the bivalve *Ensis spp.* in the grid. There was a difference between the lines (DF=4, F=48.07, P<0.0001). A maximum of the *Ensis spp.* in A2 (546 ind/m²) in one of the two replicates.

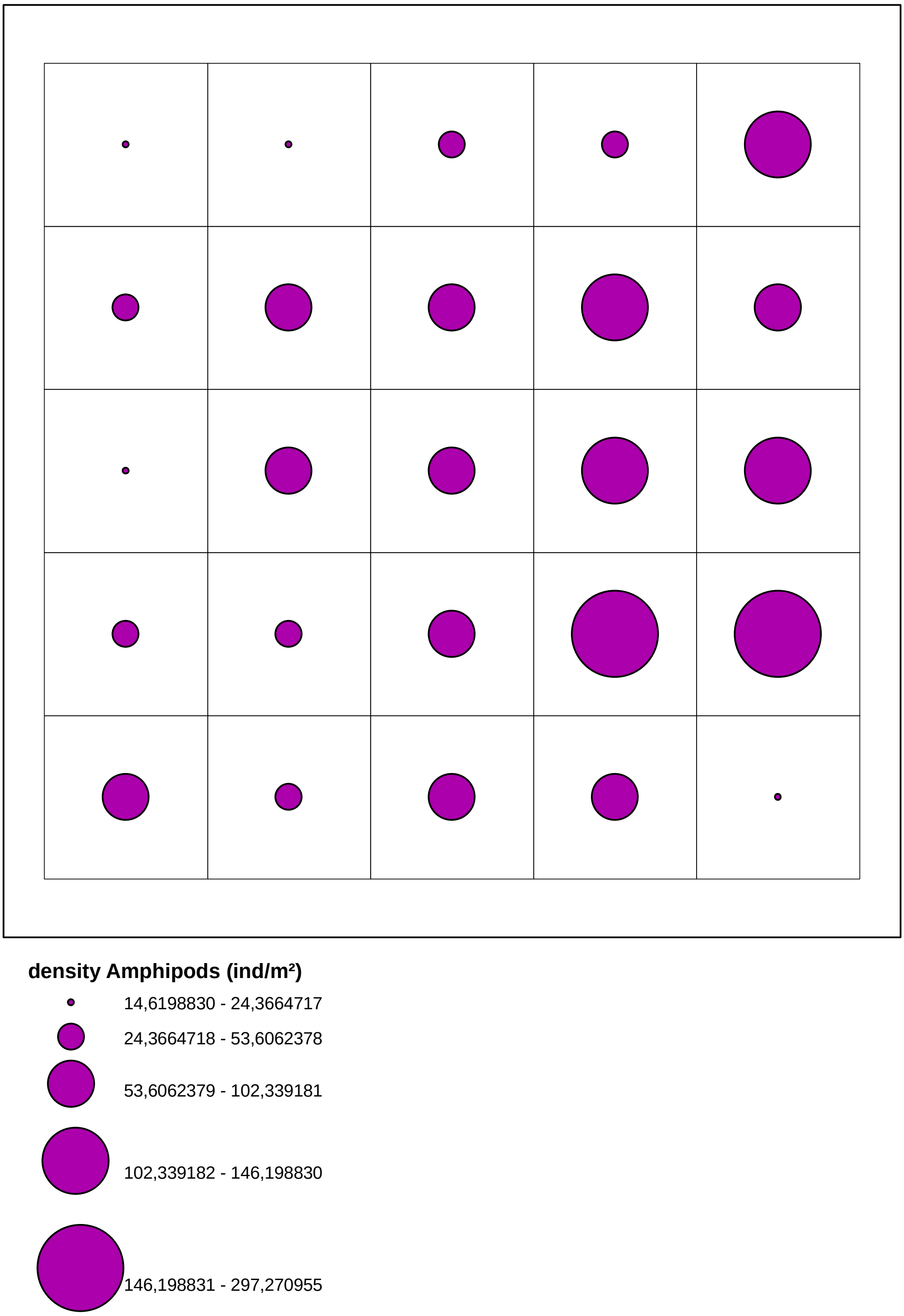


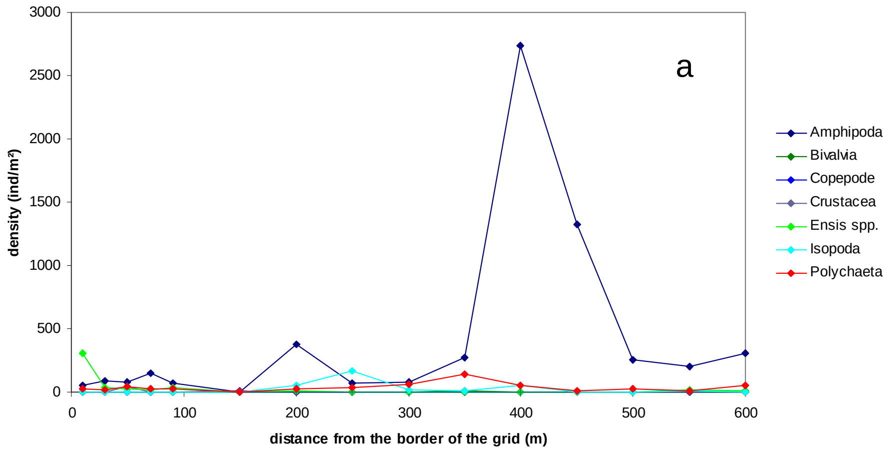
Figure 18: Density of amphipods in the grid. The distribution was patchy (line: DF=4, F=3.26 and P=0.028; column: DF=4, F=4.90 and P=0.005 and line*column: DF=16, F=2.35 and P=0.027). A maximum of Amphipods were recorded in D5 (409ind/m²) in one of the two replicates.

4.2.1.4 Density along the total transect including the grid

Table 7: Mean density in the total transect (grid+transect) (±SD). The amphipods were outstanding by their high density (403.7 ind/m²), followed by the polychaete worms (35.5 ind /m²), the *Ensis spp.* spp. (29.4 ind/m²) and finally the Isopods (20.3 ind/m²). The total density was on average little lower than 500 ind/m² (495.0 ind/m²).

Species in the total transect	Mean density (ind/m²)	± SD
Amphipods	403.7	719.5
Bivalves	1.6	2.7
Copepods	0.1	0.5
Crustaceans	3.2	11.5
Echinodermata	0.7	2.5
Ensis spp. spp.	29.4	77.1
Hydrozoa	0.5	1.1
Isopods	20.3	43.8
Juvenile Pleuronectidae	0.1	0.3
Polychaete worms	35.5	33.2
Total density	495.0	714.6

If we consider the total transect including the grid, mean densities of amphipods and isopods became much higher, whereas densities of *Ensis spp.* decreased (Table 7 and Figure 19) grid-total transect: amphipods 86.4-403.7 ind/m² and *Ensis spp.* spp. 83.2-29.4 ind/m²). Patterns along the intertidal gradient become much more apparent (Figure 19). Amphipods occurred in high densities at the higher part of the beach between 350 and 500m from the beginning of the grid. *Ensis spp.* clearly prefers the lowest part of the beach, with densities above 300 ind/m² in the A line. Isopods mainly occurred between 150 and 450m, whereas Polychaete worms were present along the entire transect but with maximum around 350m.



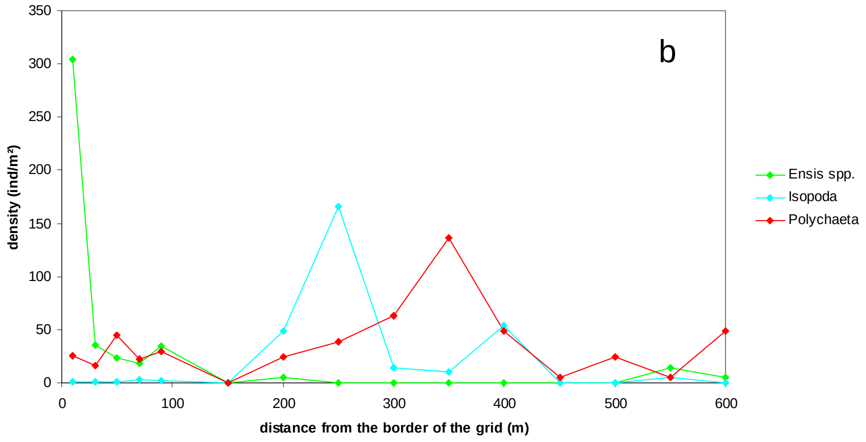


Figure 19: Density (ind/m²) along the total transect (grid+transect). The amphipods were clearly the dominant species maximum of 2734 ind/m² (19a) high on the intertidal zone (350m). The *Ensis spp.* were abundant at the lowest part of the intertidal (304 ind/m²) (19b). The isopods were most abundant at 250m (166 ind/m²) and the polychaete worms (136 ind/m²) (19b) at 350m.

4.2.2 The occurrence of sanderlings inside the grid

The number of sanderlings inside the grid was clearly higher before low tide than after low tide (DF=1, F=9.11 and P=0.017) (Figure 20). The number of birds was always higher just when the zone appeared during down going tide (negative numbers) or when the zone was just getting recovered with water during incoming tide. This shows that the birds were mainly foraging along the water line. The total number of birds inside the grid was highest when three lines were uncovered, E+D+C during downgoing tide and A+B+C during incoming tide (Figure 20).

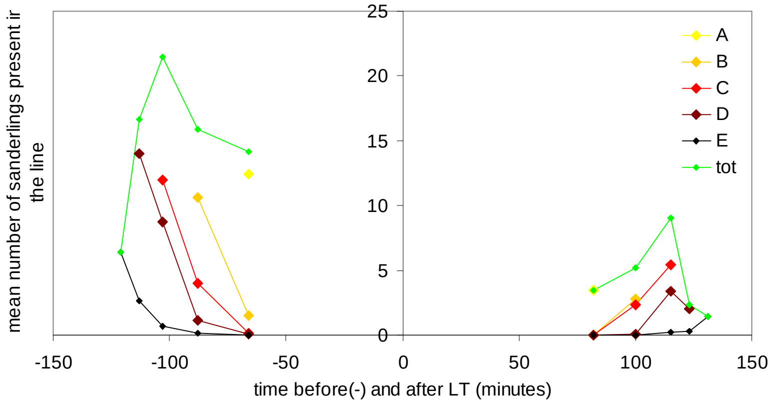


Figure 20: Mean number of sanderlings present in the grid during the tidal cycle depending on the zone (A,B,C,D and E). The birds were more numerous in the grid before low tide (0) than after (DF=1, F=9.11 and P=0.017).

The distribution of the sanderlings in relation to the tide (Figures 21a-21g and Table 8) shows some remarkable details. In the first place, it shows that the birds clearly prefer the lowest intertidal area (zone A) where high densities of *Ensis spp*. were found in the benthic samples (compare Figure 17). When the entire intertidal zone is available for the foraging sanderlings (Figures 21 c, d and e) almost all birds are concentrated near the waterline where they feed on small *Ensis spp*. However when zone A is flooded and no longer available for foraging either during downgoing or incoming tide (Figures 21 b and f) the birds are more dispersed over the remaining intertidal area. During that tidal sage, most sanderlings were found foraging in the upper right corner of the grid (cells B3-B5, C3-C5 and D3-D5). This distribution pattern matches the distribution pattern of Amphipods very well (compare Figure 18), suggesting that during this tidal stage the distribution of Sanderlings is either directly related to the patchy availability of Amphipods or reflects a co-relationship with another environmental feature. When both zone A and B are flooded (Figures 21 a and g) the distribution of the sanderlings no longer matches the distribution of any prey species.

Table 8: Explicative table for the figures 21a to 21g.

Name	Time	Zones available	Figure
1down	9:50-10:10	E, D and C	21a
2down	10:10-10:30	E, D, C and B	21b
3down	10:30-10:50	All	21c
4down	10:50-11:04	All	21d
1up	13:10-13:30	All	21e
2up	13:30-13:50	B, C, D and E	21f
3up	13:50-14:12	C, D and E	21g

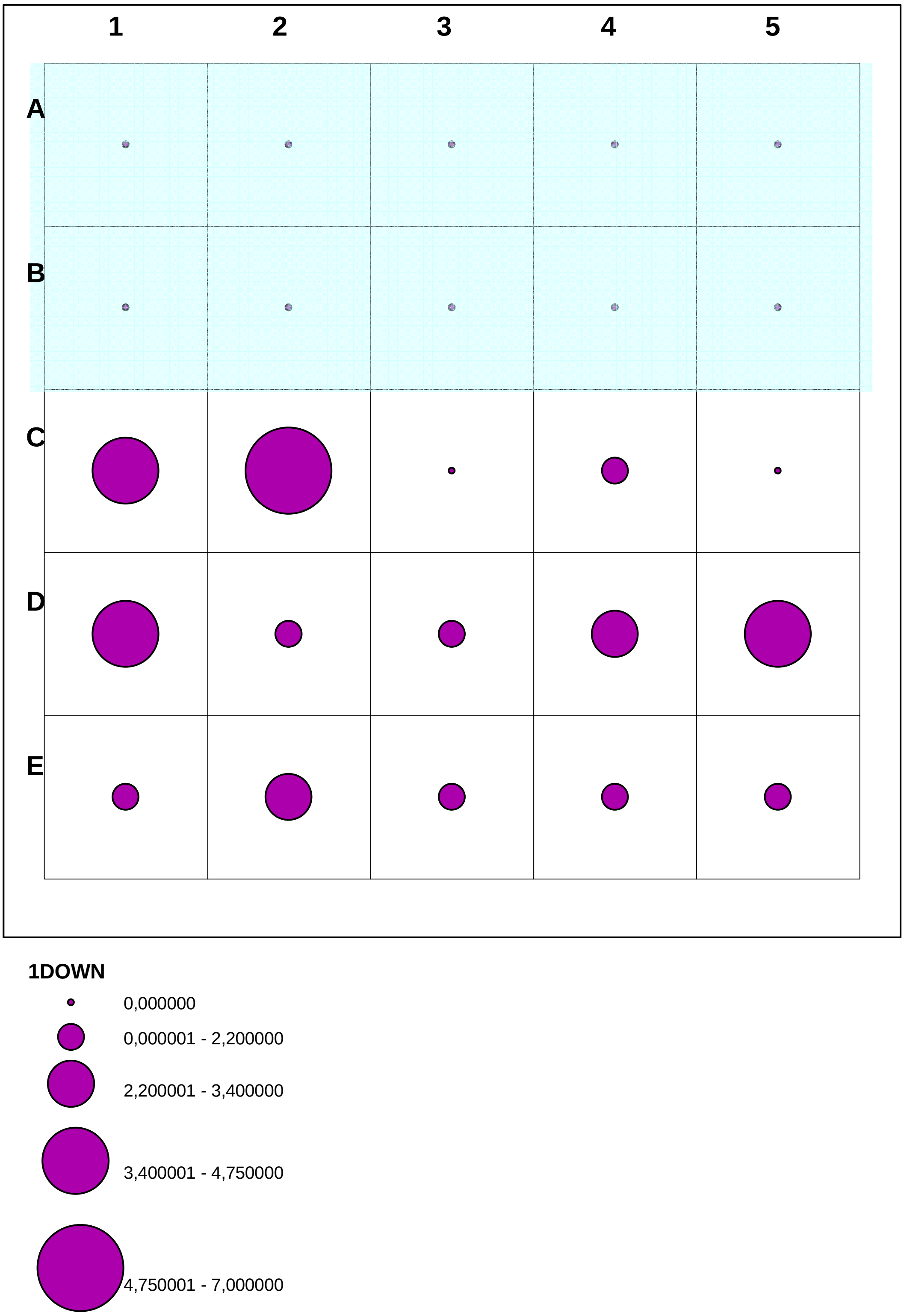


Figure 21a: Number of sanderlings present in the grid during downgoing tide from 9:50-10:10. A and B were still covered and the waterline was in C.

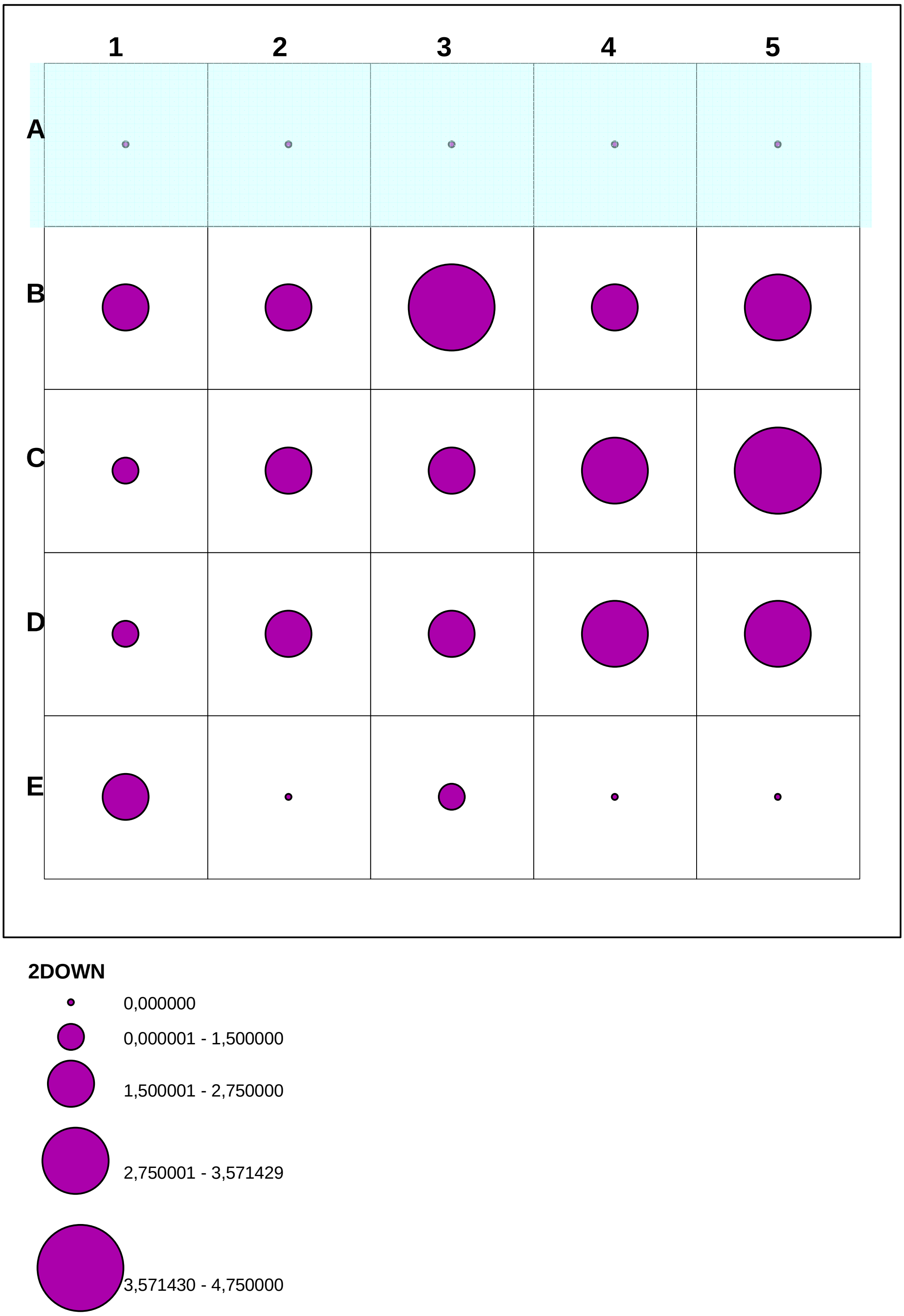


Figure 21b: Number of sanderlings present in the grid during downgoing tide from 10:10-10:30. A was still covered and the waterline was in B.

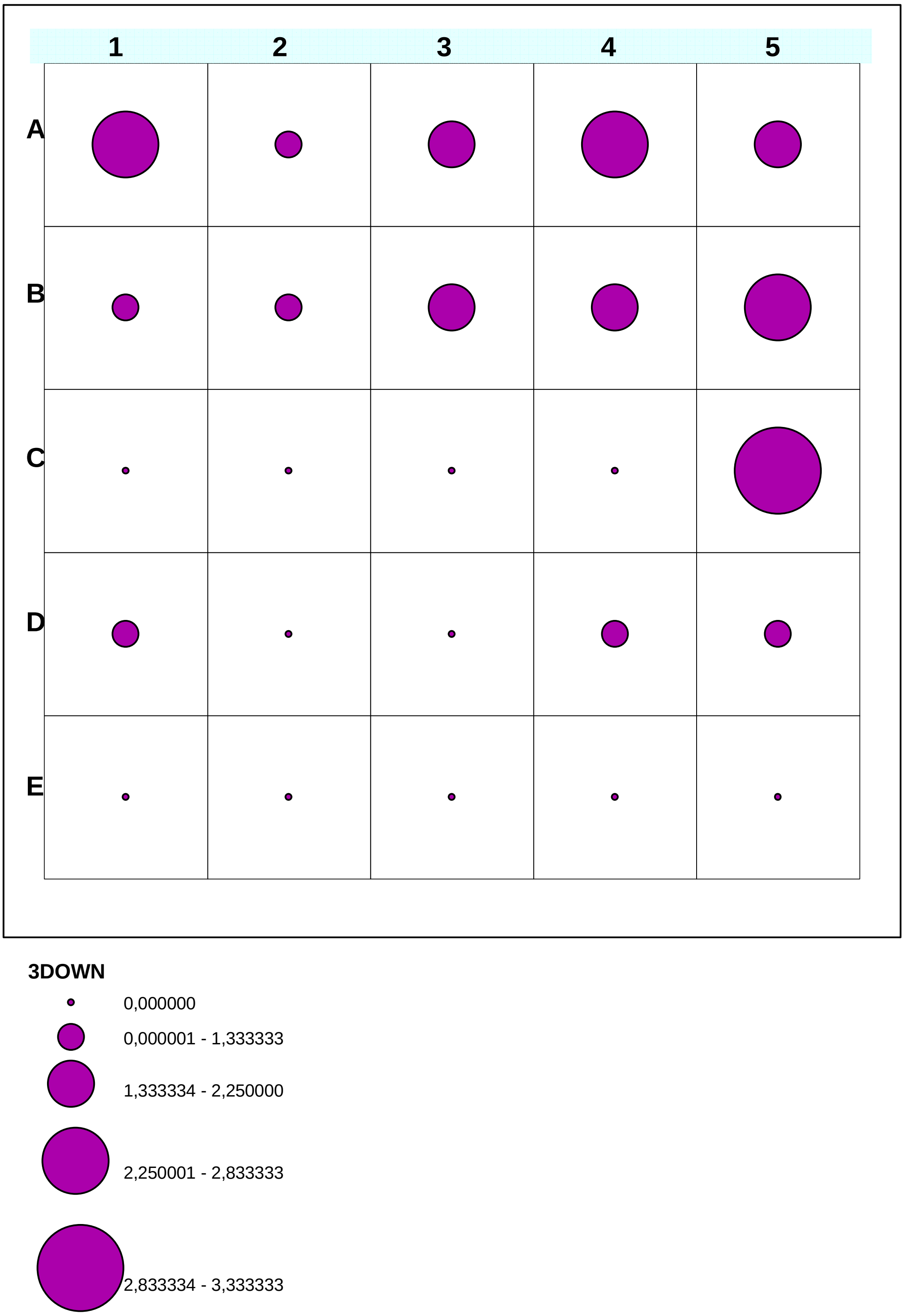


Figure 21c: Number of sanderlings present in the grid during downgoing tide from 10:30-10:50. The waterline was in A.

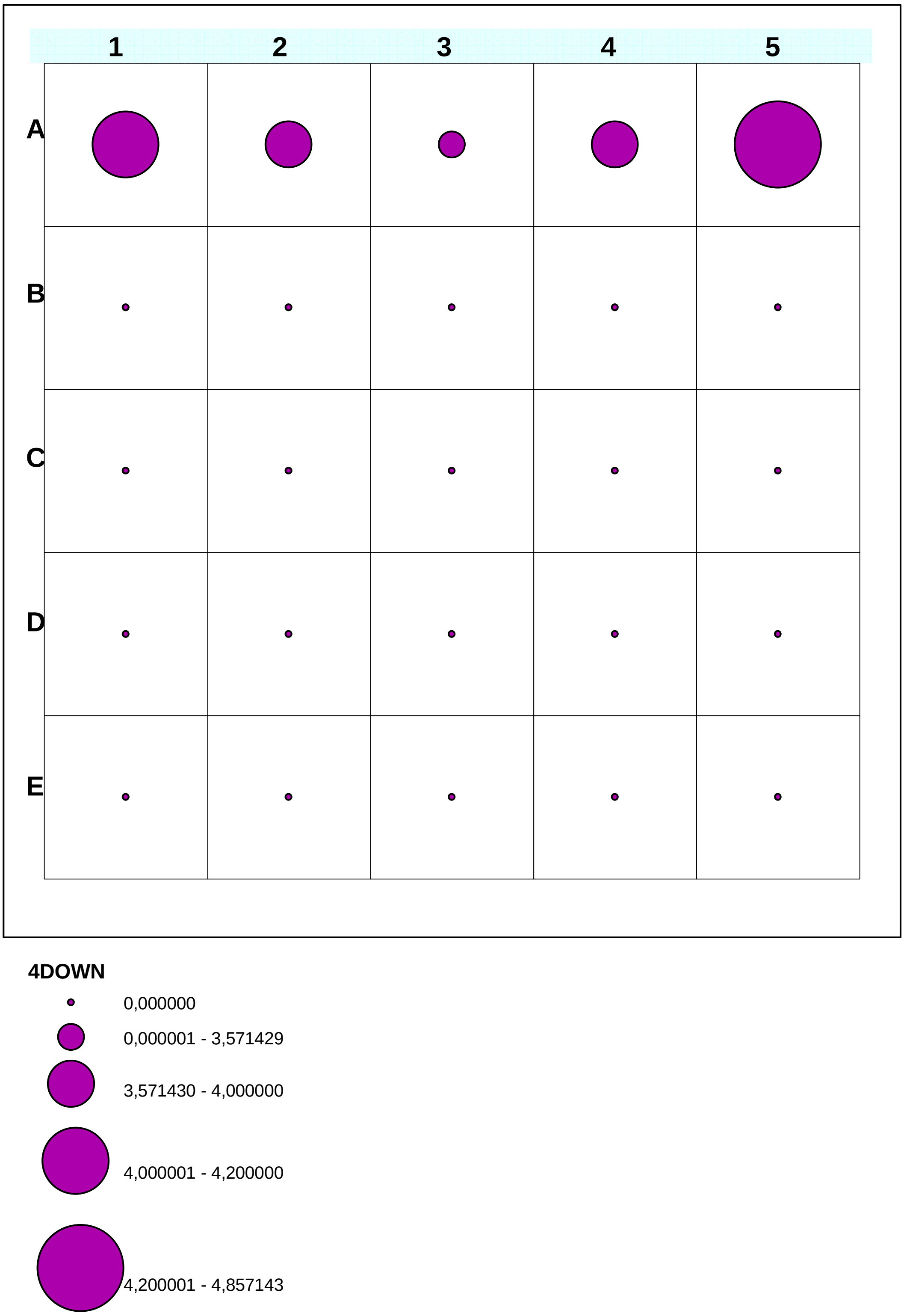


Figure 21d: Number of sanderlings present in the grid during downgoing tide from 10:50-11:04. The waterline was in A.

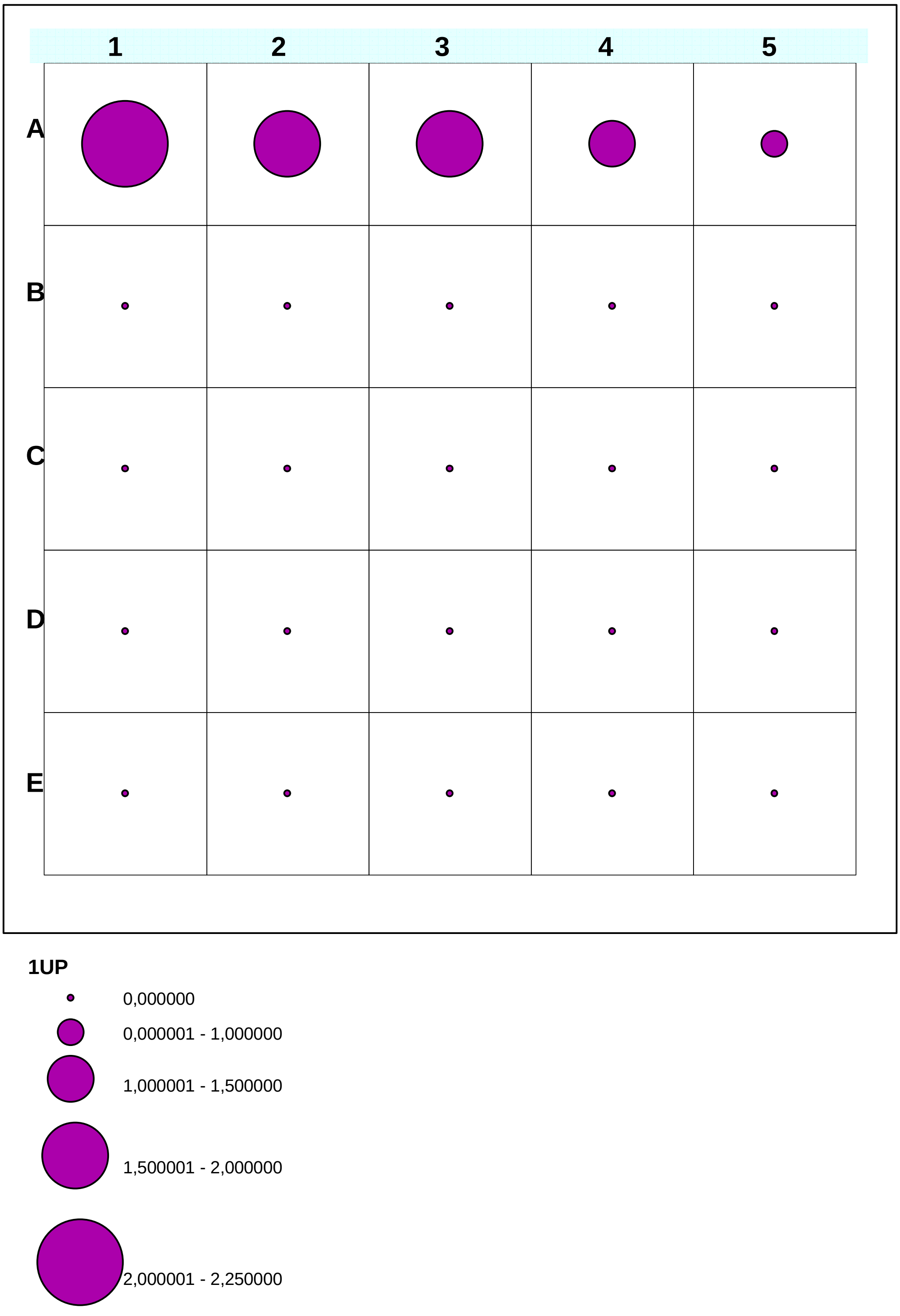


Figure 21e: Number of sanderlings present in the grid during upgoing tide from 13:10 to 13:30. The waterline was in A.

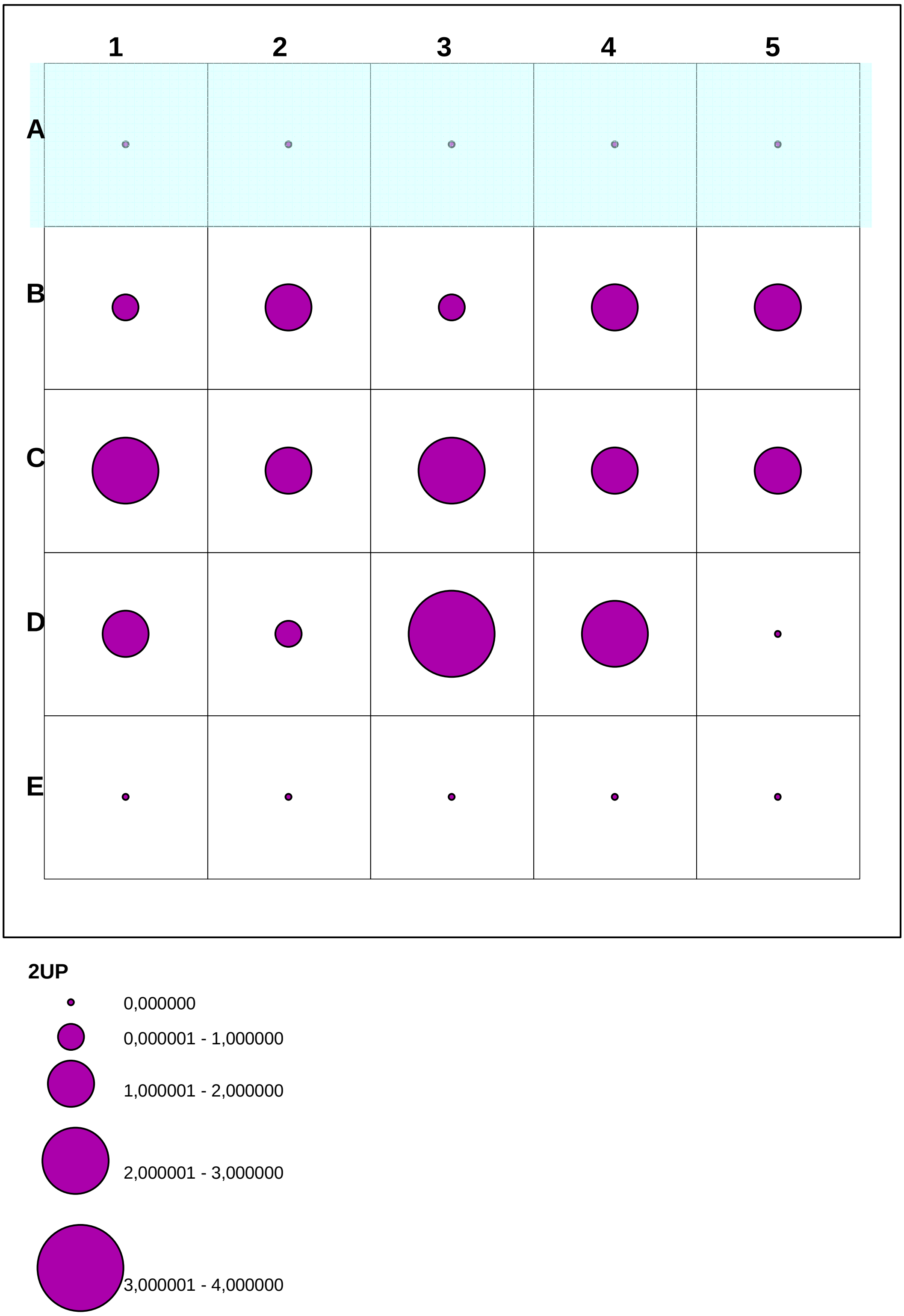


Figure 21f: Number of sanderlings present in the grid during upgoing tide from 13:30 to 13:50. The waterline was in B and A was covered with water.

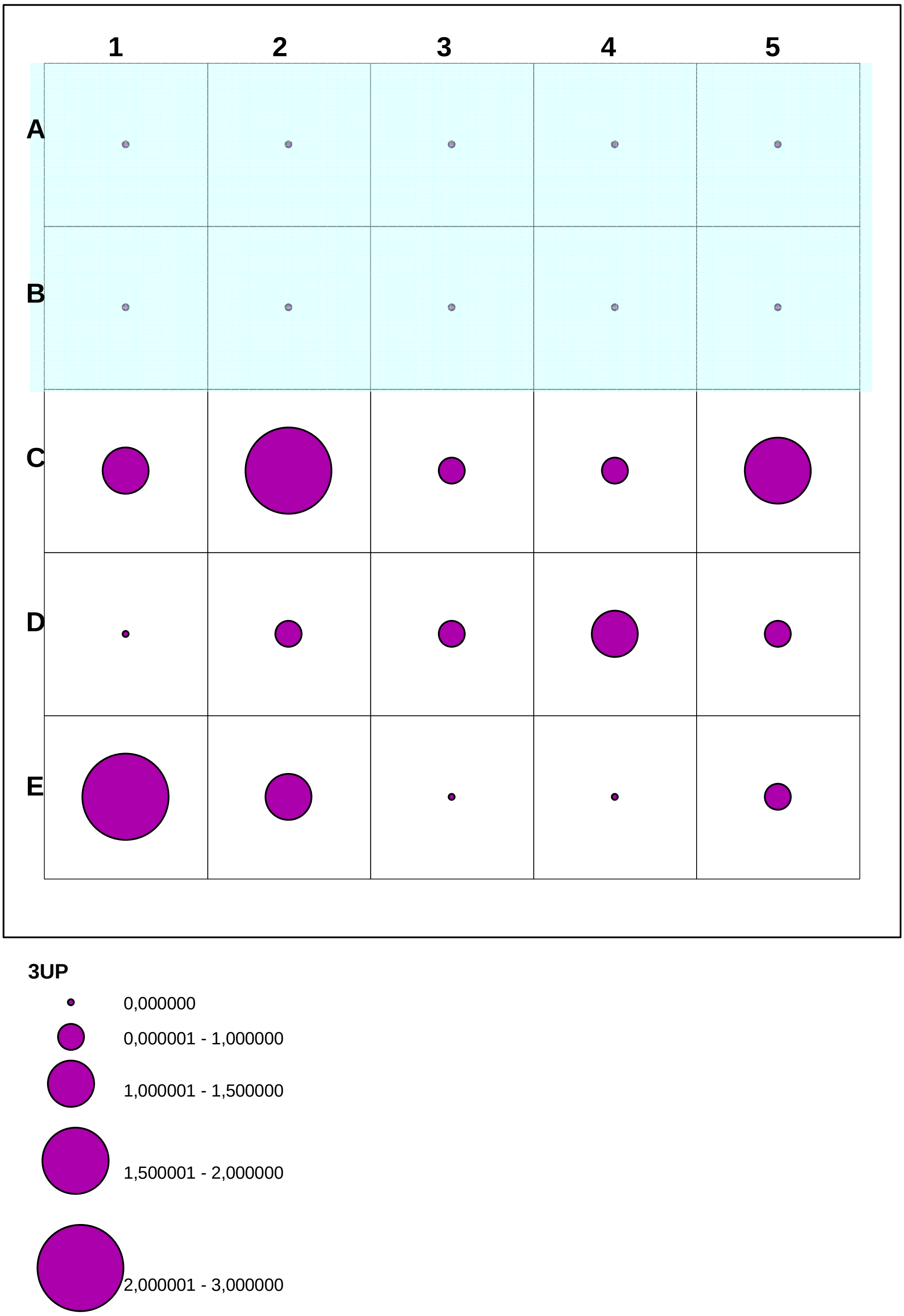


Figure 21g: Number of sanderlings present in the grid during upgoing tide from 13:50 14:12. The waterline was in C and A+B were covered with water.

5 Discussion

When looking at the waterline during low tide, groups of sanderlings could often be observed on the beach of Oostduinkerke Bad. Typically, these birds were almost constantly foraging. Three main behaviours were used to forage: pecking, probing and tactile walking. The main prey that could be identified visually were small *Ensis spp.* (2-4 cm long) which were removed from the sediment alive. Also of importance were beached prey items such as small *Ensis spp.* (2-4 cm long), big *Ensis spp.* (more than 7 cm long), debris and polychaete worms. Foraging on beached *Ensis spp.* was as successful as foraging on buried ones. But the quantity of flesh ingested is probably much higher when consuming an *Ensis spp.* out of the sediment than when only pecking part of the fleshy material of beached specimens. Small *Ensis spp.* were generally removed from the sediment. After the shell was removed by a shaking movement of the head, the flesh was swallowed entirely. Pecking on beached items was a somewhat quicker method to obtain food. The profitability of foraging on those two prey types, however, is difficult to determine. Pecking on beached items requires almost no handling time, but only gives a small amount of energy at a time, whereas probing on buried *Ensis* requires longer handling and probably longer searching time as well, but is rewarded with a higher energy intake. There was a clear separation in time between the two foraging methods, the beached items (mainly big *Ensis spp.* and debris) were brought in by the upcoming tide, while the “hunting” for alive *Ensis spp.* mainly occurred during low tide.

Beached prey items, not hidden in the sediment, were collected by visual behaviours (pecking and probing) in which the birds walk on the beach and suddenly stop to peck or probe. In other occasions, the birds used tactile detection of the prey present in the sediment. Visual foraging could be used all along the tidal cycle, but was in fact mainly used during upcoming tide when beached items were brought in by the tide. Tactile foraging only occurred along the waterline where the sediment was saturated and thus wet enough and soft enough to allow the bird to push its beak in the sediment. Dias et al. (2009) showed that tactile waders increase their foraging effort in close vicinity of a place where a prey was captured. In this study, the main prey taken by tactile behaviour were small *Ensis spp.* which, according to the bethos samples, lived predominantly in the lower part of the intertidal zone. Here very active and concentrated foraging took place. It was worth for the sanderlings to increase their foraging effort in the low intertidal because the foraging efficiency was close to 50%, much higher than the *Scolelepis* foraging efficiency of 5.5% occurring higher on the intertidal zone according to Vanermen et al. (2009). The spatial separation between visual behaviours, higher in the intertidal and tactile behaviours in the lowest intertidal one, probably mainly reflects the penetrability of the sand. At the lowest part of the intertidal zone the birds were predominantly feeding along the waterline where the wet penetrable sediment made probing possible. Higher on the beach, the importance of foraging on intertidal flats (harder dry sediment) increased. The prey type and its availability influenced the use of visual or tactile foraging. At the lowest part of the intertidal zone, *Ensis spp.* dominated the prey spectrum (our data are confirmed by Armonies & Reise 1999). These bivalves are buried in the sediment and almost impossible to detect visually. Higher on the intertidal amphipods, isopods and polychaete worms were dominant prey species and at least amphipods and isopods must be detected visually. In Belgium, amphipods that are available for sanderlings are either *Bathyporeia spp.* (Dahl 1952-1953, Degraer et al. 1999, Degraer et al. 2003, Speybroeck et al. 2008a) or beach flea *Talitrus saltator* (Dahl 1952-1953, Speybroeck et al. 2008b) whereas isopod availability is restricted to *Eurydice pulchra* (Degraer et al. 1999 and Degraer et al. 2003).

The sandy ultra-dissipative beaches of Belgium are characterised by a low species diversity (Degraer et al. 1999 and Degraer et al. 2003), in our case the benthic animals were not determined to the species which is required to calculate the Shanon-Wiener diversity index. Therefore the diversity index calculated was lower than the one from other studies (Degraer et al. 1999, Degraer et al. 2003, Speybroeck et al. 2007, Speybroeck et al. 2008a, Speybroeck et al. 2008b) (Table 9). Nevertheless our results were similar to Degraer et al. 1999 for the density (Table 9). Crustaceans and polychaete worms were found to be dominant both in density and biomass (Degraer et al. 1999 Degraer et al. 2003), but *Ensis spp.* had almost the same density as the polychaetes.

Table 9: Comparison of the Shanon-Wiener diversity index and the main prey density between our study and Degraer et al. 1999.

	Our study	Degraer et al. 1999
Shanon-Wiener diversity index	Grid: 0.9 Transect :0.4 Maximum in zone C (grid): 1.3	0.7-1.2
Mean prey density (ind per m²)	Grid: 212 Grid+transect: 495	250

All the small *Ensis spp.* (dead or alive) that were taken by sanderlings were between 13 and 44 mm long which corresponds to <1 year old individuals (Armonies and Reise 1999). This age class of *Ensis spp.* is subjected to high mortality rates in late winter and early spring (Mühlenhardt-Siegel et al. 1983) as it is easily washed out of the sediment (Armonies and Reise 1999). On the other hand, this age class is highly mobile as it is able to “byssus-drift” (Essink 1985) by which it can migrate to better grounds if necessary. Apparently, during autumn 2009 many young *Ensis spp.* settled at the Belgian Continental Shelf, leading to high densities in the sediment but also to elevated numbers of beached individuals. Such increased availability of *Ensis spp.* was never been demonstrated in Belgium. The opportunistic sanderlings immediately profited from it.

In this study we did not point out the importance of foraging on polychaetes, particularly *Scolelepis* (Glutz von Blotzheim et al. 1984 and Vanermen et al. 2009) or on amphipods/isopods (Cramp 1983, Glutz von Blotzheim et al. 1984, Nuka et al. 2005) because the filming mainly took place during the lowest part of the tide and also because these preys may easily be missed in visual observations. Instead we focussed on the importance of patchiness for the foraging behaviour of sanderlings. The reason for this was that Vanermen et al. (2009) hypothesised that foraging on polychaetes was not enough to fulfil in the daily energy demands of the birds. Either the birds were taking advantage of patches with very high prey densities or/and small important prey items are missed by the observers. Vanermen et al. (2009) already suggested that small amphipods (*Bathyporeia*) might be a good candidate for this. Here we show that, except in the lower tidal part that was dominated by invasive *Ensis spp.*, during a large part of the tidal cycle it is probably the patchy occurrence of amphipods that rules the occurrence of sanderlings. According to literature (see above) those amphipods could be *Bathyporeia spp.* and/or *Talitrus saltator. Bathyporeia* is known to live in the intertidal flat (Speybroeck 2008a) and *Talitrus* (Dahl 1952-53) young ones at the lowest part of the beach and adult ones at higher levels.

The number of birds observed in the grid was higher before low tide than after, which was also found by Vanermen et al. (2009). However, in contrast to Vanermen et al. (2009), most probing occurred around low tide. In our study sanderlings caught high numbers of small *Ensis spp.* in the lower tidal zone (A-zone of the grid) where this species was very abundant. The A-zone (Figure 1) was at the waterline 28 minutes (from 80 to 52 minutes before low tide) during downgoing tide and 16 minutes (from 74 to 90 minutes after low tide) during incoming tide (Figure 21), consequently the sanderlings probing at the waterline would have at least 44 minutes to forage on small *Ensis spp.* alive (the grid wasn't at the low tide water line) twice a day. Apparently these bivalves were especially accessible during retreating tide probably because the wet sand during downgoing tide is better penetrable and also because of the time (more than 28 minutes) the lowest tidal zone is available. During upcoming tide, the foraging success on *Ensis spp.* sharply decreased and instead feeding on wrecked material became the dominant foraging behaviour. Then, the birds were feeding on *Ensis spp.* (small and big), mussels and other undetermined bivalves that were washed ashore. Wrecked material seems a very important food source for sanderlings as was already found by Vanermen et al. (2009). Even during upcoming tide, the birds were observed pecking on wreck. The amphipod *Talitrus saltator* is often encountered on wreck (Speybroeck et al. 2008b), and the birds might have taken advantage of that presence. Vanermen et al. (2009) showed that probing and capture of polychaetes predominately occurred in the upper intertidal areas. This is in agreement with the presence of polychaetes in our transect samples high up the beach, but not with the bird observations. Out of 14 worms eaten, 13 could be *Scolelepis* and only two of those were caught just before high tide.

The reliability of the benthic species as a prey item for sanderlings is depending on their mobility and their life cycle. The predictability of the presence and the number of preys at one location can vary in time. This seems especially true for the invasive *Ensis spp.* species. The bivalve *Ensis directus* (also called *Ensis americanus*) was introduced in the European ecosystem in the late 1970s (Von Cosel et al. 1982) in Germany and arrived on the Belgian coast in 1987 (EnSIS report 2008). Armonies (2001) describes *Ensis directus* as a species having “outstanding dispersal capabilities”. In the case of a beach nourishment this allows the *Ensis spp.* to quickly “re”-colonize the new space created. The only problem is the reliability of the production of these young *Ensis spp.* (<1 year) because there is a strong year to year variation in the recruitment (adding new individuals to a population by reproduction) (Armonies and Reise 1999, Beukema and Dekker 1995). The number of small *Ensis spp.* accessible to the birds from year to year is not predictable. Until this year only older *Ensis spp.* (size from 7cm and up) has been observed beached and no small individuals. In 2010, exceptionally high quantities of small *Ensis spp.* (< 5cm) were reported beached along the Belgian coast. Apparently huge amounts of young *Ensis spp.* settled at the Belgian Continental Shelf and this was confirmed by high numbers in our samples. The “lack” of young *Ensis spp.* in previous years is confirmed by Vanermen et al. (2009), who did not observe the birds foraging on this prey type in the period 2005-2006. The presence of small *Ensis spp.* beached or alive in the lower intertidal zone might be exceptional and occasional during our study period, but time must tell. Armonies and Reise (1999) found a maximum density of 33 *Ensis spp.* per m² in the intertidal zone in March 1993; much less than the maximum density of 546 individuals per m² found in our study.

Scolelepis is characterised by its “short life span, great reproductive effort, and opportunistic behaviour” by Souza and Borzone (2000) in Brazil which is not the same as in Speybroeck et al. (2007) where the polychaete worm lives for 24 months (instead of one year) and only reproduces once (in opposition to the great reproductive effort) on the Belgian coast. Nevertheless the abundance of Scolelepis was lower in February 1992 (<20 ind/m²) than in February 1993 (>70 ind/m²) in Brazil (Souza et Borzone 2000) which could be an indication of inter annual variation. In North Carolina, Peterson and Manning (2001) show that Scolelepis is the only benthic species reacting positively to beach nourishment by an increased abundance. The polychaete worm *Scolelepis* seems to follow the same pattern as the *Ensis spp.* with no predictability on recruitment but great capability of “recolonizing”. The crustaceans: *Bathyporeia spp., Talitrus saltator* and *Eurydice pulchra* are all mobile species and less is known about their distribution in the intertidal zone. Do they concentrate in zones parallel? In patches?

The most important finding in our study was that the amphipods were found patchily distributed and that sanderlings apparently used these patches of high amphipod densities when the more profitable *Ensis spp.* that exclusively occurred in the lowest intertidal zone was no longer available. This strongly suggests that amphipods are a very important prey species for sanderlings, which unfortunately could not be confirmed by visual observations on feeding sanderlings. Probably, these small prey were picked from the substrate and swallowed very quickly. Vanermen *et al*. (2009) used the Ash Free Dry Weight (AFDW) to estimate the number of preys that should be ingested and also estimated the total daily consumption between 5.2 and 12.6 g of AFDW of benthic preys. Estimating the AFDW per *Bathyporeia* the from literature (Degraer et al. 1999 and Ysebaert et al. 2000) with the density and the biomass, the AFDW of a single *Bathyporeia* should be between $0.10*10^{-3}$ g (Degraer et al. 1999) and $0.22*10^{-3}$ g (Ysebaert et al. 2000) (Table 10). If the daily energy needed by the birds was calculated in Ash Free Dry Weight (AFDW) as Vanermen et al. (2009) did, the birds should eat between 23,661 and 132,300 *Bathyporeia* a day (Table 10). The maximum successful pecking rate observed was 34.6 pecks/min, that meant that the sanderlings would have to use between 11h23min and 63h44min pecking for *Bathyporeia* to fulfil its daily needs (Table 11). The maximum density of amphipods in our study was 2734 ind/m², if considering that they were all *Bathyporeia*, this would mean that a sanderling needed at least to deplete 8.65 m² of the beach surface from *Bathyporeia* to gain enough energy. If the sanderlings should feed essentially or mainly on amphipods some criteria should be fulfilled:

- Very high densities of amphipods, if possible very concentrated in patches on the intertidal zone or on wreck
- Bigger amphipods than those from Degraer et al. (1999) so the energy gained by a single amphipod could be higher.

If we use the AFDW needed from Vanermen *et al*. (1999) to calculate the number of *Ensis spp.* that need to be eaten, the number of *Ensis spp.* eaten should be situated between 271 and 656 (average from several years, several sites and age classes from 1-2 years Armonies & Reise 1999) (Table 10). The sanderlings were able to reach an intake rate of 283 *Ensis spp.* per hour and consequently needed between 57min and 2h18min (Table 11) to fulfil their daily needs. The A-zone was at the waterline 44 minutes twice a day, which means that the sanderlings could fulfil their daily energy needs by only foraging on *Ensis spp.*. It should not be forgotten that the very high abundance of *Ensis spp.* was not usual on the Belgian coast and that the sanderlings used this opportunity.

Apart from a decrease in prey abundance, other possible effects of sand suppletion on the sanderlings would be on the foraging mode. The sand added will probably be more compact and courser than the original one, which will decrease the ability of the bird to search for prey tactilely. Furthermore adding sand will decrease the total beach surface immerged by water, less wet sand and makes it less penetrable for the birds. Turbid disturbed water is less suitable for visual foraging behaviours. Sand suppletion will therefore have direct effect one the foraging efficiency of both visual and tactile behaviours, as well on the surface as on the time available for the birds.

The rationale behind this study is to find out how beach nourishment might affect foraging birds along the Belgian coast. This study as well as the former study of Vanermen et al. (2009) shows that beach nourishment will mainly affect the availability of the predictable food resources of sanderlings. This only a part of their daily energy source as sanderlings also strongly depend on the presence of beached prey items. Low in the intertidal beach nourishment will at least temporarily affect the availability of bivalves (mainly *Ensis spp.* in the winter 2009/2010), somewhat higher the availability of amphipods will decrease and in the highest part it will lead to a decreased availability of polychaete worms. As beached prey will not always provide enough energy for sanderlings this means that when large parts of the coastline will be suppleted in a short period of time it may have serious consequences for the occurrence of sanderlings in front of our coast. On the other hand, this and earlier studies show that sanderlings are truly opportunistic species that may easily switch to alternative prey species or alternative locations. In other words: beach nourishment will have least effects on sanderlings when it is carried out in phases. Organising the nourishment (either spatially or temporally) in a way that only short stretches of beach are affected, will ensure the presence of alternative feeding zones for sanderlings.

Table 10: Number of *Ensis directus* and *Bathyporeia spp.* needed to fulfil the daily energy needs. The densities and the biomass were used to calculate the individual biomass in Ash Free Dry Weight (AFDW) (Ysebaert et al. 2000, Degraer et al.1999 and Armonies & Reise 1999). The daily energy needed expressed in AFDW was used from Vanermen et al. (2009) and was situated between 5.2 and 12.6 grams of AFDW.

Species		Location		Density (ind/m²)	Biomass (g AFDW/m²)	Individual biomass (g AFDW/ind)	Number of preys needed if daily intake is 5.2 g AFDW	Number of preys needed if daily intake is 12.6 g AFDW
Bathyporeia spp.	Ysebaert et al. 2000	Schelde estuary (Belgium)		86	0.019	$0.22*10^{-3}$	23661	57333
	Degraer at al. 1999	De Panne (Belgium)	Summer	63	0.006	$0.10*10^{-3}$	54600	132300
			Winter	34	0.004	$0.12*10^{-3}$	44200	107100
			Mean			$0.11*10^{-3}$	48853	118374
Ensis directus	Armonies & Reise 1999	Island of Sylt, West(Germany)	1996	1883	6.2	$3.30*10^{-3}$	1579	3827
		Island of Sylt, List(Germany)	1992	19	0.6	$31.58*10^{-3}$	1645	399
		Island of Sylt, List(Germany)	1993	1500	18.5	$12.33*10^{-3}$	422	1022
		Island of Sylt, List(Germany)	1994	2025	249.9	$123.41*10^{-3}$	42	102
		Island of Sylt, List(Germany)	1995	204	22.2	$108.82*10^{-3}$	48	116
		Island of Sylt, List(Germany)	1996	38	13.7	$360.53*10^{-3}$	14	35
		Island of Sylt, Watt(Germany)	1993	1925	38.1	$19.79*10^{-3}$	263	637
		Island of Sylt, Watt(Germany)	1994	1159	36.8	$31.75*10^{-3}$	164	397
		Island of Sylt, Watt(Germany)	1995	467	468.8	$1003.85*10^{-3}$	5	12,6
		Island of Sylt, Watt(Germany)	1996	688	666.7	$969.04*10^{-3}$	5	13
		Island of Sylt, (Germany)	Mean			$266.44*10^{-3}$	271	656

Table 11: Time needed to eat enough *Ensis directus* or Bathyporeia to fulfil the daily needs. The number of preys needed were used from Table 10. The maximum pecking rate observed in our study was 34.6 pecks per minute and the highest number of *Ensis spp.* alive removed were 4.72 per minute. The sanderlings would need between 11 hours 23 minutes and 57 hours 01 minutes foraging on Bathyporeia or between 57 minutes and 2 hours 18 minutes foraging on *Ensis directus* to gain enough energy.

Species	Study	Number of prey eaten per minute	Number of prey eaten per hour	Time needed if daily intake is 5.2 g AFDW	Time needed if daily intake is 12.6 g AFDW
Bathyporeia spp.	Ysebaert et al. 2000	34.6	2076	11h23min	27h37min
	Degraer at al. 1999			23h32min	57h01min
Ensis directus	Armonies & Reise 1999	4.72	283	0h57 min	2h18min

6 Sum up

The main results of this study were:

- *Ensis spp.* was the main prey of Sanderlings both in numbers ingested and in terms of energy intake. Young specimens of this invasive bivalve were found in high densities along the waterline at the lowest part of the intertidal zone. When available during a tidal cycle this part was preferred by foraging sanderlings.

- Feeding on amphipods was not verified by visual observations. However, when the lowest intertidal zone was flooded and *Ensis spp.* was no longer available, the distribution of foraging Sanderlings followed the patchy distribution pattern of amphipods suggesting that it is an important prey item.

- Also the importance of beached prey items should not be neglected. In this study especially beached *Ensis spp.* were very abundant.

- Sanderlings were exploiting the entire intertidal zone, following the waterline at the lowest part and dispersing more afterwards.

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