

SHOREBIRDS OF THE BRAGANTINIAN PENINSULA I. PREY AVAILABILITY AND SHOREBIRD CONSUMPTION AT A TROPICAL SITE IN NORTHERN BRAZIL

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Resumo. – Pássaros litorâneos da Península Bragantina I. Disponibilidade de presa e consumo de pássaros litorâneos em um local tropical no norte do Brasil. – Estudos sobre a ecologia da alimentação dos pássaros litorâneos foram feitos freqüentemente em regiões temperadas, aonde as interrupções de viagens em locais tropicais e os lugares para passar o inverno ficam períodos altamente de baixa representação. Entretanto, os habitats tropicais diferem significativamente de suas contrapartes temperadas com características únicas que tem que ser enfrentadas pelos pássaros. Para descrever as características de uma planície de maré tropical e o uso deste habitat pelos pássaros litorâneos, foi realizado um estudo sobre pássaros que passam o inverno na península Bragantina na costa norte do Brasil durante 2001/2002. Por causa da elevada entrada de água doce durante o período de chuva, condições abióticas deste habitat foram variáveis. Como uma consequência, a abundância e biomassa da comunidade bentônica foram geralmente baixas e distribuídas irregularmente. Pássaros litorâneos foram predominantemente migratórios e ocorreram em densidades elevadas durante Janeiro e Fevereiro. Para a maioria, somente uma parte pequena da escassa fonte de alimento estava disponível para o consumo. Durante a presença das espécies migratórias, o cálculo teórico do consumo das aves foi superior ao das presas existentes, embora que um experimento de exclusão não revelou um efeito significativo de predação dos bentos. Conseqüentemente, os pássaros litorâneos deviam ter se alimentado em outro lugar.

Abstract. – Studies on the foraging ecology of shorebirds have often taken place in temperate environments, with tropical stop-over and wintering sites remaining highly underrepresented to date. However, tropical habitats differ significantly from their temperate counterparts by unique characteristics which have to be faced by the birds. In order to describe characteristics of a tropical tidal flat and habitat use by shorebirds, a study was conducted on overwintering birds at the Bragantian Peninsula on the north coast of Brazil during 2001/2002. Because of the high freshwater input during the wet season, abiotic conditions of this habitat were variable. As a result, abundances and biomasses of the benthos community were generally low and patchily distributed. Shorebirds were predominantly migratory and occurred in high densities during January and February. For the majority, only a small fraction of the sparse food supply was available for consumption. During the presence of migratory species, the calculated theoretical avian consumption far exceeded existing prey, although an enclosure experiment did not reveal a significant effect of predation on the benthos. Consequently, shorebirds must also have fed elsewhere. *Accepted 14 June 2006.*

Key words: Tropical habitat, benthos, shorebirds, consumption, enclosure experiment, prey availability, Brazil.

INTRODUCTION

Many shorebird species are long distance migrants. To overcome seasonal adverse environmental conditions, they often leave their arctic or temperate breeding grounds to winter in tropical and subtropical habitats. Within one year they experience significant habitat shifts and adapt to the differing conditions. Tropical tidal flats are likely to show specific properties which are different from those found at their temperate counterparts, such as the impact of a rainy season. Nevertheless, most investigations on nonbreeding shorebirds have taken place on temperate breeding and stop-over areas, and only in the last fifteen years have increasing efforts been put into the investigation of tropical tidal flats as shorebird environments (Wolff & Smit 1990, Wolff 1991, Piersma *et al.* 1999, de Goeij *et al.* 2003). What are the characteristics of these habitats? Are tropical tidal flats favorable foraging habitats or do they provide constraints the birds have to face? Do the birds show special adaptations to tropical environments?

The northeastern coast of South America is one of the major wintering areas of migratory shorebirds breeding in North America with an estimated 86% of shorebirds wintering in South America (Morrison & Ross 1989). Especially in spring, it is a key area for many birds to gain fuel before they return to their breeding grounds, because the Caribbean is bypassed or overflowed by most northbound shorebirds, presumably due to a limited food supply in this region (Wunderle Jr. *et al.* 1989). Although, there are some detailed studies on shorebirds in Surinam (Spaans 1979, Swennen *et al.* 1982), an area famous for its enormous numbers of over-wintering individuals, very limited data have been published about the northern Brazilian coast, an area eminent for its variety of habitats (Rodrigues 2000).

In 2001/2002 we conducted a shorebird

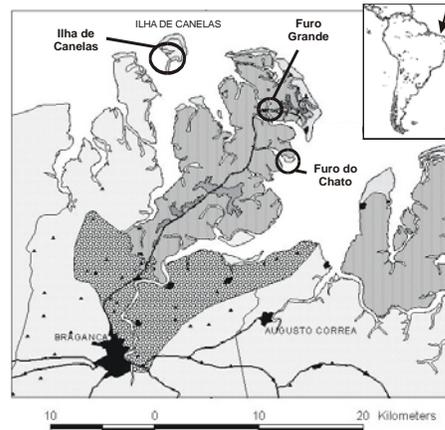


FIG. 1. Bragantian peninsula with sampling sites.

study at the coast of Pará in northern Brazil ($0^{\circ}52.427S$, $46^{\circ}39.012W$). Our objective was to investigate the foraging ecology and habitat use of shorebirds in the intertidal zone adjacent to mangroves. This paper presents the characteristics of this specific tropical bird foraging habitat, in particular the availability and consumption of prey by shorebirds since it affects future fitness and reproductive output (Drent *et al.* 2003). A second paper (Kober & Bairlein in press) will focus on behavioral reactions of shorebirds to these habitat characteristics in more detail.

METHODS

Study area and sampling sites

The Bragantian Peninsula is on the northern coast of Brazil. This coast is bordered by the world's second largest continuous mangrove region, covering an area of 1.38 million ha along a coastline of approximately 6800 km (Kjerfve *et al.* 1997). The forest is crossed by small creeks, named "Furos", with direct access to the sea. The soils along the fringe of these streams, as well as those inside the forest, are made up of soft and heavy mud.

Towards the edge of the mangrove forest, streams widen out to extensive open intertidal flats with firm and sandy soils.

The Bragantian Peninsula is tropical with a pronounced rainy season from January to May/June and a dry season from July to December. Data were collected in January–June 2001 and 2002, thus covering the northward migration of shorebirds. We used three sampling sites in order to represent all intertidal habitats available to shorebirds (Fig. 1). The first site, about 1 km² of open tidal flats close to the Ilha de Canela, was characterized by constant sediment relocations due to strong water currents. The second site, Furo Grande, was located within the mangrove forest at the margins of a large mangrove channel. It stretched over 200 m along the shore, and covered the full width (50 m) of the intertidal zone. The third site, Furo do Chato, consisted of about 0.5 km² tidal flats at the mouth of a stream, representing a transition area between an open intertidal area and a tidal flat bordering mangrove streams.

Sampling design

In 2001, 46 plots were marked with poles (25 plots at the Ilha de Canela, 6 at the Furo Grande and 15 at the Furo do Chato). Each had a size of 50 x 50 m (2500 m²); two plots were smaller because of limited space available (2000 m² and 750 m²). To obtain optimal data for correlation analysis and multivariate statistics, plot locations were not situated randomly but instead chosen to cover the variety of distinguishable, local intertidal habitats. Consequently, data of the sites are given as ranges because means would be altered, and statistical comparisons between sites are not valid. In 2002, five plots (2500 m²) were marked at the Ilha de Canelas, since this was the only area of significance for birds in 2001. The following data were recorded monthly:

Abiotic variables. One sediment sample was

taken per plot by pooling three sub samples, employing a corer of 2.5 cm diameter and 20 cm length at different locations (“Sacrificial Pseudoreplication”, Hurlbert 1984). A sample of 30–45 g dry weight (dried for 4 days at 60°C) was taken from this mixture and soaked for 24 h in a solution of sodium-hexametaphosphate (0.24 g/l) to dissolve agglomerated particles. A wet-sieving-analysis was performed by using the Analysette 3 Pro with six sieves of differing mesh widths (1000, 710, 500, 315, 71 and 20 µm). The resulting sediment fractions were dried (48 h, 60°C) and weighed to the next 0.001 g. The proportional contribution of each fraction was calculated and median grain sizes were determined (Buchanan & Kain 1984). At each plot pore water was collected, and the salinity determined with a conductivity meter (TetraCon® 325, WTW, calibrated on 25°C). Concentrations of organic carbon and nitrogen within the sediment were not assessed in this study as these data were made available by Acheampong (2001).

Prey organisms. At three locations within each plot, benthic samples were taken with a corer of 15 cm diameter up to 20 cm depth. Each sample was divided in three horizons of 0–5 cm, 5–10 cm, 10–20 cm depth. Within a few hours, samples were sieved through a 1-mm sieve, the remains sorted on a tray, and extracted animals stored in 70% ethanol. Additional samples processed with a 0.5-mm sieve by Acheampong (2001) produced benthic abundances similar to those of our samples. Only one out of six t-tests found significant differences between samples ($t = -3.34$, $P = 0.03$; all other tests $P = 0.32–0.88$), however, n was rather small with only three replicates (Kober unpubl.). We assumed that, although benthic communities of tropical tidal flats are usually composed of particularly small individuals, sampling with 1-mm sieves will not disregard considerable prey fractions

in this area. Benthic organisms were identified to the lowest taxonomic level possible, and data converted to densities/m². To avoid double counts, only anterior regions of damaged polychaetes were counted. Sizes of all intact individuals were determined using a graded microscope ocular. We measured Brachyuran crabs carapace width, bivalves shell width, gastropods shell height and, for all other animals, body length. "Worms" were straightened without stretching. Prey identification and measurements were done with a stereomicroscope (Stemi 2000 from Zeiss, 10x) and a microscope (Zeiss Axioskop 2 with 10x/0.30, 20x/0.50 and 40x/0.75 oculars).

In March and April 2002, additional samples were taken at the Canelas area in order to transform prey length records into biomass data. Ash free dry masses (hereafter AFDM) of individual prey items were determined as recommended by Higgins & Thiel (1988). For each benthic taxon the best length-AFDM relation was obtained by the nonlinear estimation tool of Statistica (Kober 2004). With the resulting functions, lengths of all benthic organisms were transformed into biomasses (AFDM/m²).

Avian abundance and behavior. From January–June 2001/2002, bird counts were conducted during mid-day low tides of four successive days, and a monthly mean low tide density was calculated for each plot. Each individual was recorded with its activities such as foraging, locomotion, preening, aggression and resting.

In 2002, the detailed foraging behavior of birds was investigated by visual observations at the Ilha de Canelas. A total of 617 birds were watched, each for 3 min, with help of stop watches and the following data were recorded: foraging behavior, prey type, prey size and probing depth in the sediment estimated in relation to bill length (mm). Observed prey sizes and probing depths were

used to determine accessible and ingestible prey, the 'harvestable prey fraction', defined as the fraction of prey organisms within reach of the bill and small enough to be handled as well as swallowed by individual bird species (only the upper size-limit was considered).

The determination of the harvestable prey fraction has got some drawbacks since benthic depth distributions were not measured on a continuous scale e.g., birds probing only 2.6 cm into the sediment were assumed to reach the same benthic fraction as those probing 4.9 cm into the sediment. Also, observed sizes of large prey items might have been overestimated, a methodological problem described also elsewhere (Zwarts & Blomert 1992). Finally, core-sampling might have been underestimating the quantity of organisms in the upper layer of sediment because some bury themselves deeper while the core is being taken (Leyrer & Exo 2001). Hence, harvestable prey fractions of this study can only be approximations.

Avian consumption. The birds' prey consumption and predation pressure exerted on the benthic community was estimated by applying the procedures used by Zwarts *et al.* (1990): it was assumed that the cost of living in the tropics is about 1.8 BMR (Basal metabolic rate) and that average digestibility of flesh reaches approximately 80%. Gross food intake (GFI, gAFDM/day) was calculated from body mass (M in kg) as obtained from the literature (Blake 1977, Gratto-Trevor 1992, Paulson 1995, del Hoyo *et al.* 1996, Skeel & Mallory 1996, Oring *et al.* 1997, Nol & Blanken 1999, Nettleship 2000, Harrington 2001, Jehl *et al.* 2001, Lowther *et al.* 2001, Macwhirter *et al.* 2002): $GFI = 47.6 \times M^{0.729}$. Since data from the nearby area Maranhão suggest that birds in this region and time of the year weigh very little (A.A. Ferreira Rodrigues, Universidade Federal de Maranhão at Brazil pers. com.), lowest values given in the

literature were taken.

For each plot and month, the mean bird density (birds/ha) of each species was multiplied by the corresponding consumption/day. The outcome, a total consumption (AFDM)/ha for each plot, is given for the entire benthic community as well as separately for the benthic groups. Relative predation pressure was calculated by dividing the birds' consumption (AFDM/ha) by the food stock (AFDM/ha). Where no food stock was recorded for a plot/month, data were omitted from the analysis.

Exclosure experiment

In exclosure experiments, potential main predators are excluded from an area for a certain time. By observing the effect on prey during this time, the influence of the predator on its prey can be evaluated (Hall *et al.* 1990). In February 2002, three treatments (exclosures, controls and procedural controls) were set up at the Ilha de Canelas. A treatment consisted of seven replicates, each covering one m², situated 2 m apart from each other in a line parallel to the other treatments. Replicates were situated close to each other to minimize variation of sediment and benthic features, individual treatments were separated to minimize potential cross-treatment influences.

The design of exclosures resembled that of Mercier & McNeil (1994). Four poles (length: 60 cm, diameter: 5 x 2 cm) were put in place, one at each plot corner, with a height of 20 cm above the sediment surface. Galvanized metal netting was attached to the top (diameter: 2 cm) and nylon cords were tightened horizontally around the poles (4 cm and 12 cm above the ground) to prevent bird entry. The design was chosen to avoid a significant influence on sedimentation patterns inside the exclosures and to allow access for other predatory species such as fish and crabs. No birds were observed to enter exclosures

during observations, despite foot prints in the surrounding area. Procedural controls were used to investigate the effects of cages on sedimentation and benthos. Four poles were set up in the same manner as exclosures but without top-netting and cords. Bird access was thus possible, while the cages' effect on water currents and sedimentation was imitated. Control plots were not marked at all. They were located by taking a fixed distance to neighboring exclosures.

Sedimentation was in fact strong and exclosures as well as procedural controls appeared to "sink" into the sediment progressively. In May, only six and, in June, only two exclosures were left, the others had to be excluded from the analysis. For that reason only data from February until May were used in data analysis.

Each month sediment conditions and pore water salinity were investigated in exclosures, procedural controls and controls as described above. Benthos was evaluated by taking three sediment samples up to 20-cm depth with a corer of 8 cm diameter per replicate. They were divided into three horizons (0–5 cm, 5–10 cm and 10–20 cm) and sub samples from the same depth were mixed together. Samples were processed as described above.

To minimize destructive effects of sediment and benthos sampling on consecutive sampling occasions, a cord-grid-net was constructed and laid over each plot before sampling. Each grid had a size of 25 x 17 cm and monthly samples were restricted to randomly predetermined grids. Grids beside poles were not sampled to avoid edge effects.

Statistical analysis

All data were fed into the database Access 2000 (Microsoft®) and the program Statistica (Version 5.1 from StatSoft Inc.) was used for data analysis. Since Shapiro Wilke's *W*-test for normality showed that most data were not

TABLE 1. Benthos found in 2001. Given are the range of densities found, total individuals found with percentage of total individuals given in brackets, range of gAFDMs found and total gAFDM found with percentage of total gAFDM given in brackets.

Benthic groups	Range of densities/ m ²	Total individuals	Range of gAFDM/ m ²	Total mgAFDM
Bivalva	0–179	219 (7.7%)	0–23.6	7581.3 (33.8%)
Crustacea	0–498	741 (26.1%)	0–25.6	13,448.7 (59.9%)
Gastropoda	0–139	52 (1.8%)	0–3.5	940.8 (4.2%)
Insecta	0–20	1 (< 0.1%)	–	–
Nemertinea	0–119	121 (84.3%)	0–0.2	52.7 (0.2%)
Oligochaeta	0–20	1 (< 0.1%)	0–< 0.1	1.2 (0%)
Polychaeta	0–538	1662 (58.6%)	0–0.4	408.9 (1.8%)
Sipunculida	0–80	40 (1.4%)	0–< 0.1	0.1 (< 0.1%)
Total	0–677	2837 (100%)	0–25.7	22,433.7 (100%)

normally distributed, non-parametric tests such as Kruskal-Wallis ANOVAs or Mann-Whitney *U*-tests were used for further investigations. Where several *U*-tests are used as *a posteriori* tests of a Kruskal-Wallis ANOVA, a Bonferroni correction was applied to decrease $\square\alpha$ appropriately: $\alpha = 0.05/(\text{number of } U\text{-tests applied})$. Beside these tests, contingency tables were employed to test whether benthic data from neighboring plots were independent. For all tests a significance level of $\alpha = 0.05$ was chosen.

RESULTS

The habitat

Abiotic conditions. Environmental conditions at the study area showed a remarkable variability. Because of strong currents with heavy sediment loads, sediment characteristics changed quickly. As a result a mosaic of small patches with differing sediment conditions was created, ranging from soft mud to compact sand with grain size medians between 2.76–4.41 Φ (Kober 2004).

With the onset of the wet season, average pore water salinity decreased, until a minimum was reached in April, before increasing again in May and June ($H = 177.37$, $P <$

0.001). Although overall salinity levels ranged between 15–38 ppt, spatial differences within a month were small compared to temporal differences (Kober 2004).

Benthos composition, abundance and availability.

The zoobenthos represented the primary prey of the shorebirds at the tidal flats (Kober & Bairlein in press). Overall 55 different taxa were distinguished, belonging to the groups of Polychaeta, Crustacea, Bivalvia, Gastropoda, Sipunculidae, Nemertinea and Oligochaeta.

Total densities ranged between 0–677 individuals/m² (Canelas: 20–557 individuals/m², Furo Grande: 0–637 individuals/m², Furo do Chato: 20–677 individuals/m²). Although significant monthly temporal fluctuations occurred ($H = 12.20$, $P = 0.032$), no clear trend was apparent. Mean benthic density was highest in January with 239 ± 135 individuals/m² (mean \pm SD) and lowest in February with 167 ± 87 individuals/m², which is equivalent to a 30% decline of the standing crop ($U = 665.00$, $P = 0.003$, ns) (for details see Kober 2004).

Polychaetes and Crustaceans dominated the benthos with 59% and 26% of all individuals found (Table 1), with Pinnotheridae,

TABLE 2. Ranges of avian densities (Individuals/ha) at the three study sites in 2001. Abbreviations of the bird names are given in brackets.

Bird species	Abbreviation	Ilha de Canelas	Furo Grande	Furo do Chato
Charadriidae				
Collared Plover	(copl)	0-8	0-3	0-3
Grey Plover	(grpl)	0-5	0-4	0-5
Semipalmated Plover	(sppl)	0-14	0-4	0-5
Scolopacidae				
Marbled Godwit	(mago)	0-3	0	0
Red Knot	(knot)	0-33	0	0
Ruddy Turnstone	(turn)	0-35	0-2	0
Sanderling	(sand)	0-4	0	0
Semipalmated Sandpiper	(spsa)	0-40	0	0-34
Short-billed Dowitcher	(sbdo)	0-104	0	0
Spotted Sandpiper	(sdsa)	0	0-70	0
Whimbrel	(whim)	0-35	0-6	0-2
Willet	(will)	0-12	0-3	0
Total		0-126	0-73	0-40

Gammaridea (both small crustaceans), Capitellidae and Nephtyidae (both polychaetes) being the most abundant benthic groups. Individual benthic taxa showed a large spatial and temporal variability with seasonal patterns independent from each other (Fig. 2, for details see Kober 2004).

Total biomass samples varied between 0–25.7 gAFDM/m² in 2001. The monthly mean of all plots ranged between 0.5–2.3 gAFDM/m². Although monthly plot means differed significantly from each other ($H = 14.06$, $P =$

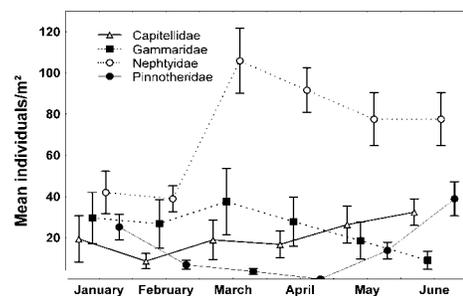


FIG. 2. Exemplary phenologies of the most abundant benthic taxa. Given are mean densities + SE at the Ilha de Canelas in 2001.

0.015), no seasonal trend was apparent. Spatial variability was also very high: while most plots had low biomasses, a few plots sometimes showed extraordinarily high biomass values (Kober 2004).

The two groups contributing most to benthic biomasses were crustaceans and bivalves, making up 60% and 34% of the total biomass respectively (Table 1). They contributed together more than 90% of the total biomass in each month in 2001 and the taxa with highest individual biomasses were Callianassidae and *Uca maracoani* (both Crustaceans), the bivalve *Tagelus plebeius* and the gastropod *Nassarius vibreus*. Some 68% of all individuals were found in the top 5 cm of the sediment layer, 19% in 5–10 cm and only 13% in 10–20 cm depth. Polychaete densities showed a peak abundance in the uppermost 5 cm, whilst their biomass was found in the top 10 cm. Bivalves and crustaceans were also most abundant in the upper layer. However, 1/3 of the bivalve biomass and nearly 2/3 of the crustacean biomass was found in 10–20 cm depth (Kober 2004).

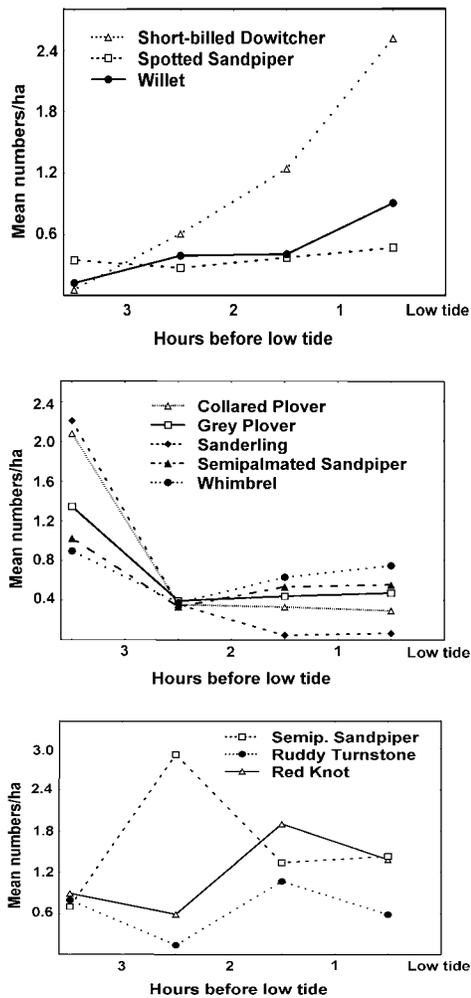


FIG. 3. Avian mean densities over the course of ebb tide in 2001. Time is given in hours before low tide. All individuals present for more than 3 h before low tide are summed in the first value.

The bird community

The shorebird community consisted of 12 abundant species (Table 2). Of these, only Collared Plover (*Charadrius collaris*) was resident, all other species were migratory. The most abundant sandpipers were Semipalmated Sandpiper (*Calidris pusilla*) with 23%, Short-billed Dowitcher (*Limnodromus griseus*)

with 21%, and Red Knot (*Calidris canutus*) with 15% of all counted individuals. The most abundant plover was Semipalmated Plover (*Charadrius semipalmatus*) with 8% of all counted shorebirds. Marbled Godwit (*Limosa fedoa*) was observed for the first time in Brazil (Kober *et al.* subm.).

In 2001 the shorebird densities ranged between 0–126 birds/ha. In January their mean density was highest with 23 birds/ha, decreasing steadily until May and June with only 2 birds/ha (Kober *et al.* subm.).

Like benthic organisms, shorebirds were not evenly distributed. While some plots were hardly frequented by birds (most plots at the mouth of creeks), others experienced comparatively high bird densities (the muddy plots at the open intertidal, Table 2).

Birds used the study area predominantly for foraging, locomotion, resting and preening. Aggression was rarely observed. Foraging was the most prominent behavior, depending on the species 76–100% of all birds were engaged in that (Kober unpubl.).

Bird presence fluctuated over the course of ebb. At the Ilha de Canelas, plots were emerged for a period between 3 h 39 min and 4 h 59 min, depending on plot location. When the tide began to recede, all plovers, Sanderling (*Calidris alba*), and Whimbrel (*Numenius phaeopus*) were present in highest numbers, before many of them moved on towards newly emerged areas and only a constant low number remained in the study area (Fig. 3). Because of the large dimension of exposed tidal flats, exact positions of new locations could not be determined. While the abundance of Short-billed Dowitcher and Willet (*Catoptrophorus semipalmatus*) increased progressively, with maximum abundances towards low tide, densities of Spotted Sandpiper (*Actitis macularia*) remained constant. All other sandpiper species passed through the area 1–3 h before low tide (Fig. 3).

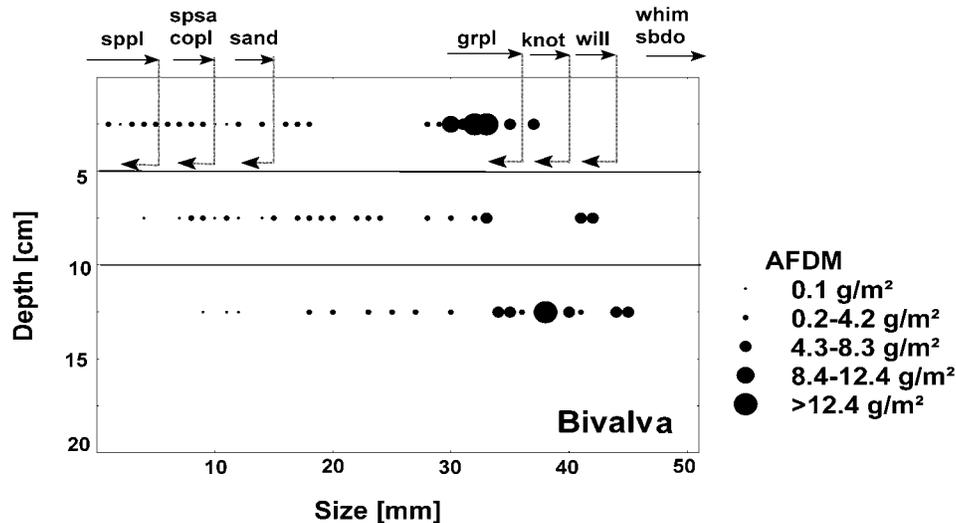


FIG. 4. Size-depth distribution of benthic Bivalvia. Dot-sizes give the sum of AFDMs found in 2001/2002 within a specific size/depth range. Arrows indicate searching depth and maximal size of prey chosen by individual bird species. The prey fraction to the left of the lines is the harvestable prey fraction for these species. Minimal sizes were not considered since all birds were observed to feed on tiny prey items. An explanation of bird name abbreviations is given in Table 2. The diagram was inspired from Piersma *et al.* (1993).

The harvestable prey fraction

The benthos within the sediment was divided into fractions of certain depth- and size classes. These fractions constituted different amounts of biomass, depending on the number and mass of corresponding items. Biomass-rich depth/size fractions of bivalves were located at both < 5 cm sediment depth and > 10 cm depth, and they included only species of > 3 cm length (Fig. 4). The bird species could however not benefit from all of these fractions since they either fed on smaller bivalves [Semipalmated Plover, Sanderling, Semipalmated Sandpiper and Collared Plover (*Charadrius collaris*)], or were only able to penetrate the upper 5 cm sediment depth (Fig. 4). However, as noted in the methods, maximum prey sizes given are probably overestimated: e.g., in this study Red Knots were observed to feed on large bivalves, but given maximum circumference of bivalves determined by

Zwarts & Blomert (1992), size of observed bivalves was probably not 40 mm but a maximum of 20–30 mm, corresponding with those individuals frequently found in the study area.

Highest AFDM of crustaceans were found in sediment depths > 10 cm (Fig. 5). Shorebirds could not prey on this fraction since they could not reach such deeply burrowed crustaceans.

Highest AFDMs of “worms” were found in the upper 5 cm of the sediment and individuals had a size of 2–3 cm. They were accessible to all species; only Willet appeared to be restricted to “worms” < 2 cm (Fig. 6).

Overall, harvestable prey fractions were extremely low for all shorebirds (Fig. 7). Even though core samples are known to underestimate the prey fraction in the upper sediment layer because some polychaetes bury themselves deeper while the core is being taken

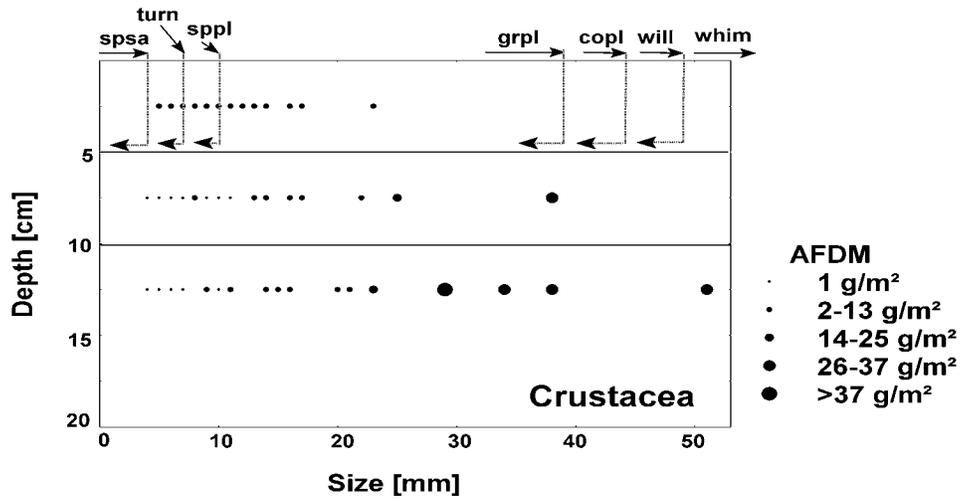


FIG. 5. Size-depth distribution of benthic Crustacea. Explanations of symbols and bird name abbreviations are given in Table 2 and Figure 4.

(Leyrer & Exo 2001), and some birds might be able to prey on organisms which occasionally emerge from the sediment and become available after all, such as certain crustaceans,

this cannot compensate for the lack of accessible biomass. For most birds there were at least some biomass-rich spots. However, for Knots and Willets, almost all plots had hardly

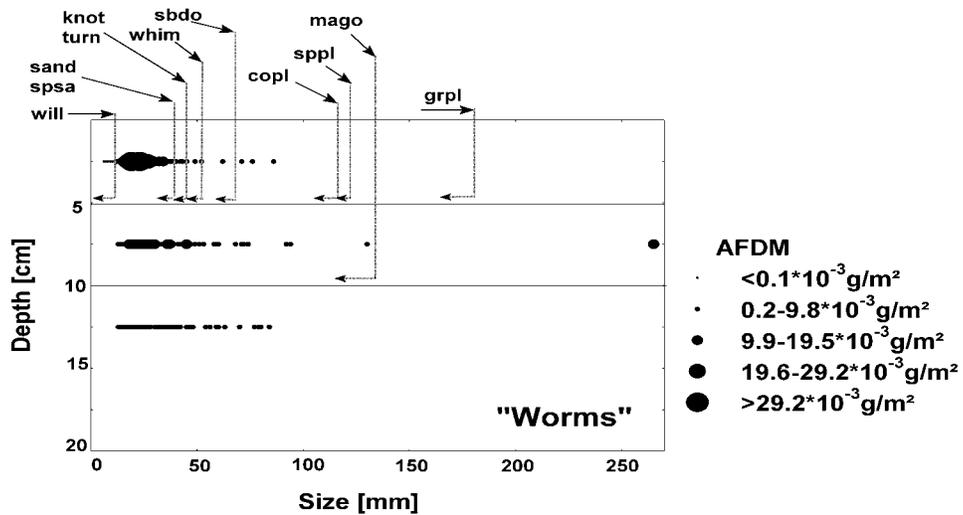


FIG. 6. Size-depth distribution of benthic "worms". Explanations of symbols and bird name abbreviations are given in Table 2 and Figure 4.

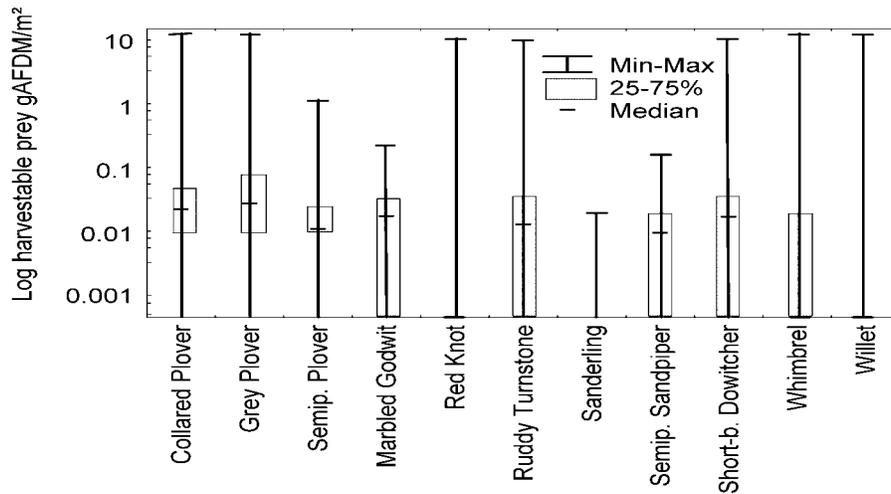


FIG. 7. Harvestable biomasses (gAFDM/m²) per shorebird species in 2001. Given are biomasses of all plots and months ($n = 276$ per species).

TABLE 3. Avian consumption in comparison to standing food stocks in 2001. Consumption was determined by multiplying consumption rate per day and plot by the number of days of each month.

Months	Benthos standing stock	Monthly consumption	
	gAFDM/m ²	gAFDM/m ²	% of standing stock
January	1.8	2.4	134.6
February	2.2	2.4	107.2
March	2.3	1.6	67.1
April	1.6	0.5	30.2
May	0.5	0.2	31.9
June	1.3	0.2	15.2

any harvestable biomass and, for Sanderlings, no biomass-rich plots were present. Essentially, the study area is a poor foraging site.

The avian consumption and its impact

Calculated consumption. When the total avian AFDM-consumption per month was expressed as proportion of the standing food stock of the study area, the highest proportion was found in January 2001 with 134.6% of the standing stock, while the lowest occurred in June with 15.2% (Table 3).

These general figures were refined by calculating the relative predation pressure in each plot and on each benthic group separately. Relative predation pressure is the relation of the consumption to the standing stock (Zwarts 1988). A predation pressure many times higher than the food stock occurred regularly (up to > 10,000 times the standing stock at some plots). Moreover, these values are underestimated: plots with a certain avian consumption but a measured standing stock of zero had to be excluded from calculations.

TABLE 4. Differences between enclosure-treatments, compared with a Kruskal-Wallis ANOVA and post-hoc Mann-Whitney *U*-tests. Given are the results of the Mann-Whitney *U*-tests, significant results (with Bonferroni-correction) are marked with an asterisk (*). Supplementary tests on the data with Capitellidae excluded are bold.

Months	Effects	With/without Capitellidae	Total		Deposit feeder		Polychaeta	
			<i>Z</i>	<i>P</i>	<i>Z</i>	<i>P</i>	<i>Z</i>	<i>P</i>
February	Control vs procedural control	+ Capitellidae	2.044	0.041	2.683 *	0.007	-2.683 *	0.007 *
	Control vs procedural control	- Capitellidae	1.981	0.048	2.492 *	0.013 *	2.364	0.018
	Control vs enclosure	+ Capitellidae	0.128	0.898	1.086	0.277	-0.511	0.609
March	Procedural control vs enclosure	+ Capitellidae	2.044	0.041	-1.725	0.085	1.150	0.250
	Control vs procedural control	+ Capitellidae	-0.255	0.798	-0.383	0.701	-0.511	0.609
	Control vs enclosure	+ Capitellidae	-0.958	0.338	0.192	0.848	-1.789	0.074
April	Procedural control vs enclosure	+ Capitellidae	1.022	0.307	0.575	0.565	-1.214	0.225
	Control vs procedural control	+ Capitellidae	-1.917	0.055	-2.875 *	0.004 *	-2.747 *	0.006 *
	Control vs procedural control	- Capitellidae	0.639	0.500	1.022	0.307	-1.533	0.125
May	Control vs enclosure	+ Capitellidae	0.064	0.949	1.022	0.307	-0.703	0.482
	Procedural control vs enclosure	+ Capitellidae	-2.556 *	0.011 *	-2.300	0.021	-2.747 *	0.006 *
	Procedural control vs enclosure	- Capitellidae	2.172	0.030	1.853	0.064	-2.747 *	0.006 *
May	Control vs procedural control	+ Capitellidae	0.831	0.406	-0.767	0.443	0.639	0.523
	Control vs enclosure	+ Capitellidae	-1.571	0.116	-0.500	0.617	1.143	0.253
	Procedural control vs enclosure	+ Capitellidae	-0.571	0.568	0.286	0.775	0.714	0.475

Exclosure experiment. The exclosure experiment was carried out in a part of the study area with medium bird densities. Abiotic conditions and composition of the benthic community within exclosures were comparable to those observed in the rest of the study area. While sediment grain-sizes were similar, pore-water salinity differed slightly between treatments during all months. However, these differences were minor compared to the high monthly variation in salinity.

Concerning the benthos, most trophic groups (suspension feeders, carnivores and omnivores) and taxa were similar between treatments, only few differed significantly. In February, deposit feeders and polychaetes showed significantly higher abundances in controls in comparison to procedural controls, but not to exclosures (Table 4). In April, the total benthic community (i.e., deposit feeders, Polychaeta, and Capitellidae) had distinctly raised densities in procedural controls in contrast to other treatments. These differences were significant between procedural controls and exclosures for the total benthic community, between procedural controls and controls for deposit feeder and Capitellidae, and between procedural controls and controls, and procedural controls and exclosures for Polychaeta. To assess if only Capitellidae, which are deposit feeding polychaetes, effected the outcome of the tests, crucial Mann-Whitney U-tests were repeated excluding Capitellidae (Table 4).

Capitellidae were responsible for many observed effects in April. All other significant results could be explained by a pooling of organism abundances which showed no differing abundances on their own. Overall, very few and only weak significant results were observed in the exclosure experiment.

DISCUSSION

Mangrove forests play an essential role at

many tropical coasts. They represent a highly productive ecosystem with net primary production rates as high as 30 t C/ha/year (Clough 1998). A rich trophic net including invertebrates (mainly crustaceans, mollusks and polychaetes) and vertebrates (mainly fish, birds and small mammals) is supported by them. At the Caeté estuary of the Bragantian Peninsula, there is a strong outwelling of organic and inorganic material derived from litter decomposition of the mangrove forest (Dittmar 1999). Nevertheless, sediment concentrations of organic carbon (0.07–0.87%) and organic nitrogen (< 0.01–0.06%) are low in comparison to other tropical estuaries, and spatially fluctuating (Acheampong 2001). We assume that this is a result of strong local currents, flushing out most organic material. In certain areas heavy erosion occurred, resulting into a highly variable mosaic of differing sediment conditions, ranging from fine sand to fine mud (Krause & Glaser 2003, Krause & Soares 2004). With the beginning of the rainy season, freshwater input increases and pore water salinity responds with a distinct and ongoing decline until the onset of the dry season. The benthic community of the Bragantian tidal flats is thus exposed to a number of stressors, including low organic sediment contents, ongoing sediment alterations and strong seasonal salinity fluctuations.

The low benthic abundance and biomass might be a direct result of such environmental stress, which is enhanced during the wet season, due to the increased fresh water input and current velocities. In tropical areas, benthic abundances are generally lower compared to temperate regions, e.g., the macrofauna ranges between 1000–2000 individuals/m² (Reise 1991, Dittmann 2002a). But, even in this respect, abundances found at the study area were extremely low and, although similar values have been found at sampling stations of other tropical tidal flats, they were uncommon and always at the lowest part of the spectrum

in these areas (Wolff & Smit 1990, Wolff *et al.* 1993, Dittmann 1995, Pepping 1999, Dittmann 2002b).

For macrozoobenthic biomasses, Piersma *et al.* (1993) gave an overall range of 5–80 gAFDM/m² worldwide, with an average of 24 gAFDM/m² for the investigated areas. Again, when compared to these values, biomasses found for the Bragantian Peninsula were extremely low (0.5–2.3 gAFDM/m²). Although AFDMs were not measured directly in this study, calculated values are well within the range of the data obtained by Acheampong (2001) by direct biomass measurements in the same study area, and likely to be valid.

Despite the low benthic biomass, shorebirds were found in densities as high as 23 shorebirds/ha. Even if no total bird numbers can be given for the estuary, the impression given by these densities supports the finding of Morrison & Ross (1989), that the northern coast of South America is one major wintering area of North American migrants in South America. Quantitative investigations into total bird abundances on tropical tidal flats are rare, but most present lower bird densities than those observed in this study (Zwarts 1985, Sasekumar & Chong 1986, Tye & Tye 1987, Zwarts 1988). Only Altenburg *et al.* (1982) found far higher densities at the Banc d'Arguin in Mauritania with 41.6 birds/ha.

Are the low amounts of food found on the tidal flats sufficient to sustain the avian populations? During certain months, calculated predation pressure showed that birds need far more food than available. Moreover, only a small fraction of the food stock is actually harvestable for shorebirds, in particular for small species, not able to probe deeply into the sediment. Consequently, most plots provide for the birds less than 0.1 gAFDM/m² harvestable biomass, a very low value for shorebirds which have to feed between 3 g (Semipalmated Sandpiper) and 20 g (Whimbrel) AFDM per day to survive, and probably

even more in order to gain weight before migration (Kober 2004). For Sanderling, Knot and Willet, this value was even far lower. At night the harvestable prey fraction might be higher due to fact that many invertebrate prey might move closer to the substrat surface and become thus available for the birds (McNeil *et al.* 1995). However, the comparison between avian consumption and entire food stock shows that prey living in 0–20 cm depth cannot compensate for the lack of food and it is not likely that many benthic organisms live deeper than 20 cm in the sediment. At the Banc d'Arguin, some shorebirds took remarkably small prey (Zwarts *et al.* 1990); maybe the birds forage primarily on prey organisms which were too small to be sampled with a 1 mm sieve? Additional samples showed that Bragantian prey abundances and biomasses obtained with a 0.5 mm sieve were not much larger than the original samples (Acheampong 2001), thus the small benthic organisms cannot provide the missing biomass to support the birds. For even smaller prey, it might be doubted if that is still profitable, given a certain time for searching and prey intake (Kober 2004). Furthermore, benthic production is a more meaningful factor than the standing stock to be compared with predation (Piersma 1987). Is the production large enough to allow for a strong predation pressure? Even if a high yearly P/B ratio of 5 or 6 is assumed, as often found in tropical environments (Wolff & Smit 1990), consumption would most likely reach or even exceed production in January and February (Kober 2004). We conclude that (1) birds are probably not able to gain sufficient amounts of prey and, (2) benthos is probably exposed to an extremely high predation pressure.

The enclosure experiment failed to reveal a strong impact of the avian consumption on the benthic community. Significant effects were restricted to few taxa, or were in fact a result of variable abundances of some taxa in

certain months. Overall, abiotic fluctuations and disturbances seemed to have a larger impact on structure and abundance levels of the benthic community than shorebird predation. The 30%-drop of benthic abundances in February might have been rather the result of decreased salinity levels than a consequence of avian consumption.

The outcomes of consumption calculations and the enclosure experiment seem to be contradicting. However, many birds stayed in the study area only for limited time, presumably en route to their primary foraging areas elsewhere. Typically, most territorial plovers left the area with the receding tide, most likely to occupy their territories at uncovered tidal flats elsewhere, and only a small number occupied constantly territories in the study area. Within sandpipers, there was one group preferring dry sand for their solitary, visual foraging technique (Whimbrel and Sanderling), and one group favoring soft and damp sediments [Semipalmated Sandpiper, Ruddy Turnstone (*Arenaria interpres*) and Red Knot] (Kober 2004). During low tide, both groups frequented areas elsewhere, which might have been more favorable for their preferences. Short-billed Dowitcher and Willet were the only species reaching highest numbers during low tide, even though they had a preference for the vicinity of water (Kober 2004). The many ponds and tidal creeks in the study area might have been responsible for that.

If most birds foraged primarily elsewhere, where could such feeding grounds be located? In Panama, Butler *et al.* (1997) recorded high bird densities on mudflats adjacent to mangroves, presumably due to the abundant food availability associated with mangroves. At the Bragantian peninsula, macrobenthic densities of 858 individuals per m² were found inside the mangrove forest, close to the Furo Grande plots of this study (unfortunately, no biomass data are available, Guimarães Figueira 2002). This gives the impression of a

poor mangrove foraging habitat and mean bird numbers found inside the mangrove forest (Furo Grande) were indeed far lower than those found at the open intertidal (Ilha de Canelas). Hence we reject the possibility of foraging habitats in the mangrove forest in accordance to other studies (Evans 1976, Piersma *et al.* 1993) and put on record on only limited numbers of birds within the mangrove forest. Since raptors were observed at the forest, we hypothesize, that staying away from mangroves might be a form of predator avoidance.

Besides potentially feeding in the mangrove forest, birds could also use other tidal flats. The sediment of the Bragantian intertidal contains more sand than other coastal areas nearby (Muehe & Neves 1995). As a result, these areas might have a different benthic composition and / or differing abundances of benthic organisms. Morrison & Ross (1989) found in their investigations that most avian species showed a clumped dispersion with comparatively low numbers of shorebirds at the intertidal around the Bragantian Peninsula (2500–6000 shorebirds to the west, 700–1500 to the east of the peninsula). Some 100 km further east or 50 km further west, far higher concentrations of shorebirds were found, possibly as a result of better foraging conditions. Birds using the Bragantian intertidal might represent competitively inferior individuals, which may have been displaced from richer tidal flats by dominant individuals. Another possibility is that they have already fed on primary foraging grounds, using the tidal flats investigated in this study because of other characteristics, such as a low predator abundance. However, these considerations must remain speculative until primary foraging areas have been identified and investigated.

Whether the environmental conditions of the Bragantian intertidal are typical for tropical tidal flats is not known and remains to be

tested in future. However, there are some patterns characterizing our study area as well as other tropical sites, which differ from temperate tidal flats: (1) The high freshwater input during the wet season leads to strong currents causing heavy sediment erosion, high salinity fluctuations and scouring of organic matter (Alongi 1990); (2) low benthic abundances as observed in this study might be due to these incidences, because benthos responds negatively to these disturbances (Alongi 1990). [Generally, benthic abundances are lower in tropical areas compared to their temperate counterparts (Reise 1991, Dittmann 2002a)], (3) due to the lack of strong temperature fluctuations, abundances of tropical benthos do not show strong seasonal trends with a peak in mid summer, as observed in temperate benthos communities (Beukema 1974), but phenologies are observed to fluctuate independently from each other, possibly because reproduction is not necessarily synchronized (de Goeij *et al.* 2003).

It is likely that shorebirds have evolved strategies to cope with the specific environmental features met when foraging on tropical tidal flats; a discussion on emerging behavioral patterns and strategies will be provided in the corresponding second paper by Kober & Bairlein (in press).

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