

Foraging ecology and habitat use of wading birds and shorebirds in the mangrove ecosystem of the Caéte Bay, Northeast Pará, Brazil



Dissertation

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Abbreviation list

In some instances, for example in some figures, the use of the full names and expressions was not possible or practical. In these cases short forms were used, which are listed below:

Bird names

Collared Plover	copl
Great Egret	greg
Grey Plover	grpl
Greater Yellowlegs	grye
Little Blue Heron	lbhe
Marbled Godwit	mago
Red Knot	knot
Ruddy Turnstone	turn
Sanderling	sand
Short-billed Dowitcher	sbdo
Scarlet Ibis	scib
Spotted Sandpiper	sdsa
Snowy Egret	sneg
Semipalmated Plover	sppl
Semipalmated Sandpiper	spsa
Tricolored Heron	tche
Whimbrel	whim
Willet	will
Yellow-crowned Nightheron	ycnh

Study areas

Furo Grande	FG
Furo do Chato	FC
Ilha de Canelas	C

Experimental treatments

Exclosures	Ex
Control	C
Procedural Control	PC

Others

Gross food intake	GFI
Ash free dry weight	AFDW

Summary

Only little is known of wintering and resting shorebirds in tropical environments. The objective of this thesis was to describe the environment and the food availability the birds encounter in the tropics, the bird community in this habitat, the relationship between birds and environment/prey and the effects of bird consumption at tropical tidal flats. The study was conducted at the Bragantinian peninsula in the Northeast of Brazil, an area previously characterized as of major importance for migratory shorebirds.

The study area was a poor and very variable foraging habitat, comprising an overall low content of organic material, many physical disturbances and high fluctuations of sediment conditions and salinity. Presumably as a result, the diversity, abundance and biomass of the benthos was very low compared to other tropical areas. The benthos also showed a strong spatial and temporal variability, especially on the lower taxonomic level. "Worms" were the numerically dominating group, which were accessible for all birds but provided only low biomass values. Bivalves and crustaceans included also large and biomass rich individuals, but they were less abundant and harvestable for only few large bird species. Thus, for many birds a large part of the food stock is not available.

Overall 19 bird species were observed in the study area. Over 90% of the observed individuals were migratory shorebirds, the remaining residential birds consisted of mostly wading birds. As a result, avian abundances and the community structure were strongly seasonal dependent, with mainly migratory shorebirds during January-March and an enhanced influence of residential wading birds after the departure of the migrants. The spatial distribution of the birds was variable and could not be linked directly to environmental variables. However, the birds showed preferences for sampling sites (the fringe of the mangrove forest vs. open intertidal) and microhabitats (association and depth of water, probing depth) and on that basis also guilds could be identified.

The harvestable fraction of the prey, the organisms accessible and ingestible for the birds, was very low at the study area, especially for the small birds, which rely exclusively on "worms". The observed diets of the birds contained always a large variety of prey items, a result supported by the prey remains found in the droppings. According to their diets, the bird community could only be distinguished in three large groups, which were partly related to the guilds based on microhabitat use. A calculated optimal diet included as well a large variety of prey items, showing that opportunistic foraging is most favourable in this poor and variable environment. Only few birds should have more specialized diets, a result of their ability to prey on large bivalves and crustaceans. The observed foraging behaviours were probably chosen to maximize prey intake rates, however, the intake rates did not differ between foraging techniques. The attempt to find a relationship between the spatial distribution of the

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avian predators and their prey failed, presumably due to variety of prey items and the resulting complexity of the relationship.

The avian community splits clearly in residential herons and egrets and predominately migratory shorebirds, manifested by time, the use of microhabitats and diets. The residential birds did not tend to fill the niches which were occupied by the migrants during the winter time, this space probably remain mostly abandoned during their absence. Beyond this obvious segregation, lesser distinct niches appeared within the shorebird community, defined by microhabitat characteristics, somehow related with diet. However, most birds comprised very broad niches and a variable resource use, possibly a result of the restricted food resources at the Bragantinian peninsula. Birds not able to forage on large prey items are forced to feed opportunistically, since a restriction on few prey organisms most probably leads to food shortages.

The time spend foraging was mostly dependent on the foraging technique of the birds. In most cases it did not increase prior migration, since the birds probably already spend maximum time with foraging during the entire study period. Most species did not spend the entire ebb tide at the study area. During their absence, they probably used other, more profitable areas to obtain food. This might be crucial for the birds in this area, since it was calculated that some of the birds cannot gain enough of the necessary energy with the intake rates observed at the study area. Also, the food stock would have been depleted in only few weeks time, if the birds would forage exclusively in the study area. However, an exclosure experiment did not show such strong impact, another indicator that the birds might forage elsewhere.

Resumo

Pouco é conhecido de pássaros migratórios costeiros em ambientes tropicais. O objetivo deste trabalho foi descrever o ambiente e a disponibilidade de alimento que estes pássaros encontram nos trópicos, a comunidade de pássaros nestes habitats, a relação entre pássaros e o ambiente/presas e o efeito do consumo dos pássaros no estuário. Este estudo foi conduzido na península Bragantina, Pará, Brasil, em uma área previamente caracterizada como de grande importância para aves migratórias.

A área de estudo é um habitat bastante variável quanto à disponibilidade de alimento, incluindo sedimento com pobre em matéria orgânica, diferentes características físicas, altas flutuações nas condições do sedimento da salinidade. Provavelmente como resultado disso a diversidade, abundância e biomassa dos bentos foi muito baixa comparada à outras áreas tropicais. Os bentos também mostraram uma alta variabilidade espaço-temporal, especialmente à nível taxonômico. Organismos vermiformes foram dominantes, apesar de acessíveis à todos os pássaros, provêm pouca biomassa. Bivalves e crustáceos representam também grande biomassa, mas foram pouco abundantes e acessíveis apenas

para poucas espécies de grandes pássaros. Por isso, para muitos pássaros grande parte do estoque de alimento não é acessível.

No total, foram observadas na área 19 espécies de pássaros. Cerca de 90% dos indivíduos observados foram pássaros costeiros migradores. Pássaros não migradores consistiam em Garças e Guarás. Como resultado, a estrutura e abundância e estrutura da comunidade de aves foram fortemente influenciados pela sazonalidade. Pássaros migradores estiveram presentes entre Janeiro e Março. Pássaros não migratórios mostraram maior influência depois da partida dos pássaros migradores. A distribuição espacial dos pássaros foi variável e não está diretamente ligada às condições ambientais. Contudo os pássaros mostraram preferência por algumas áreas de estudo (franja dos bosques de mangue vs. áreas zonas entremarés) e microhabitats (associações entre profundidade da água e probing depth), assim, guildas puderam ser também indentificadas.

A fração de presas consumíveis pelos pássaros, foi muito baixa na área de estudo, especialmente para pequenos pássaros, estando quase que limitada aos vermiformes. Observações do hábito alimentar, assim como a análise fecal dos pássaros revelou uma dieta com grande variedade de presas. De acordo com a dieta, a comunidade de pássaros pode ser distinguida em tres grandes grupos, parcialmente relacionados às guildas baseadas no uso do microhabitat. A dieta ideal calculada incluiu grande variedade de presas, mostrando que alimentação ocasional e uma dieta mais variada são mais favoráveis neste ambiente pobre e variado. Apenas poucos pássaros mostraram uma dieta mais especializada, como resultado de sua habilidade de capturar bivalves e crustáceos. O comportamento alimentar observado foi provavelmente escolhido para maximizar a captura de presas, porém a taxa de sucesso não difere entre as técnicas de captura. Não foi encontrada nenhuma relação entre a distribuição espacial da aves e suas presas, provavelmente pela variedade de presas, resultando em uma relação complexa.

A comunidade de aves se divide claramente em Garças e “Garças” não migradoras e aves costeiras migradoras. Essa diferença manifestada de acordo com a estação, o uso de habitats e a dieta. As aves não migradoras não ocuparam os nichos previamente ocupados pelas aves migradoras. Menos nichos são encontrados na comunidade de “shorebirds”, definidos por características de microhabitats, assim como relacionados à dieta. Porém, a maioria dos pássaros ocupam muitos nichos e uma grande variedade no uso de recursos, possivelmente como resultado do restito recurso alimentar na Península Bragantina. Pássaros não capazes de capturar grandes presas são forçados a capturar oportunisticamente, pois a restrição à poucos organismos provavelmente leva à baixa oferta de alimento.

O tempo gasto capturando na captura foi mais relacionado à técnica de captura. Em muitos casos isso não teve relação com a migração, provavelmente porque os pássaros já gastaram muito tempo com a captura durante o período de estudo. A maioria das espécies

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não permaneceram todo o tempo da mare baixa na area de estudos. Durante sua ausência, provavelmente utilizaram outras areas para obtenção de alimento. Isso deve ser crucial para os pássaros nesta area, pois calcula-se que muitos pássaros não ganhassem energia suficiente com a alimentação ingerida na area de estudo. Além do que o estoque de alimento seria totalmente consumido em apenas algumas semanas se os pássaros capturassem exclusivamente na area de estudo. Apesar disso um “experimento de exclusão” não mostrou nenhum impacto sobre a abundância dos bentos, outro indicativo de que os pássaros capturam alimento em outros lugares.

Zusammenfassung

Obwohl es viele Untersuchungen an Limikolen in ihren Brut- und Rastgebieten in der nördlichen Hemisphäre gibt, weiß man sehr wenig über sie in ihren tropischen Überwinterungs- und Rastgebieten. In dieser Arbeit sollte zunächst das Habitat und die Nahrungsverfügbarkeit beschrieben werden, die die Vögel in den Tropen vorfinden. Weiterhin sollte die Vogelsonsistenz selbst, die Beziehung zwischen den Vögeln und dem Habitat/ihrer Beute dargestellt werden und schließlich der Einfluß der Vogelkonsumption auf die tropischen Watten untersucht werden. Die Untersuchung wurde auf der Bragantiner Halbinsel im Nordosten von Brasilien durchgeführt, einem Gebiet, das schon zuvor als sehr wichtig für die ziehenden Limikolen charakterisiert wurde.

Das Untersuchungsgebiet war sehr arm und zeigte eine ausgesprochene Variabilität, mit einem insgesamt sehr niedrigen Anteil organischem Materials, vielen Störungen und stark fluktuierenden Sediment- und Salinitätsbedingungen. Vermutlich daraus resultierend war die Diversität, die Abundanz und die Biomasse des Benthos ebenfalls sehr niedrig im Vergleich zu anderen tropischen Gebieten. Das Benthos war ebenfalls sowohl räumlich als auch zeitlich sehr variabel, besonders auf dem Niveau der niedrigeren Taxa. Am zahlreichsten waren die „Würmer“, die zwar für alle Vögel zugänglich waren, doch wenig Biomasse boten. Einige Bivalvia und Crustacea waren hingegen groß und reich an Biomasse, doch sie kamen nur viel vereinzelter vor und waren nur für einige große Limikolenarten zugänglich. Ein großer Teil des vorhandenen Nahrungsangebotes war daher für die meisten Vogelarten nicht verfügbar.

Insgesamt wurden 19 Vogelarten im Untersuchungsgebiet gezählt. Über 90% der beobachteten Individuen waren ziehende Limikolen, der Rest bestand hauptsächlich aus den heimischen Reiher und Ibissen. Die Vogelanzahlen und die Zusammensetzung der Vogelsonsistenz war daher stark saisonal abhängig, mit vorwiegend ziehenden Limikolen von Januar bis März und einem zunehmenden Einfluß der heimischen Reiher und Ibisse nach dem Abflug der Zugvögel. Die räumliche Verteilung der Vögel war sehr variabel und konnte zu keiner der gemessenen Umweltvariablen in Verbindung gesetzt werden. Dennoch zeigten die Vögel Präferenzen für bestimmte Untersuchungsgebiete (Rand des Mangrovenwaldes im Gegensatz zu den offenen Watten) und Mikrohabitate (Assoziation mit

dem Wasser, Wassertiefe und Nahrungssuchtiefe im Sediment), anhand derer auch Gilden definiert werden konnte.

Der verfügbare Beuteanteil, die Beuteorganismen die für die Vögel sowohl erreichbar als auch fressbar sind, war im Untersuchungsgebiet sehr niedrig, insbesondere für die kleinen Vogelarten, die ausschließlich von „Würmern“ abhängig waren. Das beobachtete Beutespektrum war generell sehr breit, ein Ergebnis welches ebenfalls durch die Analyse der Kotproben unterstützt wurde. Basierend auf der beobachteten Nahrungszusammensetzung konnte die Vogelgemeinschaft nur in drei große Gruppen eingeteilt werden, die teilweise mit den durch Mikrohabitatpräferenzen charakterisierten Gilden zusammenfielen. Ein errechnetes Optimales Nahrungsspektrum beinhaltete ebenfalls ein große Anzahl von Organismen. Dies zeigt, dass eine opportunistische Nahrungsaufnahme und ein breites Nahrungsspektrum unter solch armen und variablen Umweltbedingungen am vorteilhaftesten ist. Nur wenige Vogelarten sollten sich optimalerweise auf nur wenige Beuteorganismen spezialisieren, was mit der Fähigkeit der Aufnahme auch großer Bivalvia und Crustacea zusammenhing. Das beobachtete Verhalten bei der Nahrungssuche diente höchstwahrscheinlich der Maximierung der Beuteaufnahme, allerdings ergaben sich keine Unterschiede in den Aufnahmeraten zwischen den verschiedenen Techniken. Der Versuch eine Beziehung zwischen Vogelverteilung und Beuteverteilung herzustellen scheiterte, vermutlich wegen der Komplexität der Beziehung, die sich aus den breiten Beutespektren ergibt.

Die Vogelgemeinschaft kann klar in die Gruppen der heimischen Reiher und Ibis und die vorwiegend ziehenden Limikolen unterteilt werden. Dies schlägt sich sowohl in den Phänologien als auch in den Mikrohabitatpräferenzen und dem Beutespektrum nieder. Nach Abflug der Zugvögel im März/April besetzten die heimischen Vögel nicht die Nischen, die zuvor von den Limikolen besetzt wurden. Neben dieser deutlichen Differenzierung zeichnen sich auch noch weitere, weniger klare Nischen innerhalb der Limikolengemeinschaft ab, die sich an Mikrohabitatpräferenzen und Beutespektren festmachen. Dennoch hatten die meisten Arten sehr breite Nischen und eine sehr variable Ressourcennutzung, vermutlich ein Ergebnis des geringen Nahrungsangebotes auf der Bragantiner Halbinsel. Alle Vögel, die nur kleine Nahrungsorganismen aufnehmen können müssen sich opportunistisch ernähren, da eine Spezialisierung auf nur wenige Beutearten vermutlich immer wieder zu Nahrungsengpässen führen würde.

Die Zeit, die mit der Nahrungsaufnahme verbracht wurde, war vorwiegend von der Methode der Nahrungsaufnahme abhängig. Diese Zeit wurde vor dem Abflug nicht ausgedehnt, was vermutlich daran lag, dass die meisten Vögel bereits die maximale Zeit mit der Nahrungssuche verbrachten. Die meisten Vögel verbrachten nicht die gesamte Periode des ablaufenden Wassers im Untersuchungsgebiet. Während ihrer Abwesenheit suchten sie wahrscheinlich in profitableren Gebieten nach Nahrung. Das könnte für Vögel in diesem

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Untersuchungsgebiet entscheidend sein, da errechnet wurde, dass einige der Vogelarten nicht genug der lebensnotwendigen Energie im Untersuchungsgebiet aufnehmen, wenn sie so fressen wie beobachtet. Auch würde das Nahrungsangebot innerhalb weniger Wochen erschöpft sein, wenn die Vögel ausschließlich im Untersuchungsgebiet fressen würden. Ein Ausschlussexperiment hat keine deutliche Beeinflussung des Benthos durch die Vögel gezeigt, ein weitere Hinweis, dass die Vögel anderswo fressen.

1 General Introduction

Migration of animals has long attracted the attention of hunters, researchers and conservationists. Especially migrating birds, with annual mass movements of tens of millions of birds across continents, are particularly evident and fascinating. Examples include many waterbirds, such as shorebirds, geese, ducks and seabirds, but also birds of prey, storks and passerine birds.

Migration is a behavioural adaptation which enables the birds to breed in areas which provide considerable space for breeding and a large production of insects during spring and summer for successful reproduction. But since survival in these areas is not possible during the cold season, they undertake long migrations into wintering areas in warmer regions. There, the favourable climate prevents the high costs of thermoregulation and provides a year round food stock suitable for subsistence, but not for breeding (Beukema et al. 1993; Pienkowski and Evans 1984; Zwarts and Wanink 1993).

Most waterbird species migrate along well defined routes, the so called “flyways” and they often use for decades the same stop-over- and wintering sites. To be suitable, these sites must satisfy the specific environmental requirements of each individual bird species, and they should enable the birds to gather enough fuel for migration. Thus, these areas are of great importance for a successful migration and the survival of the birds and therefore, knowledge about the birds’ ecology at these sites is crucial.

One question is of particular interest: how are migratory birds adapted to seasonal occupancy of these different habitats? Traditionally, ornithologists regarded long distance migrants as “invaders” of the tropical habitats, but this has been questioned later on (Leisler 1990). Lack (1986) suggested to consider migrants as nomadic with several homes and tropical niches. Since the ability to gather enough food is critical for the birds in preparation for and during migration, studies on shorebird ecology at stop-over- and wintering sites focus almost exclusively on aspects of the foraging ecology. Prey choice, habitat choice, optimal foraging, consumption and prey limitation are the main subjects and many different aspects of these have been investigated:

Several studies showed that shorebirds actively choose specific prey organisms. Selectivity might be related to factors such as specific prey behaviour (Goss-Custard 1977a; Hicklin and Smith 1984), prey sizes (Lifjeld 1984; Pienkowski 1983; Weber and Haig 1997) or shell thicknesses in case of some molluscs (Zwarts and Blomert 1992). However, Backwell et al. point out, that accurate measurements of prey availability are essential for the ability to measure prey selectivity (Backwell et al. 1998).

In addition, shorebirds often choose specific habitats for foraging. Food seems to be a major determinant of shorebird distribution, for there exists a general relationship between bird densities and food availability (for review see Evans and Dugan 1984; O'Connor 1981). Many studies in the Dutch Wadden Sea (Meire and Kuyken 1984; Smit and Wolff 1983). and in Great Britain (Goss-Custard et al. 1977a; Goss-Custard et al. 1977b; Goss-Custard et al. 1991; Yates et al. 1993a) found a correlation between bird numbers and prey numbers. Distribution of sediment characteristics, which are expected to be closely related to benthic abundances, were even used to successfully predict shorebird distribution (Scheiffarth et al. 1996; Yates et al. 1993b). However, it was also pointed out that simple models of predator-prey density relationships are not likely, since several other factors also affect prey availability and shorebird distribution (Evans and Dugan 1984; Wolff 1969). For example, birds might select different mudflats according to prey detectability, as a result of prey activity (Goss-Custard 1970; Mouritsen 1994) or substrate characteristics (Quammen 1982). Other important factors might include predator avoidance (Dierschke 1998; McGowan et al. 2002; Sitters et al. 2001), microhabitats preferences (Kushlan et al. 1985; Ntiamoa-Baidu et al. 1998) and distance to suitable roosting sites (1976; Scheiffarth et al. 1996).

Shorebirds are generally expected to be under pressure to feed efficiently and a body of theory – generally referred to as “optimal foraging theory” – has been developed to address this subject (Krebs 1978; MacArthur and Pianka 1966; Pyke et al. 1977). Goss-Custard (1977b) showed that Redshank chose, at all times, the most profitable prey, but supplemented it in times of prey scarcity with less profitable prey items. Thus, birds might concentrate on those prey yielding the maximum return on average, and not merely on the largest prey.

Some studies have also illustrated the impact of shorebird predation on their prey. The results depend very much on the particular situation at the study site, ranging from very strong impacts to no impacts at all (for review see Arntz 1981; Evans et al. 1979; Quammen 1984a; Quammen 1984b; Szélkely and Bamberger 1992; Wilson Jr. 1989; Wilson Jr. 1990).

As illustrated above, the majority of the studies were conducted in temperate areas. But tropical intertidal environments differ in several aspects to these habitats in temperate zones. Tropical habitats show a large variability in temperature and rainfall. Depending on the region, characteristic patterns of seasonal rainfall occur. In combination with a high insolation, this leads to episodically high rates of evaporation and precipitation, which results into sharp gradients of salinity, temperature and dissolved nutrients in tropical waters (Alongi 1990). A disproportionately large amount of the world's freshwater and sediment discharge streams to the oceans from tropical rivers. Thus, tropical coastal environments are subject to sporadic climatic disturbances which influence water gradients and sedimentary patterns very strongly (Alongi 1990).

The diversity of marine habitats reaches its maximum in the tropics. Mangrove forests are one of these unique tropical habitats. They represent the dominant soft bottom plant community of the marine-terrestrial transition in tropical and subtropical regions (Pernetta 1993) and mudflat/mangrove systems are recognized as of strong importance for shorebirds (Butler et al. 1997; Parish et al. 1987). Mangrove trees can reach up to 45 m height and produce dense forests with unique floristic and faunistic associations adapted to life in the changing environment of the tropical intertidal zone (Reise 2002). Many mangrove forests export large amounts of organic material to adjacent estuaries (Lugo and Snedaker 1974). The organic material is derived from litter fall, which can be remarkably constant over the year in some places, while in others it is accelerated by water stress during the dry season, by hurricanes, and other seasonal events. Thus, tidal flats next to mangroves receive, at least temporarily, considerable amounts of organic material which supports a rich ichthyo- and benthic fauna, the main food sources of wading birds and shorebirds. Additionally, mangroves offer as well a dense and sheltering vegetation, which is used by several birds for high tide roosting (Altenburg and van Spanje 1989; Fournier and Dick 1981; Zwarts 1988).

Although migrating birds spend only few months at their breeding grounds and the rest of the year migrating or at their wintering quarters, ecological investigations on shorebirds in tropical environments are rare and widely scattered. The Banc d'Arguin in Mauritania is an exception with intensive studies and descriptions of the ecosystem and its bird species (Altenburg et al. 1982; Wolff 1991; Wolff et al. 1993; Zwarts et al. 1990). At the African coast of Mozambique the role of human and avian exploitation was investigated (De Boer and Longamane 1996). Piersma and Ntiamoa-Baidu (1995), illustrated the waterbird ecology in Ghana in great detail. Mercier and McNeil (1994) were able to relate shorebird densities with prey densities in Venezuela, while Rogers (1999) found only weak relationships between them at Roebuck Bay, Australia. In the tropical Brazil, so far, only descriptions of the shorebird attendance patterns have been done (Ferreira Rodrigues 2000a; Ferreira Rodrigues 2000b).

In the New World migration system, most shorebird species breeding in the Canadian arctic and northern Alaska migrate southwards along the coasts of North- and South America, to winter in Middle- and the tropical South America. Often migration continues even further south until they reach the Terra del Fuego (Morrison 1984). But while many studies investigate the shorebird ecology in North America and some studies are conducted in Middle America and at the South of Argentina, Chile and Brazil, almost nothing is known about the birds in their tropical environment. There is great need for information from this part of the migration route and the intention of this study is to provide at least some of the missing knowledge from these areas.

This investigation aims at gaining knowledge of the wintering and resting birds in the tropical tidal flats fringed by mangrove forest and to elucidate which kind of habitat they encounter and in which way they use it. The tidal flats of the Bragantian peninsula on the

northeast coast of Brazil were chosen as the study site. This part of the coast was characterized by Morrison and Ross (1989) as one of the most important wintering areas and as of critical importance for several individual species.

The specific objectives are:

(1) to provide knowledge about the intertidal of the Bragantinian peninsula as a foraging habitat for the birds.

Migrating birds rely on rich and predictable food stocks at their stop-over- and wintering sites to support the migrants for at least a short time. The habitat quality, some abiotic conditions and especially the availability of the prey and its spatial and temporal fluctuations, has to be considered as of major importance for migratory birds. What kind of habitat do the migrating waders find when they reach the coast of the Bragantinian peninsula? (Chapter 3)

(2) to describe the avian community at the Bragantinian peninsula.

The habitat encountered by North American migrants in the tropics is also host to residential shorebirds and wading birds. Stop-over- and wintering sites are known for their species richness and high individual densities of their avian community (Recher 1966). Competition for resources, also between migrants and residents, might occur. As a result, birds might specialize on particular niches and the community might be structured in guilds. What is the appearance of the avian community in the study area and which are the significant environmental factors? (Chapter 4)

(3) to investigate the relationship between the birds and their prey

Shorebirds and wading birds use tidal flats predominantly to forage on benthic organisms. But not all prey items in the sediment are accessible for the birds, due to their burrowing depths and sizes (Piersma et al. 1993; Zwarts and Wanink 1993). Those prey items available represent - beside their energetic benefit - also costs in terms of foraging- and handling time (MacArthur and Pianka 1966). The "net energy gain" (or profitability) per prey item is possibly crucial for the decision to include an organism in the birds diet. Also, prey availability and profitability might determine the spatial distribution of the birds on tidal flats. What prey is eaten by the birds, why did they choose it and do the benthic resources determine the birds spatial distribution? (Chapter 5)

(4) to evaluate the consumption of the birds in the intertidal of the Bragantinian peninsula and its meaning for the avian- and the benthic community.

The contribution of birds to the energy or carbon flow of the intertidal ecosystem is assumed to be of little importance, since their consumption affects only a relatively small fraction of the primary production and detritus import (Meire et al. 1994). In spite of this they can severely reduce the organisms they prey on, as demonstrated by Evans et al. (1979), who showed

that birds removed about 90% of the standing crops of *Hydrobia* and *Nereis* at the Tees estuary in Great Britain. For the avian predators, consumption rates could indicate how much time these birds would need to fulfil their energetic requirements and if the intertidal provides enough food to support the entire avian community. For the benthic prey, predator consumption rates can elucidate if the prey community is affected by predation. Additionally, enclosure- and inclosure experiments are able to provide similar information. The bird behaviour, like territoriality and aggression, can be interpreted in the light of these results. How much do the birds consume at the study area and what does this mean for the avian community and the benthos? (Chapter 6)

This “Introduction” will be followed by a general “Material and Methods” chapter (chapter 2). The subsequent chapters (chapters 3-6) will focus on the different objectives of this study, each is composed of a short “Introduction” and individual “Results” and “Discussion” parts. They progressively build on one another: while the first chapters describe different parts of the ecosystem, chapter 5 will focus on the relationships between these compartments. Finally, the emphasis is on the last chapter, which will elucidate the previous results in connexion to the mangrove ecosystem.

2 Materials and Methods

2.1 Study area and sampling sites

The study was conducted at the Bragantinian peninsula on the northeast coast of Pará, Brazil. Located about 150 km southeast of the Amazon delta, it is part of the Amazonian littoral. A mangrove belt is bordering the coast, forming the world's second largest continuous mangrove region with an area of 1.38 million hectares along a coastline of approximately 6800 km (Kjerfve et al. 1997).

The study was carried out within the MADAM project („Mangrove Dynamics and Management“), a bilateral cooperation project initiated by the Centre of Marine Tropical Ecology of the University of Bremen (ZMT) and the Núcleo de Meio Ambiente of the University of Pará (UFPA/NUMA). The aim of MADAM is to investigate the mangrove ecosystem and thus to provide a scientific basis for the understanding of the interactions between biological, anthropogenic and physical circumstances (Berger et al. 1999). The mangrove ecosystem of the Bragantinian region was chosen as a research area of the project. The local headquarters and laboratories are located in Bragança, 200 km east of Bélem, at the basis of the Bragantinian peninsula. The main study region includes an area of approximately 220 km², about half of it is covered with mangrove forest (Fig. 1, Krause, pers. comm.).

The dense mangrove vegetation is dominated by the mangrove trees *Rhizophora mangle* L. (Rhizophoraceae), *Avicennia germians* L., (Avicenniaceae) and, at the margins of tidal channels or roads, *Laguncularia racemosa* L. (Combretaceae) (Reise 2002). Small creeks, named “Furos” by the local people, cross the forest with direct access to the sea. After rainfall the freshwater accumulates in the Furos and as a consequence they contain more or less brackish water, depending on the tides and the amount of rain. They serve as transportation routes in and out of the mangrove, for fish as well as for the local fishermen and crab catchers. Inside the mangrove and at the margins of the streams the ground consists of soft and heavy mud. Towards the edge of the mangrove forest, the streams widen out to extensive open intertidal flats with mainly firm and sandy grounds.

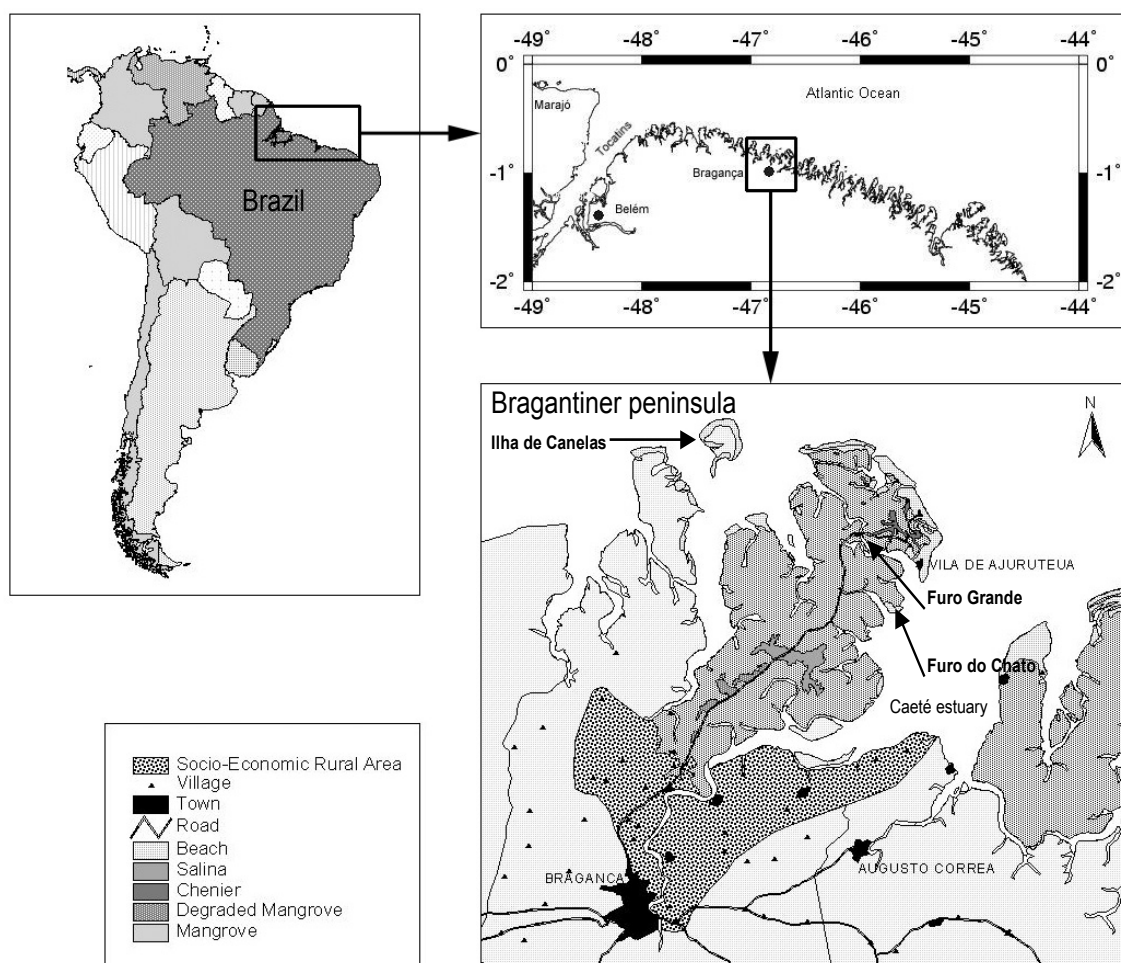


Fig. 1. Research area of the MADAM project at the Bragantian peninsula and the adjacent tidal flats. The sampling sites of this study are indicated by arrows (Modification of Krause et al. 2001).

The Bragantian peninsula belongs to the inner tropics. Its climate is characterised by a pronounced rainy season from January to May/June and a dry season from July to December (Fig. 2). Infrequent sampling of climatic data at the Furo Grande showed that the monthly mean temperatures ranged between 25.7-27.6°C (January-May) during the study period in 2001 and between 26.3-27.0°C (January-June) in 2002. The precipitations varied in 2001 between 3.2-25.2 mm/day with a peak in February and in 2002 between 0-17.8mm/day with the highest value at January and the lowest in May.

The tide is semidiurnal and has a mean altitude of 3.5 m, during spring it exceeds over 5 m.

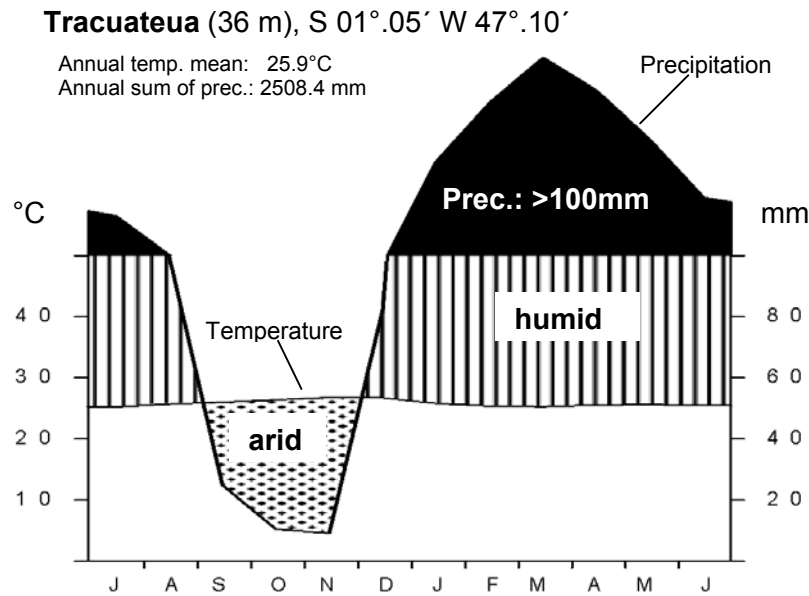


Fig. 2. “Klimadiagramm” after Walter and Lieth (1967) from Tracuateua. Given are monthly averages of temperature and precipitation sums between 1973 and 1997 (INMET 1992; Mehlig 2001).

The investigations of this study took place at three different sampling sites, exemplary for three types of intertidal areas:

Ilha de Canela – the open intertidal

The Canelas sampling site consisted of about 1 km² of tidal flats, located between Ilha de Canelas and the mainland (Fig. 3). It is under strong tidal influence and the freshwater impact can be assumed to be low. The tidal flats are with regard to sediment conditions and benthic assemblages very variable in time and space. They are affected by small scale disturbances, such as pits created by large crustaceans or sting-rays, strong currents with a heavy sediment load, boats lying on the flats during low tide or floating debris (mangrove trees or garbage) left behind on the sediment by the receding tides. These disturbances create a mosaic of patches, differing in abiotic and biotic conditions. During low tide only shallow ponds and tidal creeks remain inundated, hosting few fishes and crabs. Although some walkways are bordering the area, the disturbance by humans was quite low and was not further considered.

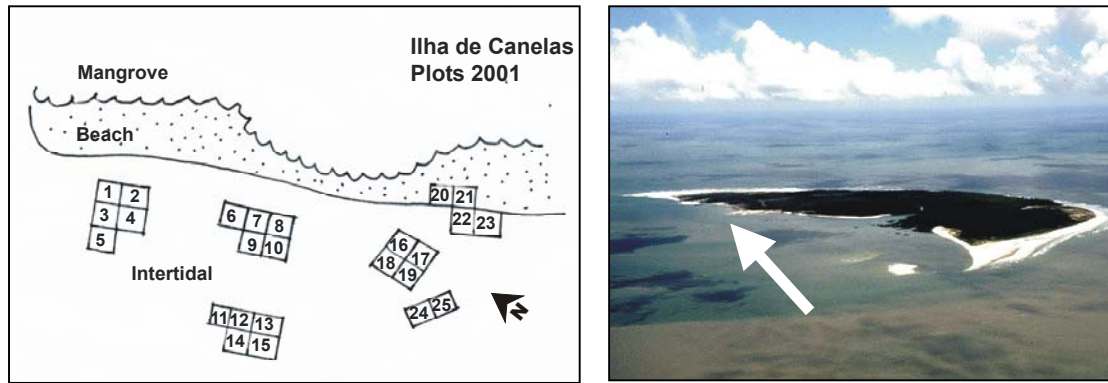


Fig. 3. Sampling site at the open intertidal of the Ilha de Canelas in 2001. The plots are indicated by their numbers, they all covered 50x50 m.

Furo Grande – the intertidal inside the mangrove

This sampling site was located at the margins of the large mangrove channel Furo Grande, very close to a crossing bridge (Fig. 4). It stretched over 200 m along the shore and covered its full width of 50 m. Like the shores of many mangrove streams it was quite steep and had three distinct vertical zones. The top “Uca”-zone, named after the characteristic mangrove crab of the taxon *Uca* (Acheampong 2001), borders the mangrove fringe with heavy and sticky mud. The intermediate zone and especially the lower zone of the stream-bed are influenced by the strong currents of the stream and include mostly firm sandy grounds. In contrast to smaller streams, the Furo Grande was never completely dry during low tide. The human impact at the area was strong since the bridge and some accommodations of local fishermen are nearby. Although the people were rarely trespassing the area, noise pollution was temporarily apparent, also created by boats.

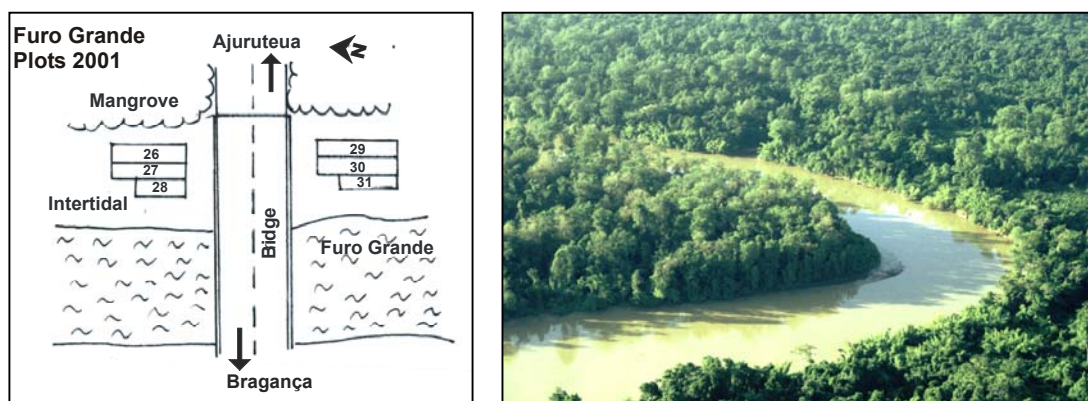


Fig. 4. Sampling site inside the mangrove at the Furo Grande in 2001. The plots had the size of 125x20 m (26, 27, 29, 30), 100x20 m (28) and 75x10 m (31).

Furo do Chato – a transition area

This sampling site comprised about 0,5 km² at the mouth of the Furo do Chato and it is part of the Caeté estuary (Fig. 5). The Furo do Chato crosses the flats even at low tide, but the remaining area is under tidal influence and it fell dry with ebb tide during the investigations. Because of its distinct position at the Furo's mouth it could neither be called an open tidal flat nor an intertidal bordering the mangrove streams, but is a kind of transition area between both. Some accommodations of local fishermen are located at the beach bordering this area. Depending on the fishermen's irregular presence, the human impact was ranging in between moderate and none at all. But here as well, the disturbance was mostly through noise and rarely through trespassing.



Fig. 5. Sampling site close to the mangrove fringe at Furo do Chato in 2001. All plots covered 50x50 m.

2.2 Study design

The general study period between January and June was chosen to cover the demanding pre-migratory fattening period of migrating shorebirds preparing for spring migration (January–March), and also the contrasting time when the tidal flats are used predominantly by tropical breeding birds, at least for some of them during the difficult time of chick raising (April–June). It was assumed that during this time the birds would forage intensively and that underlying structures in habitat use and foraging ecology would emerge more clearly.

In January 2001 a total of 46 squared plots were marked. They were indicated at their edges by poles (length: 1.20 m, diameter: 5 cm) and they were pushed into the ground leaving 40 cm above the surface. 25 plots were situated at the tidal flats of the Ilha de Canela, 6 at the Furo Grande and 15 at the Furo do Chato (Fig. 3, Fig. 4, Fig. 5). To optimise the data for correlation analysis and multivariate statistics, plot locations were chosen to cover the whole variety of occurring intertidal habitats as they could be distinguished by sight prior survey. Thus, the plots were not randomly selected and results can only refer to the investigated plots within the areas but not for the areas themselves or the entire intertidal. In most cases the plots had a size of 2,500 m², comprising 50 m x 50 m at the sides. Only two plots at Furo Grande had to be smaller because of the little space available at the side of the channel

(2,000 m² and 750 m²). The avian abundance data from these plots were calculated to match a plot of 2,500 m². Although the plots were bordering each other, Contingency tables proved that the benthic data obtained was independent from each other (Appendix I, Table 20).

Since only Canelas was of major importance for the birds in 2001, five plots were marked again in January 2002 only at the Ilha de Canelas. The plots had a size of 2,500 m² and were located at the same part of the mudflat which was investigated in 2001 (Fig. 6).

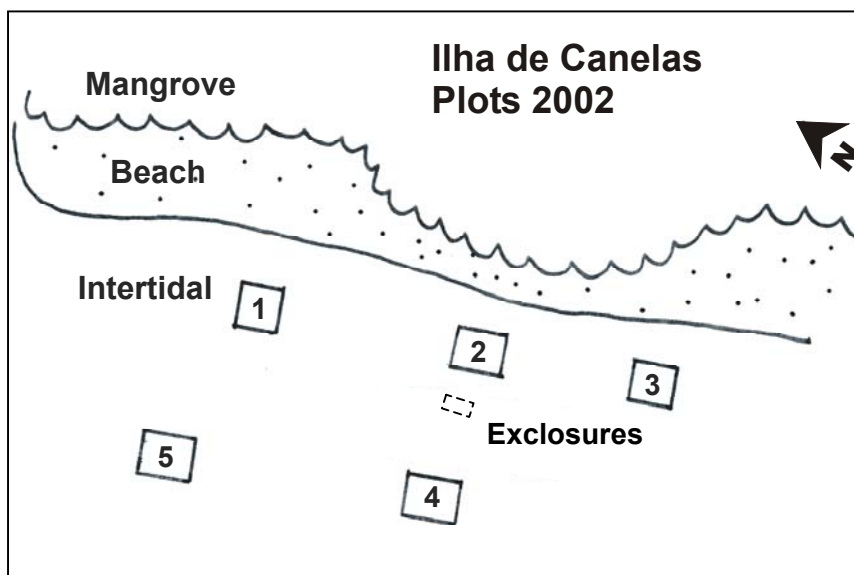


Fig. 6. Sampling site at the open intertidal of the Ilha de Canelas in 2002. The area of the exclosure experiment is denoted by a dotted line, the plots are indicated by their numbers. All plots had a size of 50x50 m, the exclosure area covered 8x19 m.

Following investigations took place at the plots according to the schedule of Table 1:

2.2.1 *Environmental conditions and the benthic community*

From January–June 2001 all 46 plots were sampled monthly, starting usually with 4 days of data collection at the Ilha de Canelas on new moon and progressing to the plots of the Furo Grande and the Furo do Chato as quickly as possible (Table 1). Due to the logistics it took about 12-14 days to take all data each month.

Table 1. Sampling schedule of the investigations in 2001/2002. Given are time, location and number of plots where investigations took place. Investigations are indicated by “# repl.”, the number of replicates taken at each plot. “Max” means that as many observations/samples were taken as possible.

time	Location	Number of plots	Environmental variables and benthic community		Avian community				Exclosures	
			Samples for spatial distribution	Samples for Biomass adjustment	Counts for spatial distribution	Counts for tidal adjustment	Focal obs. for forag. behaviour	Collection of droppings		
2001	Marking of 46 plots									
	January	Canelas	25	1 repl.	-	4 repl.	1 repl.	-	-	-
		Furo Grande	6	1 repl.	-	4 repl.	1 repl.	-	-	-
		Furo do Chato	15	1 repl.	-	4 repl.	1 repl.	-	-	-
	February	Canelas	25	1 repl.	-	4 repl.	1 repl.	-	-	-
		Furo Grande	6	1 repl.	-	4 repl.	1 repl.	-	-	-
		Furo do Chato	15	1 repl.	-	4 repl.	1 repl.	-	-	-
	March	Canelas	25	1 repl.	-	4 repl.	1 repl.	-	-	-
		Furo Grande	6	1 repl.	-	4 repl.	1 repl.	-	-	-
		Furo do Chato	15	1 repl.	-	4 repl.	1 repl.	-	-	-
	April	Canelas	25	1 repl.	-	4 repl.	1 repl.	-	-	-
		Furo Grande	6	1 repl.	-	4 repl.	1 repl.	-	-	-
		Furo do Chato	15	1 repl.	-	4 repl.	1 repl.	-	-	-
	May	Canelas	25	1 repl.	-	4 repl.	1 repl.	-	-	-
		Furo Grande	6	1 repl.	-	4 repl.	1 repl.	-	-	-
		Furo do Chato	15	1 repl.	-	4 repl.	1 repl.	-	-	-
	June	Canelas	25	1 repl.	-	4 repl.	1 repl.	-	-	-
		Furo Grande	6	1 repl.	-	4 repl.	1 repl.	-	-	-
		Furo do Chato	15	1 repl.	-	4 repl.	1 repl.	-	-	-
2002	Marking of 5 plots and exclosures									
	January									
	February	Canelas	5	1 repl.	-	4 repl.	-	max	max	1 repl.
	March	Canelas	5	1 repl.	-	4 repl.	-	max	max	1 repl.
	April	Canelas	5	1 repl.	max	4 repl.	-	max	max	1 repl.
	May	Canelas	5	1 repl.	max	4 repl.	-	max	max	1 repl.
	June	Canelas	5	1 repl.	-	4 repl.	-	max	max	1 repl.

The following samples were taken at each plot:

Sediment

One sediment sample was taken per plot by pooling three sub samples, obtained by a corer of 2.5 cm diameter and 20 cm length at different locations at each plot. This procedure ("Sacrificial Pseudoreplication", Hurlbert 1984) accounts for some variation within an area, but keeps the processing expenditure low. From this mixture a sample of 30-45 g dry weight (dried for 4 days at 60 °C) was taken and further investigated by a procedure modified by the one described by Buchanan and Kain (1984). The sample was soaked for 24 hours in a solution of Sodiumhexametaphosphate (0.24 g/l, by Synth) to dissolve agglomerated particles. To determine the sediment fractions belonging to certain grain sizes, a wet-sieving-analysis was done using the Analysette 3 Pro (Fritsch) with 6 sieves of differing mesh width (1 mm, 710 µm, 500 µm, 315 µm, 71 µm and 20 µm; the fraction <20 µm was discarded). The samples were rinsed with water for 10 minutes through every sieve, starting with the largest mesh width and preceding to the smallest one. The resulting 6 size fractions of the sediment obtained in the sieves were dried (48 h at 60°C) and the masses were defined to the next 0.001 g. The proportion of each fraction was calculated and used to define median grain sizes through a cumulative size fraction curve on a phi notation (Buchanan and Kain 1984).

Salinity

At each plot, pore water was collected by digging a hole of about 30 cm depth and taking a sample of the water which accumulated in it. The salinity of these samples was investigated with a conductometer (TetraCon® 325, WTW, calibrated on 25°C).

Time of emergence

To assess the different inundation times of the plots at the Ilha de Canelas, an observation over the complete tidal cycle was conducted at the 22.06.03. The time periods of time without water ("time of emergence") were taken with a stop watch. A plot was termed as "without water" when all 4 poles were standing in water of <30 cm depth. It was assumed that at least the large birds could start using it from that water depth on.

Burrow openings

Since visible cues of benthic organisms could be important for the habitat choice of birds, a measure of surface marks was employed. At each plot a square of 1 m² was selected randomly and marked temporary with a cord. Within its boundaries all burrow openings on the surface were counted without further distinction of responsible benthos organisms.

Benthic community

Three benthic sample were taken per plot with a corer of 15 cm diameter up to 20 cm depth at three different locations. Each sample was divided in three horizons of 0-5 cm, 5-10 cm, 10-20 cm depth . Within a few hours the samples were sieved through a 1 mm sieve, the remains were sorted on a tray and the extracted animals were stored in 70% ethanol. At the lab, the benthos organisms were identified, size measurements were taken and the obtained data were calculated to densities/m². Some animals were broken due to the handling procedure. Of incomplete polychaetes only the head regions were counted to avoid double counts. Identification and measurements were done with a stereomicroscope (Stemi 2000 from Zeiss, 10x), a microscope (Zeiss Axioskop 2 with 10x/0.30, 20x/0.50 and 40x/0.75 oculars). Identification on species level was not always possible due to limitations of time and knowledge of the local benthic community. Hence, specimens were classified to the lowest taxonomic level possible, which were families for polychaetes or higher taxa like nemertinea or hydrozoa. The following literature was used for identification:

- Molluscs: “Compendium of Seashells “ (Abbott and Dance 1986)
- Brachiura: “Manual de Identificação dos Brachyuras (Caranguejos e Siris) do Litoral Brasileiro” (Schmidt de Melo 1996)
- Polychaeta: “The Polychaete Worms – Definitions and Keys to the Orders, Families and Genera” (Fauchald 1977)

For correction or verification of the taxonomic identifications, the sample obtained in January 2001 was sent to the Faculdade de Ciências Ambientais, Centro Universitário Monte Serra and the Departamento de Oceanografia Biológica - Instituto Oceanográfico - Universidade of São Paulo. Most identifications were verified, only few had to be corrected.

The sizes of all complete individuals were determined using a ruler integrated in the ocular. Of the Brachyuran crabs the carapace width, of bivalves the width of the shell, of gastropods the height of the shell and for all other animals the body length was taken. “Worms” were straightened without stretching, however, their body length is probably not as accurate as that of molluscs or crustaceans due to their flexibility. The size data of certain polychaetes might be underestimated, since large individuals tend to break more easily than small ones and they were thus not further included in the investigations.

Biomass adjustment

To find a way to transform the length data of all macrobenthic individuals into biomasses, some extra samples were taken from the areas at the Ilha de Canelas in March and April 2002 (Table 1). Their ash free dry weights (AFDW) were determined as recommended by Higgins and Thiel (1988). The fresh animals were individually identified, measured, dried at 60°C for 24 hours and weighed to obtain the dry mass. Subsequently they were dried at 475°C for two hours and the weight of the remaining ash was determined. The difference between dry mass and ash mass is the AFDW, the measure of biomass.

For each benthic taxon the best length-AFDW relation was obtained by the Nonlinear Estimation tool of Statistica (Appendix I; Table 23). Most taxa had only few individuals, thus they were grouped together on higher taxonomic levels to find an approximation of the length-AFDW relationship. With the resulting functions all data on benthic lengths were transformed to biomasses. From that data the biomass of all benthic samples were estimated and given in AFDW/m².

Inter annual variation

To investigate inter annual variations the environmental data were investigated again at the same area within 5 newly marked plots from February–June in 2002. The samples were taken in the same manner as in 2001, but the processing of the sediment was slightly adjusted. The analysis of the sediments with the Analysette was now reduced to three sieves of 315 µm, 71 µm and 20 µm width, as in 2001 the other fractions proved to be of minor importance.

2.2.2 Avian community

For all bird observations, binoculars (10 x 40 from Zeiss and 8 x 32 from Fujinon) and telescopes were used (Optolyth TBG 80 with 20x WW and 20-60x80/65 oculars). Only diurnal foraging was taken into consideration. Beside date, time of day and weather condition (temperature, cloud cover, precipitation, wind direction and -velocity), the water coverage of the plots (in % of the plot area) was also taken. The following subjects were investigated:

Spatial distribution through low tide counts

From January–June 2001 and January–June 2002 the spatial distribution of the bird community was investigated at the marked plots (Table 1), simultaneously to the sampling of the environmental data. Each month, starting with the new moon, bird counts were conducted during mid day low tides of four successive days (“low tide counts”). The time of low tide was determined by the tide table of Salinopolis, the closest town to the study area with a tide table. Very exceptionally only a few plots were counted on three but four days, due to disturbing simultaneous benthic investigations or boats lying inside the plots. Each individual was recorded with species, activity (feeding/not feeding) and with occurrence in specific microhabitats (dry sand, waterline, in the water). With this a mean bird number/ha for each plot and month was calculated.

Tidal adjustment through ebb tide counts

When the habitat use of birds is studied, low tide counts are no ideal measure since they do not take those birds into account, which use a habitat during earlier or later stages of the tidal cycle. Because counts over an entire tidal cycle are time-consuming, it was aimed to find factors to adjust the usually applied low tide counts by the uncounted individuals. For this,

one count over the entire ebb-tide period was conducted each month (“ebb tide count”) to produce data of at least the period of receding water until low tide (Table 1). The numerical relation between this ebb tide count and the low tide count conducted on the same day was calculated. This “ebb tide factor” was used to adjust the other three low tide counts of that month.

An ebb tide count started as soon as the first plot fell dry, continuing with repeated hourly sub counts until it ended with the low tide count. All plots free of water were included, resulting into 3 to 6 sub counts per plot, depending on the elevation of the plot and the weather and wind conditions. A plot was defined as “free of water”, as soon as all 4 marking poles were standing in maximal 30 cm high water, as from this point on plots could be used by birds. The data taken during these counts were the same as for the low tide counts described above. For each plot a mean bird number/ha for this ebb tide was calculated. This was compared to the bird number of the low tide count obtained on the same day per plot, month and bird species separately. In most cases the ebb tide count as well as the low tide count produced avian abundances from which a factor could be calculated. However, sometimes birds were present during the ebb tide count but not any more during low tide. As no factor can be found to adjust “0”, the low tide count was simply substituted by the ebb tide count in this cases. This was problematic when the other low tide counts of that month had birds present, because these numbers cannot simply be substituted by the ebb tide count. These occasions had to be neglected from the analysis (66 cases), resulting into a reduction for some bird species from 4 counts to only 3, 2 or, in two cases, to only one count per month and plot. Since these cases were rare, I assumed this would not have any great influence on the results.

Foraging behaviour

From February 2002–June 2002 the detailed foraging behaviour of the birds was investigated by focal observations at the five marked plots of Canelas (Table 1). A total of 617 individual birds of 15 species were watched for three minutes and with the help of stop watches the following data were collected:

- *Steps/min*; were counted in slowly walking species (all herons, Scarlet Ibis, Marbled Godwit, Willet, Whimbrel, some Short-billed Dowitchers and Knots). In species with rapid movements the time of walking was taken with a stop watch (all plovers, Semipalmated Sandpiper, Sanderling, Turnstones, some Short-billed Dowitchers and Knots). Video tapes with several examples of these species were taken and used to count the steps in slow motion and to calculate an average step/min (Appendix I, Table 21). With these approximations the numbers of steps during the observation periods were calculated.
- *Pecks or probes/min*; were counted

- *Prey taken/min*; large prey was counted. Small prey could often not be observed directly but was detected and counted by bill movements
- *Prey size*; the size of larger prey was estimated in % bill length. Prey <20% of bill length was not further distinguished but received a mean size figure of 10% of bill. Only gastropods were excluded from the size analysis since they were usually so small that their sizes were always <20% of the bill and could not be distinguished further. With bill sizes given by the literature prey sizes were estimated (Blake 1977; del Hoyo et al. 1996; Poole and Gill 2000) (Appendix I, Table 22).
- *Prey type*; in many cases it was possible to distinguish between “worms”, bivalves, gastropods and crabs
- *Handling time*; time from the picking up of the prey item until it was swallowed entirely, estimated in seconds
- *Microhabitat*; was determined as “dry sand”, “waterline”, or “in the water”
- *Water depth*; if the bird was feeding in the water, the water depth was indicated by max % of the leg under water. With leg sizes given by the literature water depth could be estimated (Blake 1977; del Hoyo et al. 1996; Poole and Gill 2000) (Appendix I, Table 22).
- *Probing depth*; the max % of bill length inserted into the sand was estimated. With bill sizes given by the literature insert depths were calculated (Blake 1977; del Hoyo et al. 1996; Poole and Gill 2000). In cases of birds foraging in the water the probing depth was calculated by subtracting the insert depth in the water by the water depth
- *Type of behaviour*; the foraging behaviour was mostly determined as visual and/or tactile, depending whether birds detected their prey mainly by watching the sediment surface or by probing into the sediment with their beaks. Herons and few shorebirds required more detailed descriptions, since they used complex foraging behaviours. Also the association with other birds was recorded.

For the calibration of size estimations (% of bill length, % of leg length) the two persons involved in these observations were trained in simulated conditions with paper bird models and alcohol fixed benthos organisms until the estimations were exact.

Analysis of droppings

During the behavioural observations in 2002 faeces of the observed birds were collected whenever possible to search for remaining parts of the prey (cirrae, mandibulae and shell fragments) (Table 1). A total of 68 droppings of 14 different species were collected. Since observations suggested that most birds – when feeding - stayed for quite some time at the same area, it was assumed that most droppings represented local prey of the investigated areas. The droppings were treated as recommended by Scheiffarth (2001): after scraping

them off the surface, they were stored in 70 % ethanol. For further analysis they were first treated with ultrasound for 10 minutes to separate the particles. After sedimentation two fractions were obtained: the supernatant and the sediment. The tiny floating parts within the supernatant were collected with a sieve (63 µm), identified and counted in a cylindrical chamber under a microscope (Zeiss Axioskop 2 with 10x/0.30, 20x/0.50 and 40x/0.75 oculars). The sediment was scanned for larger remains of prey, which were as well counted and identified as exact as possible. A list of identified taxa is given in Appendix I, Table 24.

Specific identification of the remaining parts of the benthic organisms was eased by the collection of a reference sample. Benthic organisms, obtained at the sampling area at the same time of sampling, were identified, measured (Stereomicroscope: Stemi 2000 from Zeiss with 10x ocular, Microscope: see above) and afterwards left in warm water for 3-14 days until the state of dissolution. By then durable parts of the animal could be described. The data obtained by the droppings cannot be used for information on the quantity of prey items and can not be seen as a complete list, since not all organisms could be identified by their remains. They give only a qualitative idea about what prey was eaten with certainty. Hence it can only be used to support the data obtained by the focal observations.

Profitability of prey and the optimal diet

To obtain a measure of attractiveness of prey items the definition of profitability as proposed by Pyke et al. (1977) was adopted. They defined profitability as energetic value of a prey item divided by the sum of handling time and searching time.

$$P_i = \frac{E_i}{S_i + H_i}$$

i = number of prey types
 E_i = Energetic gain [gAFDW/prey item]
 S_i = Searching time [sec]
 H_i = Handling time [sec]

It was aimed to define a theoretical mean profitability for each bird species at each plot to see if birds distribute according to profitabilities. To obtain a H_i for all benthic individuals found at the plots a size-handling time relationship was described for each benthic group separately by a mean handling time or, when large differences occurred, with formulas calculated with the Nonlinear Estimation tool of Statistica (Appendix I, Table 26). E_i was obtained as described above with the formulas given at Appendix I, Table 23. Since individual bird species needed different handling- and searching times, they were calculated for each species separately. Consequently, profitabilities of prey items differed also between bird species.

S_i was calculated as follows:

It was assumed that search time behaves inverse proportional to the density of organisms, if prey items are evenly distributed. That means, random searching will take less time for organisms that are abundant than for rare items.

For each bird species and month a mean search time (\bar{S}) per prey item could be calculated from the data as:

$$\bar{S} = \frac{T - H}{n}$$

$$\bar{S} = \frac{S_1 + S_2 + S_3 + \dots + S_i}{i}$$

T = total time of focal observation
 H = total handling time during focal observation
 n = number of caught prey items

A factor (F_i) was calculated which accounts for the numerical relationship between the different prey items and reverses the proportions:

$$D_1 > D_2 > D_3 > \dots > D_i$$

$$D_i = x_i \times D_1$$

$$F_i = \frac{1}{x_i}$$

D_i = density of individual prey types [Individuals/m²]
 x_i = factor converting D_1 into D_i

From this the proportional search time for each prey type could be calculated

$$\bar{S} = \frac{S_1 + (S_1 \times F_2) + (S_1 \times F_3) + \dots + (S_1 \times F_i)}{i}$$

$$S_1 = \frac{i \times \bar{S}}{\sum_1^i F}$$

$$S_i = (S_1 \times F_i)$$

When profitabilities of individual prey items were calculated in this way, also an optimal diet according to Charnov (1976) could be calculated. If a predator, which already included the most profitable prey type into its diet, encounters a new and less profitable prey type it has to decide whether to eat the prey or to carry on with searching for already included prey. Charnov predicts, that prey type i should be included in the diet if:

$$\frac{E_i}{h_i} \geq \frac{\bar{E}}{(\bar{s} + \bar{h})}$$

while $\frac{\bar{E}}{(\bar{s} + \bar{h})}$ is the mean profitability of the already into the diet included items. As long as

$\frac{E_i}{h_i}$ is larger or at least equal to $\frac{\bar{E}}{(\bar{s} + \bar{h})}$, the total energy intake rate will not decrease with

addition of this prey type. If the relation reverses, the prey should be rejected since it would decrease the overall energetic gain. Based on these assumptions, an optimal diet can be predicted for each bird species (for detailed descriptions of the calculations see Pyke et al. (1977).

Gross food intake, consumption and predation pressure

The consumption by the birds and their predation pressure on the benthic community of the Bragantinian intertidal was estimated according to the procedure used by Zwarts et al. (1990a) for the birds of the Banc d'Arguin. The calculations were based on the assumptions that the cost of living in the tropics is about 1.8*BMR (Basal Metabolic Rate) and that the average digestibility of flesh reaches a value of approximately 80%. Gross food intake (GFI), given as gAFDW/day, was then calculated from body mass (M in kg):

$$GFI = 47.6 \times M^{0.729}$$

The body masses of the birds could not be measured in this study, thus data obtained from the literature had to be taken (for the Scarlet Ibis the lowest values of Haverschmidt 1968; for all other birds Poole and Gill 2000). Body mass data taken between 1997-2000 of wintering shorebirds at Maranhão, south of the Bragantinian study area, by A.A. Ferreira Rodrigues, Universidade Federal de Maranhao at Brazil, were extremely low. Hence, always the lowest literature data found were taken (Appendix I, Table 22).

The GFI, representing the essential food value per day necessary for a bird to survive, was compared with the actual consumption as calculated with the observed feeding time/day [min], with the proportional time spent feeding and the observed energy intake rate/min [gAFDW/min].

$$\frac{\text{Consumption}}{\text{day}} = \frac{(\text{feeding time}) \times (\text{proportional time spend feeding}) \times (\text{energy intake rate})}{\text{day}}$$

The observed energy intake rate/min was obtained by the focal observations which gave the amount and size of prey for each bird observed. The prey sizes could be transferred into AFDW by the formulas given in Appendix I; Table 23. Unknown prey items got a constant minimal AFDW of 0.02 mg, the lowest AFDW measured during the study.

For the estimation of the predation pressure on the benthic community the consumption/day of each bird species was divided according to the observed proportional content of the diet (chapter Table 9):

$$\text{consumption}_i = \frac{\text{consumption}}{\text{day}} \times \text{proportion}_i \text{ of diet}$$

The result were individual consumption rates for each avian species on bivalves, on "worms", on crustaceans etc. For each plot and month the mean bird density [birds/ha] given for each species was multiplied by the corresponding consumption/day. The outcome, a total

consumption [AFDW]/ha for each plot, was given for the entire benthic community or separately for the benthic groups.

The relative predation pressure was calculated by dividing the birds consumption [AFDW/ha] by the food stock [AFDW/ha]. If no food stock was recorded for that plot and month, this case had to be abandoned from the analysis. Thus, food pressure is probably higher than calculated.

2.2.3 *Exclosures*

An exclosure experiment was carried out in 2002 at the intertidal of the Ilha de Canelas. The spatial variation of sediment and benthic features in the study area made it necessary to reduce the space for the experiment as far as possible in order to minimize the variation between replicates. Thus, a sampling design was chosen with treatments separated from each other in order to minimize the sampling area while the influence between the treatments was reduced as far as possible. The experiment was carried out in an area lying in between the other plots investigated during 2002 (Fig. 6). This area was chosen because of its similarity to most plots investigated during 2001/2002 in terms of sediment characteristics, benthic community and overall appearance. Seven exclosures, seven procedural controls and seven controls were set up in mid January, each covering a 1 m² square. All squares of one treatment were situated 2 m apart from each other in a line, parallel to the lines of the other treatments (Fig. 7). The entire experimental set up covered 8x19 m. The design of the exclosures resembled that of Mercier and McNeil (1994). They were constructed of four poles (length: 60 cm, diameter: 5x2 cm) pushed into the ground at each corner until a height of 20 cm above the sediment surface remained (Fig. 7). A fishnet was attached on top of these poles with a mesh size of 2 cm in diameter. The lateral sides were closed for birds by nylon cords, tightened horizontally around the poles 4 cm and 12 cm above the ground. This construction was supposed to cause only little sedimentation inside the exclosures and still allowed entry for other predatory species, such as fish or crabs. No bird was observed to enter the exclosures during the observations although foot prints were observed at the surrounding area.

The procedural controls were set up to investigate the effects of the cages on sedimentation and benthos. Four poles, beside the cage tops presumably the parts with the strongest effects on sedimentation, were set up in exactly the same manner as the exclosures, just without the top-netting and the cords. Hence, entrance for the birds was possible but also a part of the effect on water currents and sedimentation of the cages was imitated.

The controls were not marked at all. They were located by measuring a fixed distance to neighbouring exclosures.

All replicates within a treatment were independent from each other (Appendix I, Table 20)

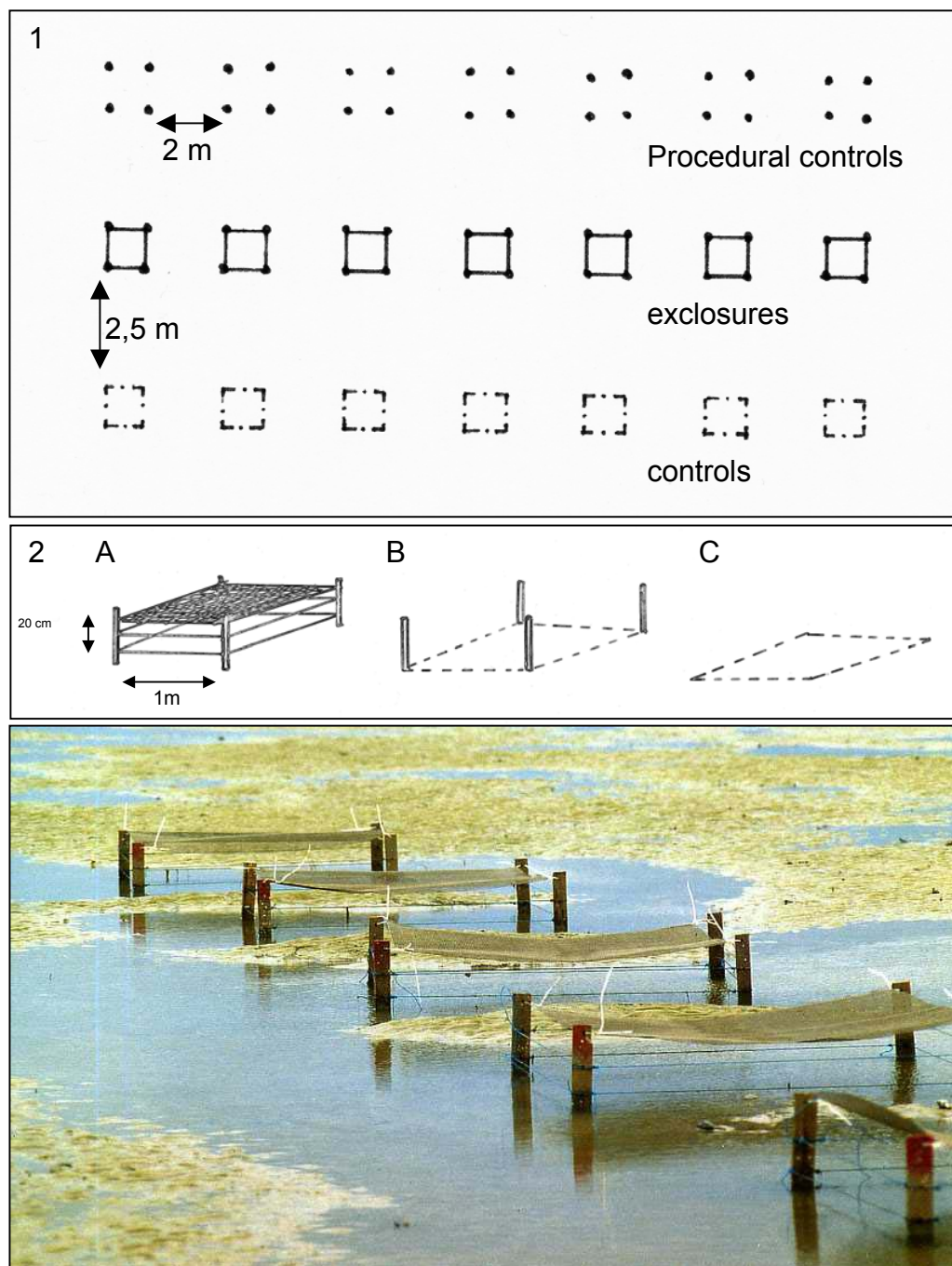


Fig. 7. Experimental design of the exclosure experiment conducted at the intertidal of the Ilha de Canelas in 2002. Given is the spatial arrangement of the three treatments (1) and the design of exclosures (A), procedural controls (B) and controls (C) (2).

Unfortunately the enclosure-cages were victims of vandalism within the first weeks after their construction. The fishnet and the cords were all destroyed in the same manner, but the poles remained unattached. Since all enclosures were affected identically, it was decided to carry on with the experiment. The enclosures were rebuilt in the middle of February, but now using galvanized metal netting with a diameter of 0.55 cm on top instead of a fishnet. The enclosures were not disturbed any more after that.

Sedimentation was very strong in the area, thus enclosures and procedural controls appeared to “sink” into the sediment progressively. In May only 6 and in June only 2 of them were left, the others had to be excluded from the analysis. For that reason only the data from January until May were used.

At each of the plots the following samples were taken on a monthly base, simultaneously to the other plot samplings in 2002:

Sediment characteristics

One sediment sample was taken by pooling three sub samples obtained at three different locations per enclosure cage/control/procedural control (“Sacrificial Pseudoreplication”). They were obtained by using a corer of 2.5 cm diameter and 20 cm length. This samples were further processed like the above samples in 2002 (chapter 2.2.1).

Salinity

Pore water was collected and investigated with a conductometer like all other salinity samples (chapter 2.2.1).

Burrow openings

The openings of all burrows were counted of the entire plot surface before taking the monthly samples (chapter 2.2.1).

Benthos

Three sediment samples up to 20 cm depth were taken with a corer of 8 cm diameter per plot. They were divided into three horizons (0-5 cm, 5-10 cm and 10-20 cm) to investigate the vertical distribution. All three sub samples from the same depth were mixed together to one sample for each depth and plot (“Sacrificial Pseudoreplication” see above). Within a few hours the samples were sieved through a 1 mm sieve, the remains were sorted on a tray and the extracted animals were stored in 70% ethanol. They were further investigated like the samples of the investigations on the spatial distribution of benthos in 2001 and 2002 (chapter 2.2.1).

To minimize the destructive effect 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 25x17 cm and samples of one month were restricted to haphazardly predetermined grids. Grids beside poles were not sampled at all to avoid strongly obscured samples through edge effects.

2.3 Statistical Analysis

All data collected were fed into the database Access 2000 (Microsoft®). For the Analysis the statistical Programs Statistica (Version 5.1 from StatSoft Inc.), Primer (Version 5.2.2 for Windows, Primer-E Ltd) and the Exel Add-In Biplot (Version 1.1 by Virginia Tech) were used. To choose appropriate tests advice from the following literature was taken:

Univariate methods:

- Biostatistical Analysis by Zar (1996)

Multivariate methods:

- Using multivariate statistics by Tabachnick and Fidell (2001)
- Primer v5: User manual by Clarke and Gorley (1994)
- Data analysis in community and landscape ecology by Jongmann et al. (1987)
- Multivariate Analysemethoden by Backhaus et al. (1996)
- Canonical correspondence analysis and related multivariate methods in aquatic ecology by ter Braak and Verdonschot (1995)
- Multivariate analysis in community ecology by Gauch (1994)

2.3.1 *Data preparation*

In preparation for statistical testing all data sets were tested with Shapiro Wilke's W test for normality. According to the results non-parametric test were chosen almost exclusively for further investigations.

In some cases data were transformed for normalisation, they were always indicated in the text and in the graph/table descriptions.

In many cases the variables included into the analysis were reduced to the most abundant taxa/species in order to improve the analysis by using only significant data. Those reductions (e.g. species with > 10 individuals or > 30 individuals) are also indicated in the text and at the graph/table descriptions.

The following tests were used:

2.3.2 Univariate statistical methods

- *Kruskal-Wallis test*
- *Mann-Whitney U-test*. In case several U-tests were used as posteriori tests of a Kruskal-Wallis test, the probability for incorrectly rejecting H_0 increases with every test. Hence, a Bonferroni Correction was used to decrease α appropriately:

$$\alpha = 0.05 / (\text{number of U-tests applied})$$

- *Spearman Rank Correlation Analysis*. In general, correlations were only assumed to be considerable if $R > 0.5$, regardless of their significance indicated by the p-value.
- *Contingency tables*. Only observed data were used, no data standardizations are allowed with this test. If the expected frequency values calculated for the data were frequently < 5 , the procedure could not be applied since Contingency tables do not perform well with such low values.

2.3.3 Multivariate statistical methods/Ordination

Ordination is a collective term for multivariate statistical methods which arrange plots along axes on the basis of species compositions (Jongmann et al. 1987). Each axis represents the presence of one species and the plots are arranged in this “species-dimensional” space according to their species assemblages. The aim is, to reduce this multidimensional space into only few dimensions with as little information loss as possible, to be able to illustrate plot similarities in a diagram. In this diagram, the distance between plots (within ideally only two dimensions) represents their dissimilarity concerning their species assemblage. The further plots are located away from each other, the more dissimilar are they. In general, Ordination is not restricted to plots in a “species-dimensional” space, but can also be applied with species in a “plot-dimensional” space.

Ordination techniques are performed in two steps: In the first step a similarity matrix of the plots is calculated with the use of a similarity index. The similarity index has to be chosen depending on the kind of data used. In this study in most cases a Bray-Curtis similarity index used on transformed data was chosen as proposed by Clarke and Gorley (1994). In this way, all species contribute to some extent to the definition of similarity, but commoner species are generally given greater weight than rare ones.

In a second step this matrix will be reduced in dimensions. This can be done in several ways which depend on the ordination technique used. Following ordination methods were employed in this study:

MDS-plots

Since this technique depends only on the rank order of the data, normality is not essential for this procedure (Clarke and Gorley 1994). Nevertheless abundance data were transformed (\sqrt{x} - or log-transformed) to downweight the influence of the abundant species before computing the Bray-Curtis similarities. Based on the similarity matrix, Euclidian distances between the plots are calculated and presented in a 2-dimensional diagram. The nearer plots are to each other, the more similar are their species assemblages. The quality of the diagram depends on the information loss during the calculation procedure. It is reflected in the stress value. If this value is <0.05 , the representation is excellent, if it is < 0.2 the ordination is good and if it is >0.2 the distances at the diagram are not very reliable (Clarke and Gorley 1994).

Cluster analysis

Cluster analyses use similarity matrices to find “groupings” of samples such that samples within groups are more similar to each other than samples of different groups. There are several clustering methods which differ in their ease to group plots together according to their similarity. In this study the group-average-linkage was always chosen, as a method which produces medium sized clusters in general, as recommended by Clarke and Gorley (1994). The resulting groups are presented in a dendrogram. In contrast to the continuous scale of MDS plots, Cluster analyses always form discrete clusters. In this study, Cluster analyses and MDS plots were normally applied and interpreted together to detect abrupt as well as continuous changes of the data.

To identify faunistic (benthic) zones in chapter 3.2.4 also a Cluster analysis was performed. In this case the analysis was based not on transformed abundances but on untransformed ranks of the benthic species. For this each individual species got a rank number according to its abundance at each plot and month. This ranks were substituted by scores, rank 1 received 10 points, rank 2 got 9 points, rank 3 got only 8 points and so on. These scores were summed for the species on each plot for the total investigation period. The Cluster analysis was performed on these sums, using a Bray-Curtis similarity index. The resulting cluster represent groups of similar plots according to their ranked benthic assemblages over the complete study period.

Principal Components analysis (PCA)

The Principal Components analysis, or Redundancy Analysis, is an ordination technique with an implied Euclidian distance. Here, a line is laid in the cluster of species points in the multidimensional space. This line is fitted by minimizing the sum of residuals of the points scattered around it. It represents the first principal component and explains most of the plots variability. The second component will be located perpendicularly to the first one and accounts for the variability not explained by the first component. There is also no need for the data to be normally distributed, however, it should not be clumped. This is the reason why

the data is generally normalized and in this study all data was transformed to normalize it as much as possible. In general, only “meaningful” species should be included since other species only increase the “noise” and decrease the value of the analysis.

The PCA-diagram shows the slope of the species in relation to the principal component as species scores (points). Since the environmental variables have a linear relationship to the components, they are exposed as arrows. They point into the direction of their strongest increase. The species points can be extracted perpendicular on the arrows, to determine their preferred intensity of that variable.

In chapter 4.2.4 this analysis was performed to describe the bird species in their microhabitat environment resembling an approach conducted by Holmes et al. (1979). There, not plots but variables expressing the microhabitats use were applied with the amount of birds found within this microhabitats expressed as proportions. Within the resulting PCA-diagram the Euclidian distances between the species scores were calculated and described in a dendrogram. Guilds were defined as those groups which were separated by more than the mean Euclidian distance. They can be located in the PCA diagram and described by their position in relation to the microhabitat variables.

Canonical Correspondence analysis (CCA)

The CCA is a special form of Correspondence analysis. The Correspondence analysis is an ordination technique with an already implied dissimilarity index, the chi-square distance. There is no need for the data to be normally distributed, but the abundance data of birds or benthos organisms were generally log-transformed to give the more abundant species more weight. Species/plot abundance data can be presented by its preferred occurrence on an environmental variable. The wider the species/plots are “spread out” on this variable, the better it explains their distribution. A CA defines a theoretical variable which maximizes the spread with the use of a method called “reciprocal averaging”. The resulting variable is termed first ordination axis or eigenvector. The second eigenvector can be calculated in the same way but it is not correlated with the first axis, thus corresponds with a so far not explained variation of the data. Each eigenvector has an eigenvalue which represents the (maximized) dispersion of the data, hence it is a measure of the explanatory value of the axes. They lie between 0 and 1. Ordination axes are thought to be good separators if their eigenvalue is > 0.5 . While within a CA a theoretical variable is calculated to maximize the dispersion between species/plot points, the CCA uses a combination of environmental factors to generate this effect. If a CA has a high Multiple Correlation Coefficient, which indicates a high correlation between included environmental factors and axes, it becomes very similar to a CCA performed on the same data. Here as well the sum of eigenvalues is an indicator of the explained variance by the model. In chapter 5.2.3 these sum of eigenvalues were used to identify the best performing model.

Multiple Regression analysis

A Multiple Regression analysis is a popular technique to investigate the relationship between one dependent variable and various independent variables. It is assumed that all variables and their combinations have to be normally distributed. Results might be strongly altered if multicollinearity occurs, the correlation between independent variables. There are several techniques to decide which of all possible independent variables have to be included in the analysis in order to reject all insignificant information. In this study always a stepwise forward selection was chosen, a technique which adds the variables one by one until all variables are included which have a significant effect on the dependent variable. R^2 indicates the explanatory value of the regression, which was also used in chapter 5.2.3 to decide which model is most appropriate.

3 The tropical tidal flats – environmental conditions and the benthic community

3.1 Introduction

What kind of habitat do the migrating waders find when they reach the coast of the Bragantinian peninsula?

The quality of a foraging habitat is predominantly determined by the food stock available. Which *prey organisms* can be found? In what quantities (*abundances* and *biomasses*) do they occur and how predictable are they? Exemplary for tropical sites some detailed studies on prey abundance and variability were done at Roebuck Bay, Australia (Pepping 1999; de Goeij et al. 2003) and at the Banc d'Arguin, Mauritania (Altenburg et al. 1982; Wolff et al. 1993a).

Benthic organisms are strongly influenced by environmental characteristics. Quantity of organic material, grain size of the *sediment*, *salinity* and *inundation time* are thought to be central factors for occurrence and densities of benthic organisms (Alongi 1990; Little 2000). Thus, these factors have to be studied in the first place, to investigate their influence on the benthic community and on the avian community. Beside this aspect sediment grain sizes and salinities might have also a direct impact on the birds, as will be discussed in chapter 4. Sediment contents of organic material were not sampled in this study, however, Dittmar (1999) and Acheampong (2001) collected such data at the Bragantinian peninsula and their results will be discussed as well in context to the data obtained in this study.

A further aspect is the accessibility of potential prey organisms, which is addressed in this chapter by investigations of the *depth distribution* of benthic organisms. Not every prey item can be reached by birds with short bills. Several investigations recognized and described the importance of the depth distribution of the prey organisms (Myers et al. 1980; Myers 1984; Zwarts and Blomert 1992; Zwarts and Wanink 1993). These aspects together, the abundance of prey organisms, its spatial and temporal variability and its accessibility will provide a fairly good idea about the prey source waders will find in the area.

3.2 Results

3.2.1 Sediment

The sediment conditions at the intertidal differed between sampling sites, samples ranged from soft mud to compact sand. However, the sample grain size medians ranged merely between 2.76Φ – 4.41Φ (Fig. 8). Although the differences were not as pronounced as expected, they still reflected the observed variability. For detailed results also on quartile deviation and sorting coefficients see Appendix II, Table 27.

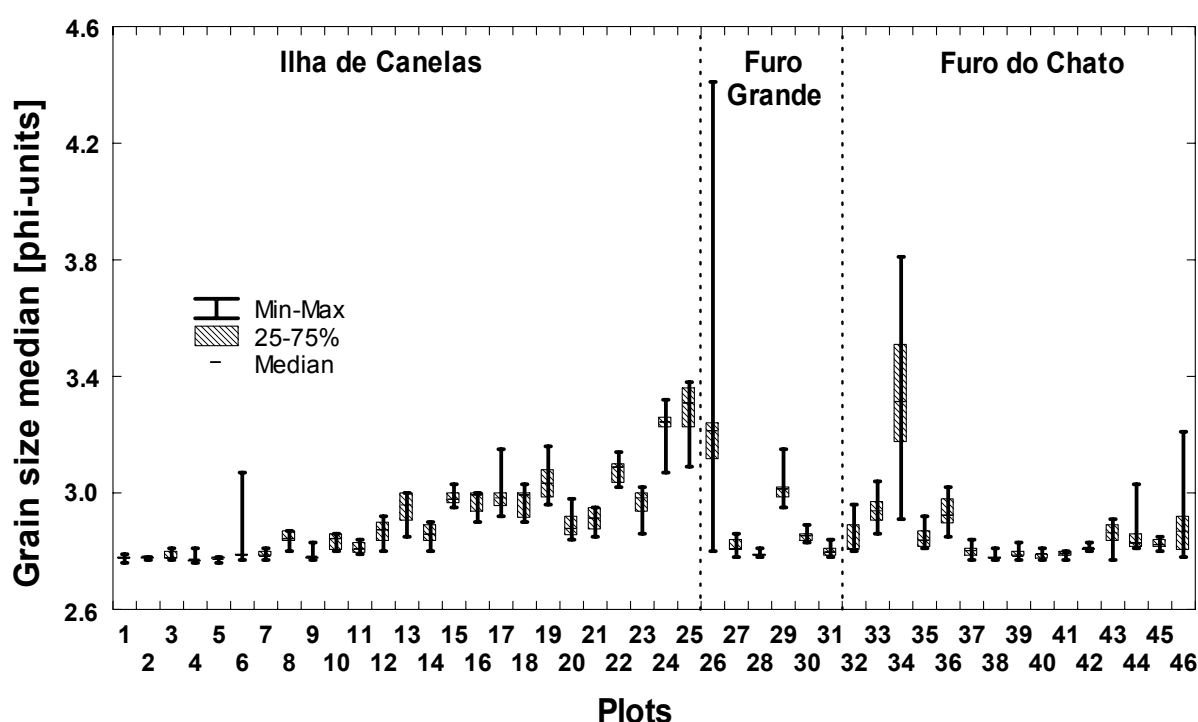


Fig. 8. Sediment conditions of the study area. Given are the grain size medians obtained at the 46 plots between January and June 2001.

During the sampling, the impression occurred that sediment conditions changed very quickly between succeeding months. This held true only for the muddier plots, the sandy sites were comparatively stable (Fig. 8). Especially the conditions of the plots close to the mangrove trees (plots 26 and 34) were strongly altered over the course of time. The sediment of all three sampling sites ranged between muddy and sandy, hence the sampling sites (Canelas, Furo Grande and Furo do Chato) were not associated with specific sediment conditions.

In 2002 the sediment ranged between 2.77Φ – 3.12Φ at Canelas which is well within the range of the Canelas plots in 2001. A Mann-Whitney U-test detected no significant difference between the years ($U=1385.5$, $Z=1.77$, $p=0.076$; $n(2001)=275$, $n(2002)=24$).

When Spearman Rank Correlation analysis between median grain sizes and benthic abundances were performed, significant differences were found, but the obtained R indicated no considerable relationship (Appendix II, Table 28). Thus, no direct association between the benthic abundances and the sediment parameters was found.

3.2.2 Salinity

The salinity of the estuary ranged between 15-38‰, indicating a strong variability. A distinct seasonal slope from January to April was due to strong rains which are typical for the time of the rainy season in this area. Most plots resembled each other in their pore water salinity, as indicated by the narrow range of the quartiles in Fig. 9. Only few plots had a much higher or lower salinity but this deviations could not be linked to any factor (sampling site, distance to tidal creeks, sediment conditions).

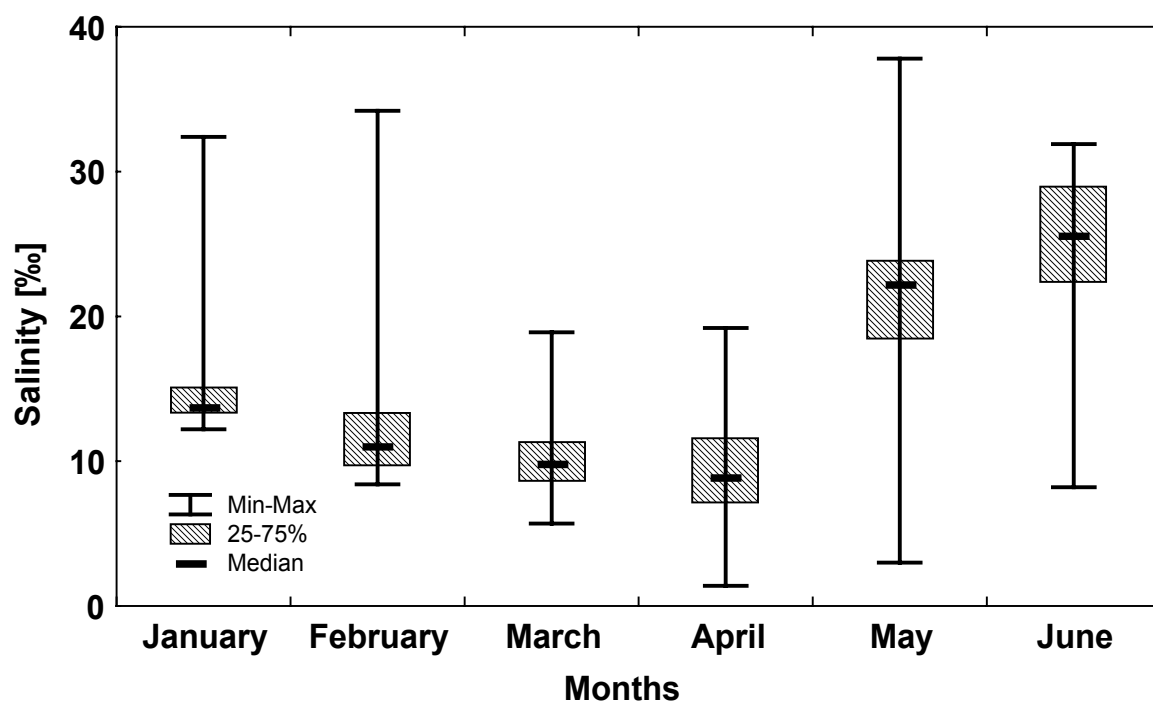


Fig. 9. Pore water salinity of the sediment at the study area. Given are the salinities obtained at the plots between January and July 2001.

Based on the data taken at each plot in 2001, Spearman Rank Correlations were performed to investigate the relationship between salinity and median grain size as well as salinity and mean water coverage of the plots. Although both tests found significant correlations, the low R indicated no substantial relationship (salinity-median grain size: $R=-0.127$, $t=-2.116$, $p=0.045$; salinity-mean water coverage: $R=0.163$, $t=2.717$, $p=0.007$; both $n=274$).

Unlike the sediment conditions, salinity samples were significant higher in 2002 than in 2001 (mean: 24,2‰ and 15,4‰ respectively) (Mann-Whitney U-test: $U=1148.5$, $Z=-5.297$,

$p < 0.001$; $n(2001) = 275$, $n(2002) = 24$). Spearman Rank Correlations were also found to be significant between some benthic abundances and salinity, but again, the low R indicated no substantial relationship (Appendix II, Table 28).

3.2.3 *Time of emergence*

The “time of emergence” is defined as the time when the intertidal was not inundated and could be used by the avian community for foraging. At the Ilha de Canelas this time period ranged between 3 h 39 min and 4 h 59 min, depending on the plot location. Spearman Rank Correlations were done between benthic abundances and time of emergence and – though significant – no substantial R was found (Appendix II, Table 28).

3.2.4 *The macrobenthic community – availability of prey organisms for the birds*

Taxonomic composition

Overall 55 different benthic taxa were found and distinguished at the Bragantinian mudflats (Appendix II, Table 29). They were dominated by polychaetes (20 taxa) and crustaceans (18 taxa), which provided together 70% of all taxa. Since they could not be identified to species level, true species numbers would certainly be higher for these groups with a more intensive identification effort. In this regard the two minor groups of bivalves (9 taxa) and gastropods (3 taxa), which were identified mostly to species level, are even more marginal (Fig. 10).

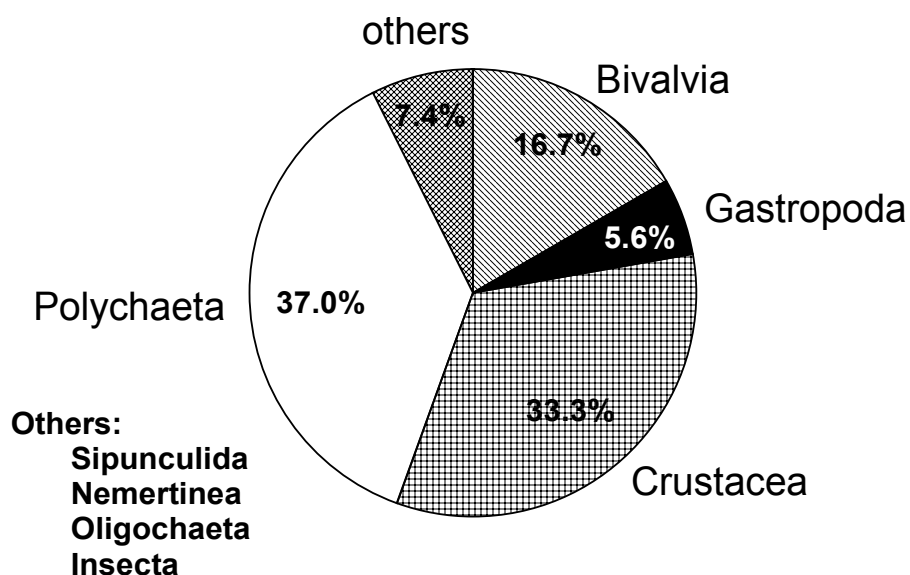


Fig. 10. Taxonomic composition of the benthos at the study area. Given is the proportional contribution of the benthic groups to the total number of individuals found in 2001.

Most taxa were found at the Ilha de Canelas and particularly polychaetes and crustaceans were present with various species at the island. The other habitats always had fewer taxa,

with emphasis on crustacean taxa at the Furo Grande and on polychaete taxa at the Furo do Chato (Appendix II, Table 29).

Total abundances

In 2001 the total benthic abundances of the samples varied between 0-677 individuals/m² with only a slight seasonality. The mean abundances of all 46 plots were highest in January with 239 ± 135 individuals/m² and lowest in February with 167 ± 87 individuals/m², resulting into a drop of 30 % of the standing crop. Even though mean benthic abundances were found to differ significantly between the months (Kruskal-Wallis test: $H=12.197$, $p=0.032$), pair wise comparisons did not detect significant changes (Mann-Whitney U tests with Bonferroni-Correction: $\alpha=0.05/15=0.003$) (Fig. 12). Over the course of time the total benthic abundances of the entire study area were fairly stable.

The total benthic abundances were higher in 2002 than in 2001 (Mann-Whitney U test between all benthic samples obtained at the Ilha de Canelas in 2001 and 2002: $U=867.500$, $Z=-4.296$, $p<0.001$).

Far more pronounced than the temporal variability were the differences between the plots. The spatial variability of mean benthic densities was very strong with large ranges at all three sampling sites (Canelas: 20-557 individuals/m², Furo Grande: 0-637 individuals/m², Furo do Chato: 20-677 individuals/m²) (Fig. 30). Also, within each plot a strong temporal variability occurred as indicated by the large ranges and quartiles at Fig. 30. Thus, the densities of the macrobenthos gave a highly variable picture if considered on a smaller spatial scale.

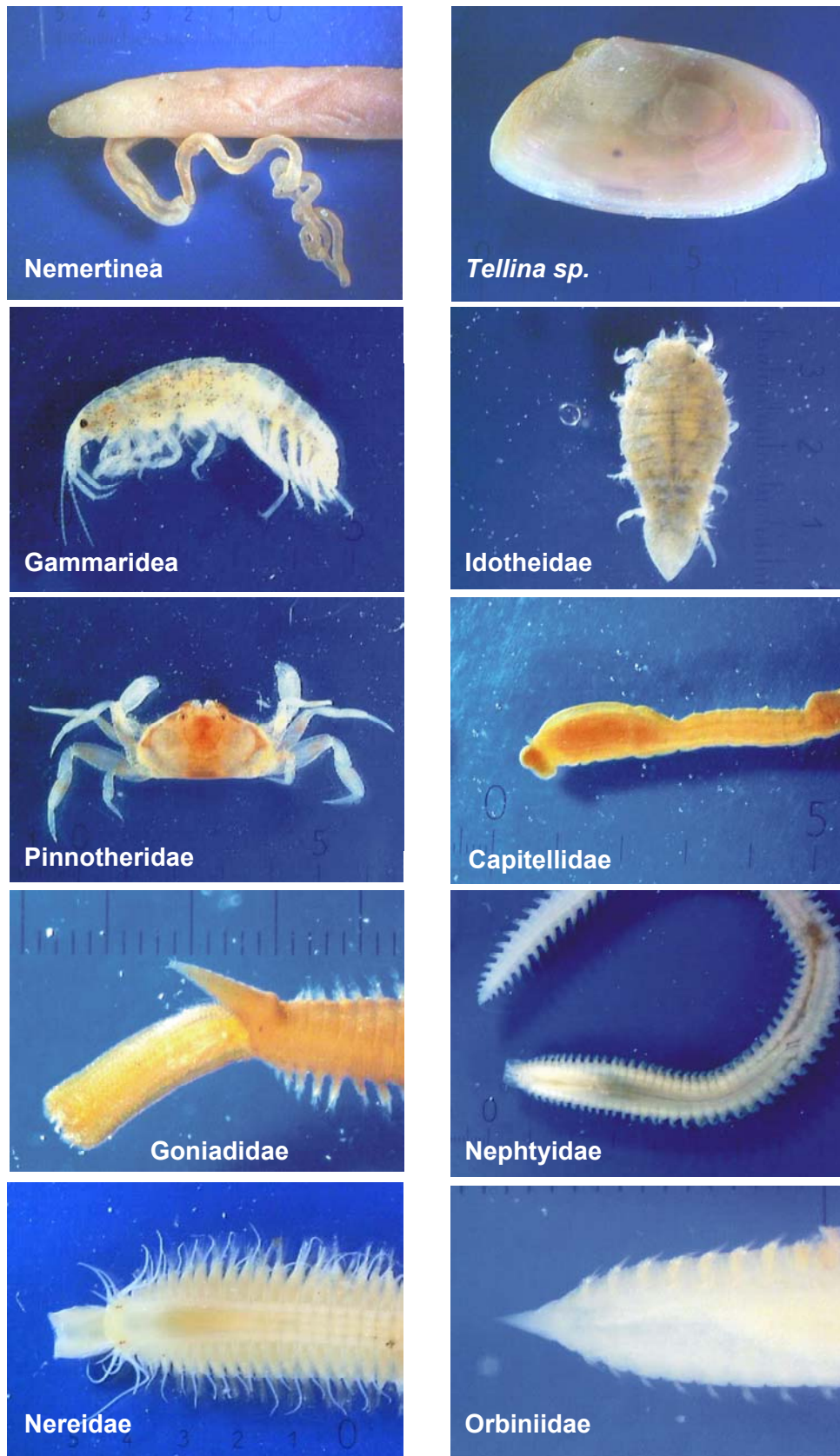


Fig. 11. The ten most abundant benthic groups at the study area.

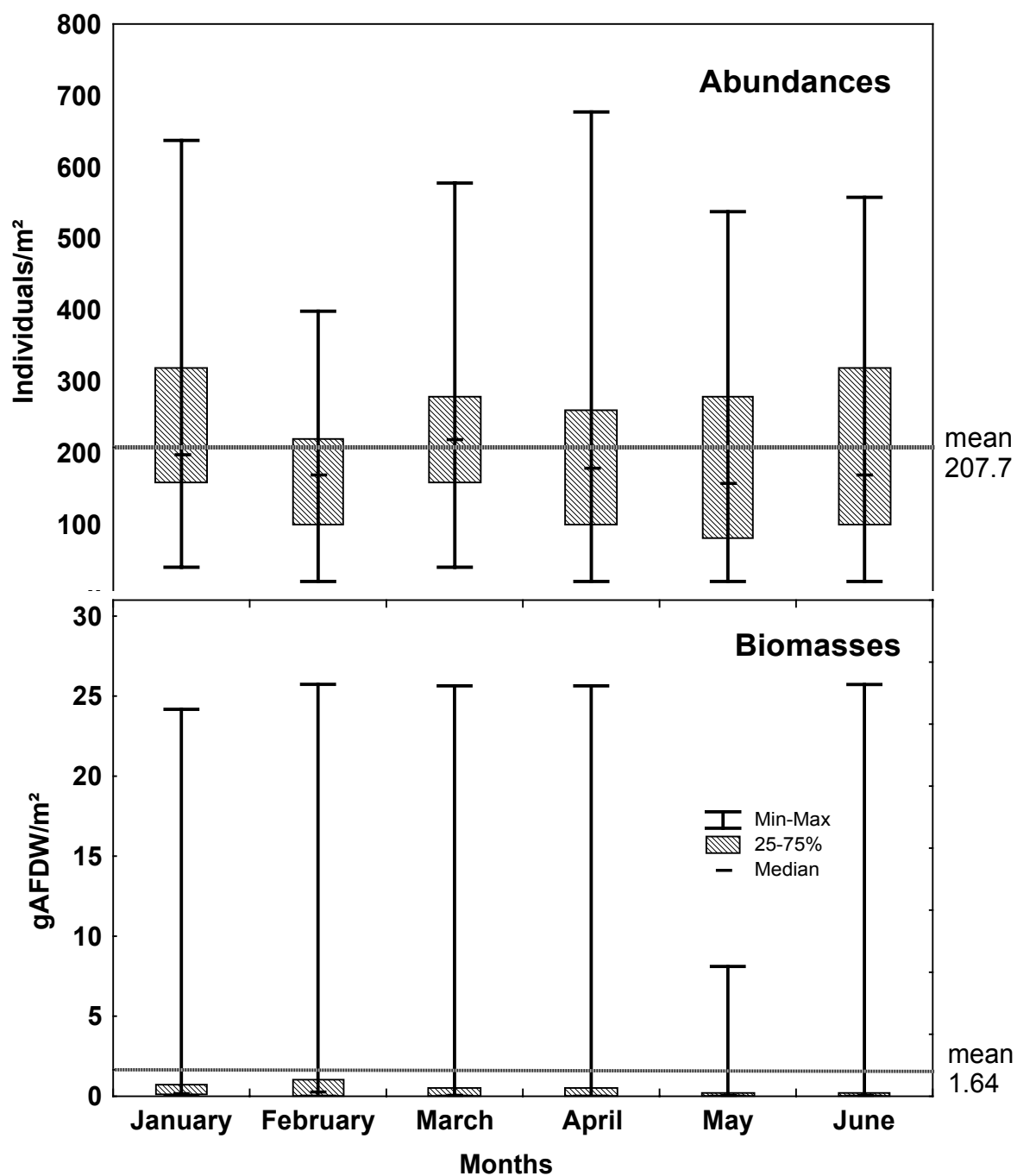


Fig. 12. Abundance and biomass of the benthos in the study area. Given is the range over the 46 plots between January and June 2001.

Abundances of taxonomic groups

Polychaeta and Crustaceans were the most abundant groups, with 59 % and 26 % of all individuals found (Fig. 13).

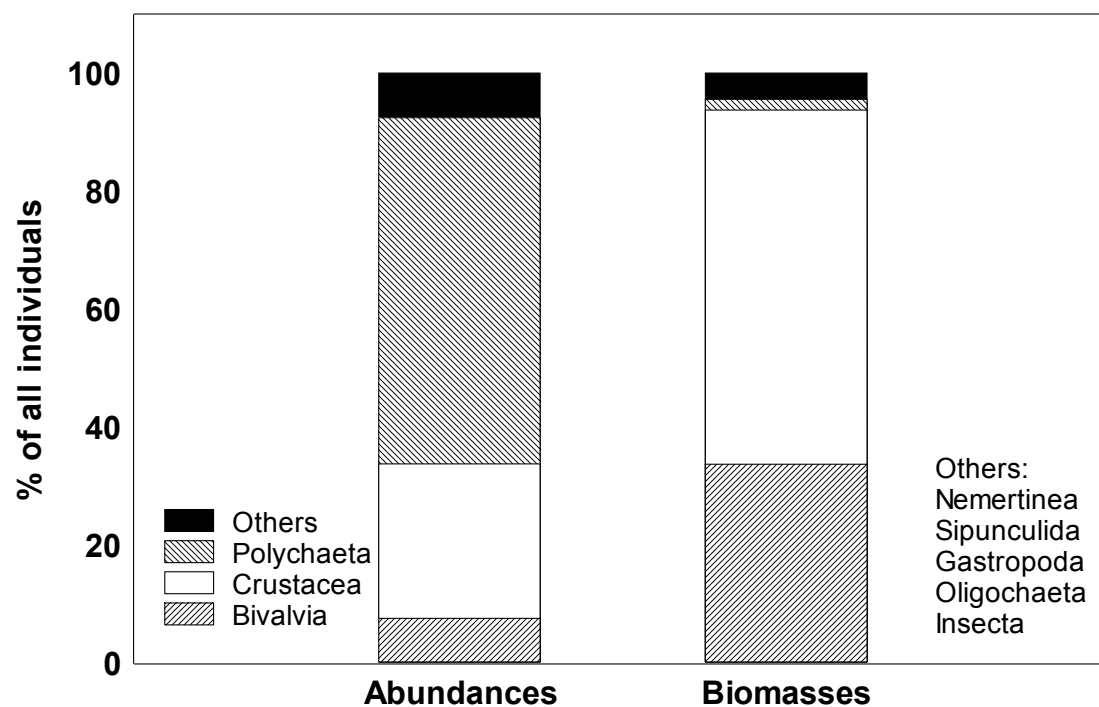


Fig. 13. Proportional contribution of the benthic groups to abundances and biomasses of the benthos in 2001.

During the study period the total abundance of the groups remained remarkable stable. Only bivalves and gastropods showed significant changes over the course of time. Bivalve abundances decreased steadily with significant differences between January and April, May and June (Mann-Whitney U-test with Bonferroni-Correction of $\alpha=0.05/15=0.003$: January-April: $Z=3.713$, $p<0.001$; January-May: $Z=3.584$, $p<0.001$; January-June: $Z=4.010$, $p<0.001$). The abundances of crustaceans showed a minimum number of abundance in April with significant differences between January-February (Mann-Whitney U-test with Bonferroni-Correction of $\alpha=0.05/15=0.003$: $Z=3.182$, $p=0.001$), January-March ($Z=3.569$, $p<0.001$) and January-April ($Z=3.764$, $p<0.001$) (Fig. 14).

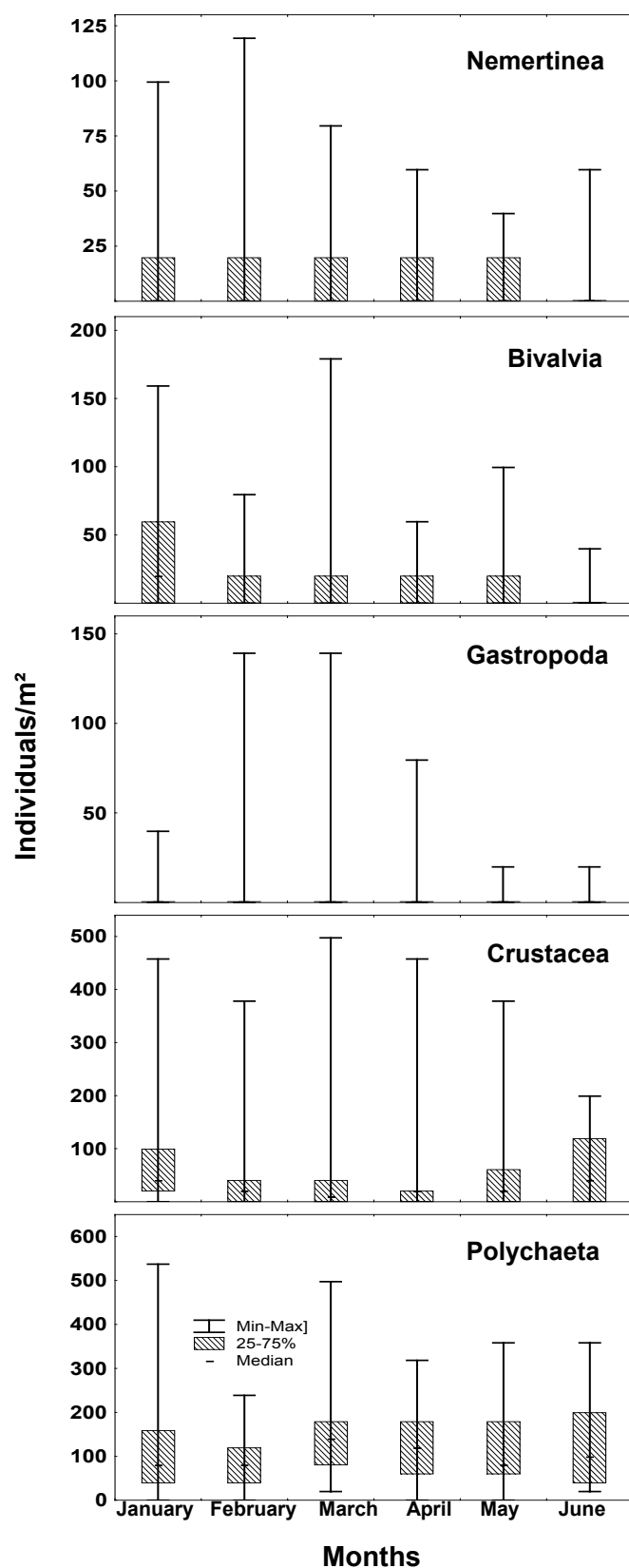


Fig. 14. Abundances of the benthic groups at the study area. Given is the range of the 46 plots between January and June 2001.

The lower benthic taxa were far more variable. Abundances and biomasses of individual benthic taxa are described in detail at Appendix II (Table 29).

In 2002 the composition of the benthic groups changed significantly in comparison to 2001 (Contingency table: $\chi^2=918.086$, $v=5$, $p<0.001$), though the dominance of the two major groups was maintained (Polychaeta: 47 %, Crustacea: 33 %) (Appendix II, Table 25). When the mean plot densities of the benthos taxa were compared between 2001 and 2002, it showed that only the Pinnotheridae (Crustaceans) had significantly higher densities from February to May in 2002 (Appendix II, Table 30).

Total Biomasses

Because of the diversity of the benthic taxa in size and weight categories, the biomasses showed a very different picture compared to the abundances. The AFDW ranged between 0.5 mg (only Polychaeta) up to 25.6 g (large Crustacea) per individual. Very large values were rare and belonged exclusively to crustaceans and bivalves.

The biomass samples from 2001 varied between 0-25.7 gAFDW/m² (Fig. 12). The monthly mean of all plots ranged between 2.3 gAFDW/m² (March) and 0.5 gAFDW/m² (May) and showed hardly any seasonal trend. The differences between the plots were very large, but constant between the months (Min: <0.1 gAFDW/m², Max: 24.2-25.7 gAFDW/m²). In May a strongly reduced range was recorded (Min: <0.1 gAFDW/m², Max: 8.1 gAFDW/m²). Like the abundances, biomasses proved to differ significantly between the months (Kruskal-Wallis Test: $H=14.060$, $p=0.015$), though no significant differences between specific pairings were found (Mann-Whitney U test with Bonferroni-Correction: $\alpha=0.05/15=0.003$).

A Mann-Whitney U test found no significant difference between the mean biomass values of the plots of 2001 and 2002.

The spatial variability was also very high within each sampling site. While most plots had low biomasses, only few plots showed a large range, indicating at least in some months extraordinary high biomass values (Fig. 31).

Table 2. Ranking of the benthos taxa according to their biomass and abundance values. Given are the monthly ranks and the mean values of abundance [individuals/m²] and biomass [mgAFDW/m²] (in brackets) obtained at all 46 plots in 2001.

Taxon	Mean abundances [individuals/m ²]						Mean biomasses [mgAFDW/m ²]					
	January	February	March	April	May	June	January	February	March	April	May	June
Sipunculida			8 (6.1)	6 (5.6)		10 (3.5)						
Nemertinea	7. (10.4)	4 (11.3)	4 (10.0)	5 (8.7)	6 (6.5)	7 (5.6)						
Bivalvia												
<i>Anomalocardia brasiliiana</i>							1 (659.6)	3 (353.3)				
<i>Lucina pectinata</i>				10 (3.0)	7 (4.3)					10 (5.7)	8 (8.8)	
<i>Protothaca pectorina</i>							4 (135.3)		5 (137.6)	3 (159.0)	1 (175.0)	
<i>Tagelus plebeius</i>	1 (6.5)		10 (3.9)				2 (402.1)	2 (496.1)	3 (275.1)	4 (149.4)	2 (141.7)	
<i>Tellina lineata</i>								6 (71.2)				
<i>Tellina radiata</i>	4 (20.8)	8 (7.4)	6 (6.9)	8 (4.3)	10 (3.5)	6 (7.8)	10 (12.5)	9 (25.8)	7 (13.8)	8 (12.7)		7 (12.6)
Gastropoda												
<i>Nassarius vibrex</i>			8 (6.1)	10 (3.0)			6 (71.1)	5 (97.8)	4 (140.4)	5 (64.9)	4 (21.4)	
<i>Natica nyarochiensis</i>												10 (3.6)
Crustacea												
Callianassidae						8.5 (4.3)	3 (264.1)	1 (927.4)	1 (1315.5)	1 (918.0)		1 (1049.0)
Copepoda	1 (6.5)											
Decapoda							7 (66.0)	7 (43.1)	6 (85.9)			
Gammaridea	2 (29.0)	2 (26.8)	2 (35.9)	2 (27.3)	3 (18.6)	5 (9.1)					10 (5.8)	6 (13.5)
Hippolytidae											6 (16.9)	
Idotheidae			7 (6.5)	4 (10.0)	10 (3.5)	8.5 (4.3)	9 (17.0)	10 (23.9)				
Mysidae					8 (3.9)			8 (26.1)		6 (56.7)	3 (53.1)	4 (24.0)
Pinnotheridae	3 (24.7)	9 (6.9)			4 (13.9)	2 (39.0)	8 (32.5)		10 (10.4)			3 (30.3)
Stomatopoda											5 (19.1)	
<i>Uca maracoani</i>				10 (3.0)			5 (84.6)	4 (100.2)	2 (286.8)	2 (194.7)		2 (87.7)
Polychaeta												
Capitellidae	5 (19.0)	5 (8.7)	3 (18.2)	3 (16.4)	2 (26.4)	3 (32.5)						
Goniadidae	9 (8.7)	6.5 (7.8)	10 (3.9)						9 (10.4)	9 (6.1)	9 (6.2)	8 (10.9)
Lumbrineridae	1 (6.5)											
Nephtyidae	1 (41.1)	1 (39.0)	1 (101.3)	1 (89.6)	1 (77.5)	1 (77.5)						
Nereidae	7. (10.4)	6.5 (7.8)	5 (7.8)	7 (5.2)	5 (7.8)	4 (13.9)			8 (13.1)	7 (15.4)	7 (15.0)	5 (16.1)
Opheliidae					10 (3.5)							9 (5.8)
Orbiniidae	6 (14.7)	3 (13.0)										
PilargiidaeB		10 (6.1)										

Biomasses of taxonomic groups

The two groups contributing most to the benthic biomasses were crustaceans with 60% and bivalves with 34% (Fig. 13). They were also dominant in 2002 (77% and 19%), however, a test with a Contingency table was not possible.

Together bivalves and crustaceans were responsible for more than 90% of the total biomass in each month in 2001. But while bivalves were the most important biomass contributors in January and May (both 67% of the total biomass), crustaceans dominated from February-April and in June (between 51% in February and 96% in June). Kruskal-Wallis tests showed that only these two groups differed significantly in their biomass contributions over the months in 2001. While bivalves decreased steadily and showed significant differences between January and April, May and June (Mann-Whitney U-test test with Bonferroni-Correction: $\alpha=0.05/15=0.003$; January-April: $U=643$, $Z=2.982$, $p=0.003$, January-May: $U=638.5$, $Z=3.147$, $p=0.002$ and January-June: $U=493.5$, $Z=4.298$, $p<0.001$), crustaceans reached a maximum in their biomasses in March with significant differences between January-March ($U=626.6$, $Z=2.983$, $p=0.003$) and January-April ($U=563.0$, $Z=3.627$, $p<0.001$).

The predominance of these groups was also reflected at the biomass ranking on lower taxonomic levels: higher ranks were always given to bivalve or crustacean taxa. Callianassidae (Crustacea) were the dominating group during most of the time, followed by *Uca maracoani* (Crustacea) and the bivalve *Tagelus plebeius* (Table 2).

Abundance vs. biomass

When densities and biomasses per individual of the prey species were plotted against each other, it appeared that most items had extremely low biomass values (Fig. 15). Only few had noticeably higher values (Callianassidae, *Uca maracoani*, *Tagelus plebeius*, *Nassarius vibrex*), all of them were molluscs or crustaceans. And all of them appeared in very low densities. On the other hand there were only some species which occurred in higher densities (Nephtyidae, Gammaridae, Capitellidae, Pinnotheridae), most of them were polychaetes and they had hardly any biomass. All other species were low in biomass and in density (Fig. 15).

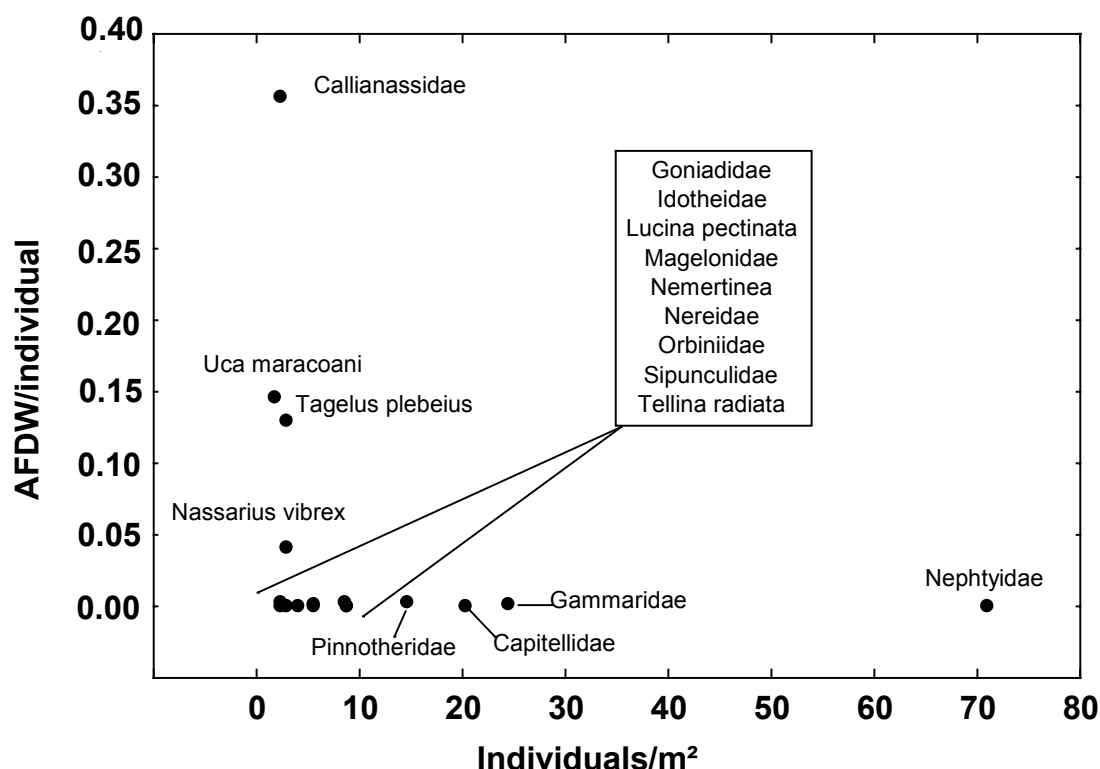


Fig. 15. Mean abundance vs. mean biomass of the benthic taxa in the study area in 2001. Only species with >30 individuals found were included.

Benthic assemblages

The plots differed significantly in the composition of their benthic groups (Contingency table: $\chi^2 = 1278.60$, $v=226$, $p<0.001$). At Fig. 16 groups of plots were roughly distinguishable from each other by sight according to their benthic assemblage:

At Canelas the plots 1-15 showed high abundances of polychaetes (mostly *Nephtyidae* with additionally *Capitellidae* at plots 7-15) with many crustaceans (in general exclusively *Pinnotheridae*), some bivalves (*Tellina radiata*) and *Nemertinea*. The main biomass source were crustaceans. The plots 16-25 had larger shares of bivalves (*Anomalocardia brasiliensis*, *Lucina pectinata*, *Tagelus plebeius* and *Tellina radiata*) and more *Nemertinea*. The groups contributing most to the biomasses were crustaceans or bivalves. Plot 23 was exceptional, with a large amount of gastropods and bivalves (Fig. 16, and Appendix II, Table 31). This was the plot with the highest biomass value, a result of high bivalve, crustacean and gastropod numbers.

Plot 26 was an outstanding plot at the Furo Grande, with large amounts of biomass from crustaceans (mostly *Uca maracoani*), bivalves (*Tagelus plebeius*) and high numbers of *Capitellidae*. The other plots were characterized by overall very low abundances and biomasses (Fig. 16, and Appendix II, Table 31).

At the Furo do Chato the plots 32-41 had high numbers of polychaetes (Nephtyidae, Nereidae and Orbiniidae) and only few bivalves (mostly *Tellina radiata*) and crustaceans (mostly Pinnotheridae). Plot 36 was the only plot with only little biomass. Plots 42-46 were outstanding with many small crustaceans (Gammaridea and Idotheidae) and with hardly any biomass (Fig. 16, and Appendix II, Table 31).

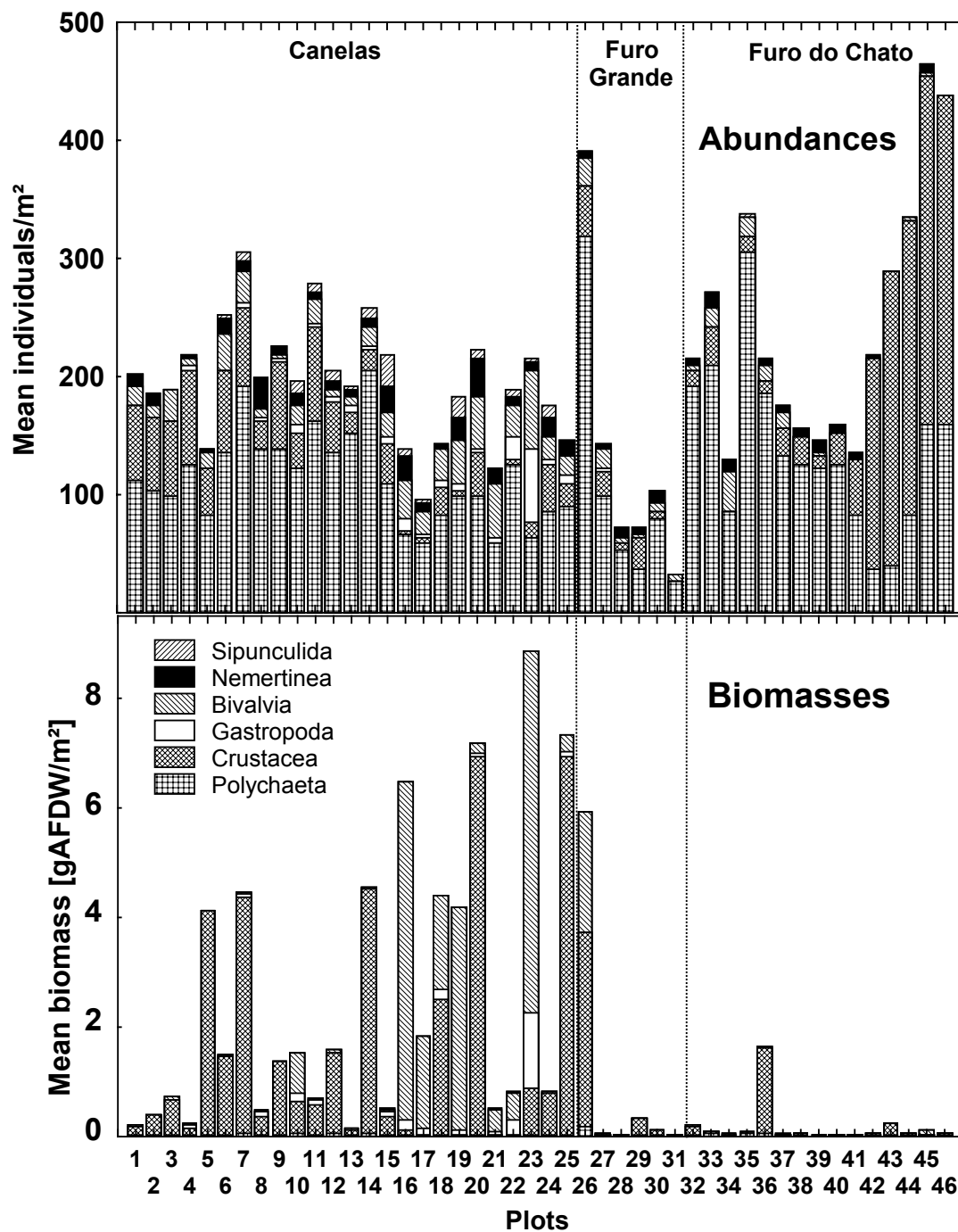


Fig. 16. Abundances and biomasses of the benthic taxa in the study area. Given are the monthly means of the data obtained at the 46 plots between January and Juli 2001.

The grouping of the plots in faunistic zones was difficult. MDS and Cluster analyses based on log-transformed abundance data did not reveal any group of plots which were similar in their benthic assemblage for longer than one month. It made no difference, if this was calculated with higher or lower taxonomic levels or with trophic groups of the benthos. The most successful attempt to separate faunistic zones was done by a Cluster analysis performed on ranked benthic abundances (Bray-Curtis similarity index on untransformed data; see chapter 2.3.3 for details on the calculation) (Fig. 17).

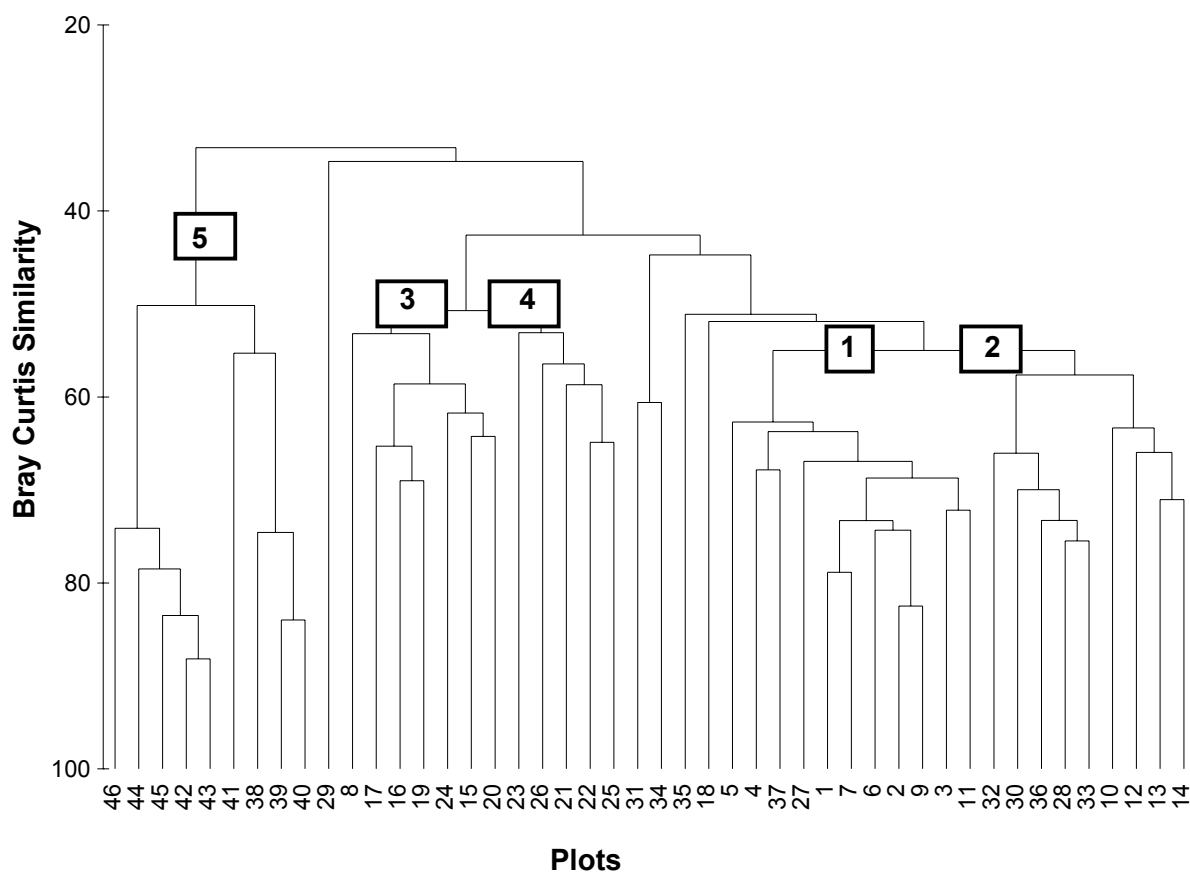


Fig. 17. Dendrogram indicating faunistic zones of the benthos in the study area. The Cluster analysis was based on ranks of benthic abundances at the different plots in 2001.

Five faunistic zones were distinguished. Although this structure did not remain absolutely stable over the course of time, some of the plot groups were recognizable at least in several months. They reflected also in parts the observations of plot similarities described above. For instance, the Nephtyidae-plots (1-15) at Canelas are roughly reflected in Zone 1 and 2 and the crustacean dominated plots of the Furo do Chato (42-46) are part of Zone 5. The zones can be described as follows:

Zone 1: A very sandy area (mean median particle size: 2.79Φ) with plots mostly situated at the Ilha de Canelas. The benthos was dominated by Nephtyidae and Pinnotheridae, at some times *Tellina radiata* was also numerous.

Zone 2: This slightly muddier area (mean: 2.87Φ) could be found in a group of Canelas plots, but also at some plots at the Furo Grande and the Furo do Chato. It was as well dominated by Nephtyidae together with some Capitellidae.

Zone 3: This zone was restricted to the Ilha de Canelas. The mean sediment grain size was finer than in Zone 2 (3.02Φ) and the benthos was dominated by Capitellidae, Nephtyidae and Nemertinea. High biomass values were found at some plots.

Zone 4: Only the muddiest plots of Canelas belonged to this zone (mean: 3.12Φ). It was dominated by Capitellidae and Nereidae and had in general very high biomasses.

Zone 5: This area was again very sandy (mean: 2.82Φ) but located only at the Furo do Chato. It was dominated - like the plots of the sandy zone 1 - by Nephtyidae and some crustaceans. In contrast to zone 1 crustaceans were not Pinnotheridae but Gammaridea and some Idotheidae and biomasses were extremely low.

While the total benthic abundances did not differ between the zones, the total biomasses showed significantly different values (Kruskal-Wallis test: $H=20.384$, $p<0.001$). The biomasses of zone 5 were significantly lower than that of zone 1, 2 and the biomass rich zone 4 (Mann-Whitney U test with Bonferroni-Correction: $\alpha=0.05/15=0.003$, Zones 5-1: $U=10.000$, $Z=3.001$, $p=0.003$; Zones 5-3: $U=0.000$, $Z=3.334$, $p=0.001$; Zones 5-4: $U=0.000$, $Z=3.000$, $p=0.003$).

Although benthic abundances did not show significant differences between the zones, the appearance of benthic assemblages was quite different (Appendix II, Fig. 40) and the zones differed significantly in their sediment conditions (Kruskal-Wallis test on the median grain sizes of the plots: $H=30.293$, $p<0.001$; for details see Appendix II, Table 32). The three different sampling sites can not be distinguished by their benthic assemblages.

Vertical distribution

Overall, 68% of the 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.

The polychaetes concentrated their abundances in the uppermost layer, but their biomass was generally found in the top 10 cm (Table 3). When polychaete taxa were investigated separately, most were found predominantly in the top layer, only Orbiniidae and Opheliidae appeared to have a prevalence for the medium and bottom layer (Appendix II, Table 33).

Bivalves and crustaceans were most abundant in the upper layer, too. But in terms of biomasses the deepest layer of 10-20 cm was also important: 1/3 of the bivalve biomass and nearly 2/3 of the crustacean biomass was found there (Table 3). Of the bivalves the only taxon not preferring the upper layer was *Tagelus plebeius*, which was found predominantly in the bottom layer. Most crustaceans were found as well in the top layer (Decapoda, Gammaridea, Idotheidae, Mysidae, *Uca maracoani*), only few were found more often in the medium layer (Pinnotheridae, Callianassidae) (Appendix II, Table 33).

These depth distributions of the taxa were not stable over all investigated plots or the course of time. Investigations with Contingency tables found some significant spatial and temporal differences (Appendix II, Table 34). The spatial variability of the vertical distribution did not reveal any distinct pattern. But over the course of time two benthic taxa moved through the depth layers in an apparently ordered fashion: Capitellidae preferred in January the bottom layer but moved their preference further upwards until most of them were found in the top layer in June. Pinnotheridae resembled this pattern, but would remain in the median depth, not in the top layer, by the time of June.

Table 3. Proportional depth distribution of the benthic groups. Given are proportions of all individuals found in 2001.

Taxa	n	Abundances [%]			Biomasses [%]		
		0-5cm	5-10cm	10-20cm	0-5cm	5-10cm	10-20cm
Sipunculidae	40	90	10	0	98	2	0
Nemertinea	121	48	31	21	29	56	15
Bivalvia	219	62	21	16	48	18	34
Gastropoda	52	75	10	15	76	10	14
Crustacea	741	67	18	15	16	28	56
Polychaeta	1662	66	21	12	52	32	16

Size classes

Birds might select prey not only by its type but also because of its size. In the section “Abundance vs. biomass” it was found that individuals of only 4 benthic species reach considerable biomasses (Callanassidae, *Uca maracoani*, *Tagelus plebeius* and *Nassarius vibrex*), thus, a size selection might be advantageous and most pronounced especially in this species (Fig. 15). All of these species showed overall very low abundances (Appendix II, Table 29).

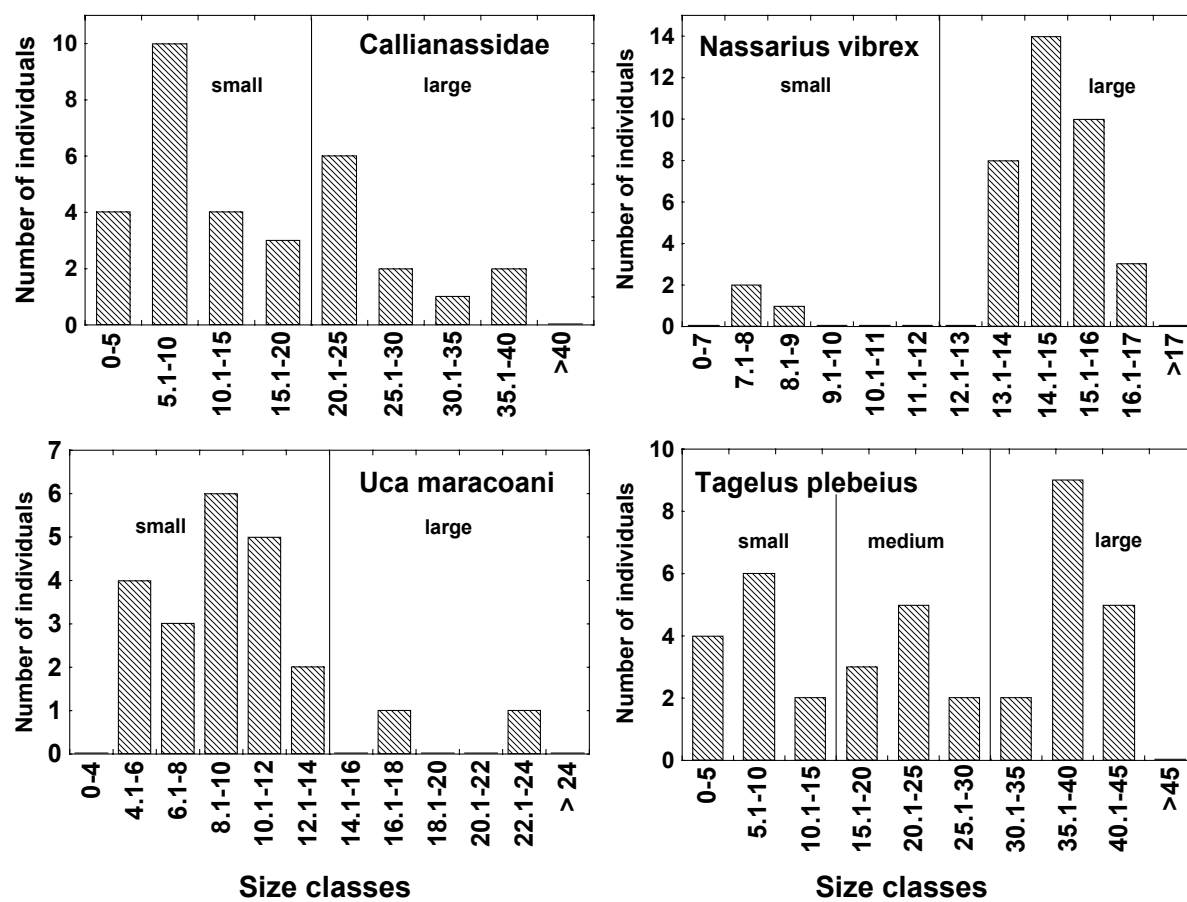


Fig. 18. Size classes of 4 benthic taxa obtained at the study area. Given are the numbers found in each size class of all individuals found in 2001.

Histograms of these 4 taxa showed that indeed distinct size differences occurred (Fig. 18). To examine the differences and changes in numerical abundances of large and small animals, the distribution was split (somewhat arbitrary) in different size classes (Fig. 18). *Callianassidae* showed two distinct classes, while *Tagelus plebeius* was split in three classes. On the contrary, most individuals of *Uca maracoani* and *Nassarius vibrex* belonged to one size class, only few individuals were larger (*Uca maracoani*) or smaller (*Nassarius vibrex*) than the majority.

When the vertical distribution of these taxa was investigated, it appeared that the taxa without distinct size categories (*Uca maracoani* and *Nassarius vibrex*) were comparatively evenly distributed throughout the sediment depths (Fig. 19), although *Uca maracoani* was not found deeper than 10 cm. Large *Callianassidae* were found mostly in 5-10 cm depth, while individuals of *Tagelus plebeius* were found in deeper layers, the larger they were (Fig. 19).

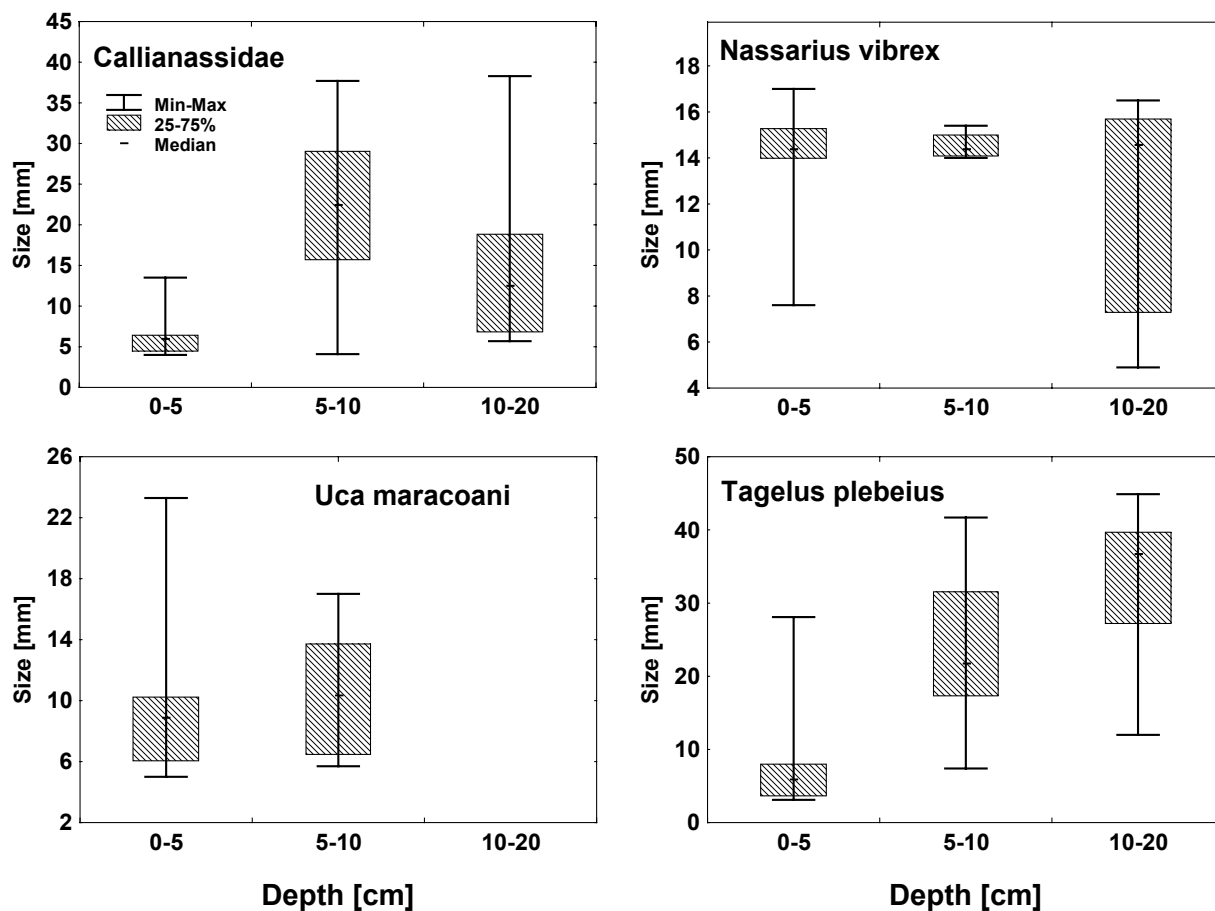


Fig. 19. Depth distributions of 4 benthic taxa obtained in the study area. Box-Whisker-plots are based on the sizes of all individuals found in 2001 in the different depth layers.

When the temporal development of the taxa was investigated, the size classes of *Tagelus plebeius* and *Nassarius vibrex* showed roughly similar appearances. While all three size classes of *Tagelus plebeius* decreased with time, both size classes of *Nassarius vibrex* showed a maximum in March and were (more or less) low at the beginning and the end of the investigation period (Fig. 20). But the temporal distributions of the size classes of *Callianassidae* and *Uca maracoani* showed differences. *Callianassidae* were generally very small in January and from April-June. Large individuals were more abundant in February and March and were indeed the only size category present during this time. Abundances of small *Uca maracoani* were extremely variable through the investigation period, but the large animals were found only during March and April (Fig. 20).

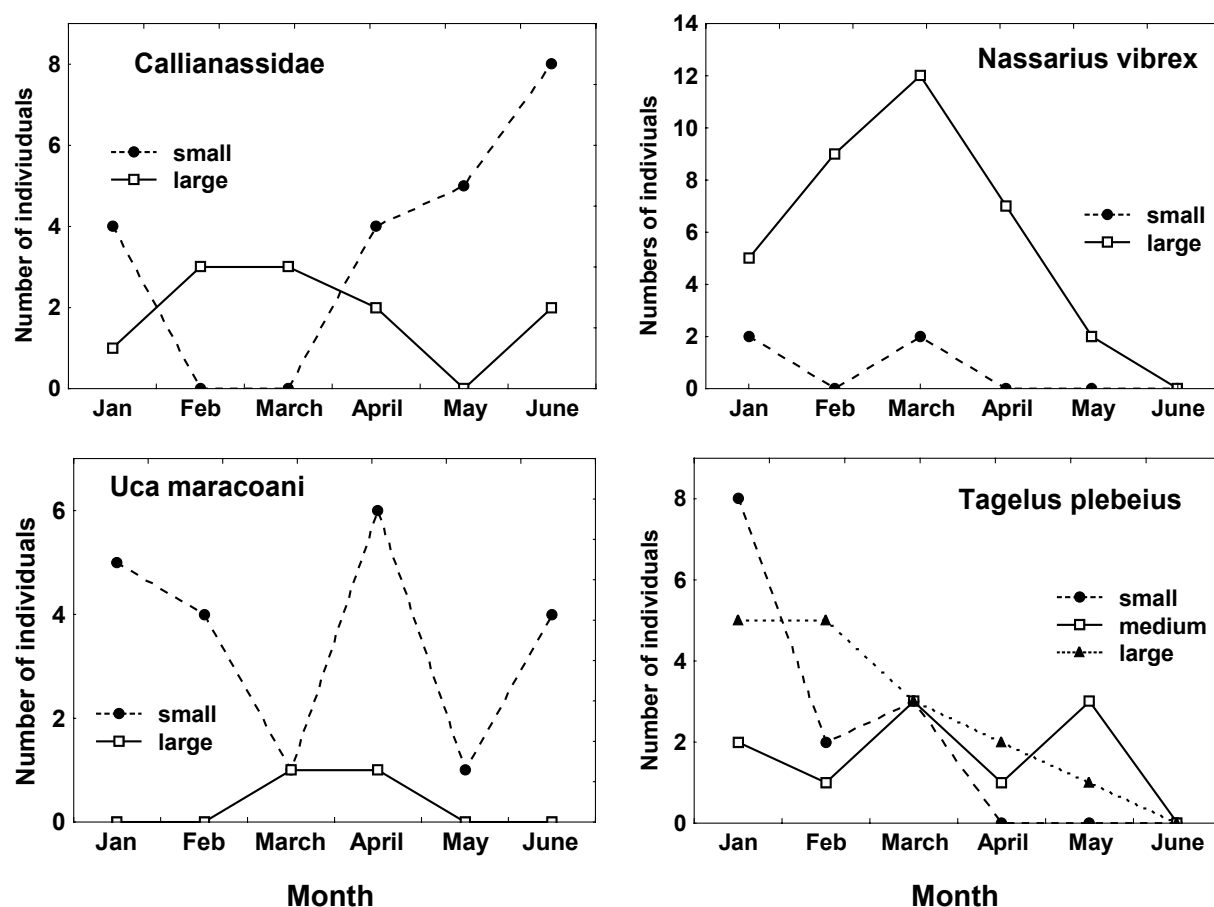


Fig. 20. Phenologies of the size classes of 4 benthic taxa obtained in the study area. Given are the total numbers found between January and June 2001 at the 46 plots.

3.3 Discussion

The environment

Mangrove forests play an essential role at many tropical coasts. They are a highly productive ecosystem with net primary production rates as high as 30 t C/ha/y (Clough 1998). A rich trophic net including invertebrates (crustaceans, molluscs and polychaetes) and vertebrates (fish, birds and small mammals) is supported by them. Dittmar (1999) showed at the Caeté estuary of the Bragantian peninsula that there is a strong outwelling of organic and inorganic material derived from litter decomposition out of the mangrove forest, even exceeding the riverine contribution of the estuary several times. While the dissolved organic material is object of long distance transport to marine habitats, an equal amount of particulate organic material is rapidly removed from the water column presumably due to sedimentation within the estuary and the coastal zones (Dittmar 1999; Dittmar et al. 2001). Hence, the Bragantian tidal flats should have a considerable input of particulate organic material derived from the mangrove forest. Acheampong (2001) measured the proportional

contents of Carbon and Nitrogen of the sediments at the sampling sites of the Furo Grande and the Ilha de Canela at the beginning of the wet season 2001. He found organic Carbon concentrations between 0.07-0.87% and organic Nitrogen values between <0.01- 0.06% of the sediment dry weight. They are variable, but in general very low in comparison to the Carbon and Nitrogen occurrences at other tropical intertidal areas. Alongi (1990) describes tropical sites with a range of organic Carbon between 0.04-13.4% and of organic Nitrogen between 0.01-2.17% (dry weight). Since the expected high organic contents are not found in the sediments of the sampling sites, parts of the organic material might have been washed out to further locations with the enhanced rains of the wet season. Thus, in contrast to initial assumptions, the benthic assemblage of the Bragantian tidal flats inhabits an intertidal with rather poor conditions concerning the Carbon/Nitrogen content of the sediment, at least during the onset of the wet season.

The sediment of the study area ranges from fine sand to fine mud, partly exhibiting heavy erosion (Krause and Glaser in press; Krause and Soares in press). Although the investigations on the median grain sizes do not resemble the impression of highly variable sediment conditions, they show that the sediment conditions of at least some patches are object of strong alterations. Just by observation, the water currents of the intertidal creeks and the tide itself appear to be strong with a heavy sediment load and they change the sediment conditions in a few days time. This, in addition to the numerous other disturbances (pits created by large crustaceans or sting-rays, boats lying on the flats during low tide or floating debris remaining on the sediment) creates a mosaic of more or less disturbed areas with differing sediment conditions and benthic assemblages. Continually occurring small scale disturbances create initial conditions which promote opportunistic benthic species. They disrupt ongoing processes between species and biotic processes, as predation or competition, are unlikely to have a strong effect on the benthic community (Reise 1985).

The salinity of the pore water shows a strong seasonal variability. The salt concentration of the water depends on the input of freshwater due to rainfall. This amount varies at the Bragantian peninsula, not only within but also between years. The average amount of rain per day, calculated monthly from January to June, is less in 2002 than in 2001 (Appendix II, Table 35). This leads to significantly higher salinities in 2002. In the tropics salinities are known to fluctuate strongly (Alongi 1990). While large amounts of freshwater mix with the saltwater during strong rains, the evaporation of the surface water and ponds during low tide, due to the radiation of the sun, is strong, leaving highly saline water. Strong salinity changes, as observed at the study area, are inevitably very stressful to the benthic community, although animals of the tropical intertidal have generally a strong resilience (Alongi 1990). Alongi (1990) describes that with the onset of monsoon most benthic communities suffer increased mortality due to low salinities and enhanced sediment erosion. In this study, a drop of 30% of total benthic abundances is found at the beginning of the wet season. And in 2002, when the rain was generally less severe, the total standing stock proved to be higher. Thus,

the reduced salinities during the rainy season are possibly a considerable constrain for the benthos.

The benthic community of the Bragantinian tidal flats lives in an environment with severe stresses, like a low organic content of the sediment, ongoing sediment alterations and strong salinity fluctuations. Benthic species living in this environment are presumably resistant, opportunistic animals, which can deal with quickly changing environmental conditions in a patchy environment.

The benthic community

There has been much debate about whether species diversity increases towards the tropics in comparison to temperate mudflats. While some authors deny an increase of diversity (Alongi 1989; 1990) others found that there are higher species numbers at tropical mudflats (Reise 1991; Dittmann 1995). In a recent review Dittmann (2002a) concluded that the benthic diversity is indeed higher in the tropics, but varies greatly between sites. Species numbers might range from much higher to very low values in comparison to temperate environments.

In this study overall 55 benthic taxa were identified. Like typical for tropical tidal flats, only few species account for the majority of individuals (Wolff et al. 1993a; Dittmann 1995; Dittmann 2002a). The number of identified taxa underestimates the species numbers of the Bragantinian intertidal, since the individuals of most taxa were not distinguished to species level. Also, the use of smaller sieve sizes (<1 mm) can increase species records and abundances since small polychaetes are especially rich in tropical tidal flats (Dittmann 1995; Dittmann 2002b). Hence, one could expect the species numbers to be higher than recorded in this study. But the more detailed study on the benthic community of the Bragantinian intertidal by Acheampong (2001) with the use of 0.5 mm sieves did not lead to much higher species numbers (77 identified taxa). Thus, also enhanced identification or smaller sieve sizes would possibly not yield in much higher species numbers. The number of macrozoobenthic species of the Bragantinian tidal flats is low in comparison to the range recorded from tropical sites elsewhere (Table 4). Alongi (1990) assumed, that the benthic diversity is decreasing the more exposed the tidal flats are, presumably resulting from the physical disturbances. Also physiological stresses, like fluctuations of water salinity are thought to cause low species richness, like proposed by Kalejta and Hockey (1999) for the low species diversity of the Berg River Estuary at South Africa. Both of these stresses occur at the tidal flats of the Bragantinian peninsula and are possibly responsible for the few benthic species.

Unlike the benthic diversities, benthic abundances are thought to be low in the tropics in comparison to temperate regions (Reise 1991; Dittmann 2002a). The general range given by Dittmann is between 1000-2000 individuals/m² for the macrofauna of the tropics (2002a and references therein). Even in this respect the monthly means of 167-239 individuals/m² at the Bragantinian tidal flats are extremely low. Comparable abundances occur also at some

sampling stations of other tropical tidal flats (Hichinbrook channel, Haughton estuary, Roebuck Bay and the Banc d'Arguin, see ranges given in Table 4), but they are not common and always at the lowest part of range in these areas. Most of these studies used smaller mesh sizes for the benthic samples which lead, especially in tropical areas rich of small polychaetes, to increased species abundances (Dittmann 1995; Dittmann 2002b). However, the results of this study were supported by the findings of Acheampong (2001), who obtained abundances of comparable magnitude with a 0.5 mm sieve at the same study sites.

The biomass values of the macrozoobenthos of this study are also low, monthly means ranged between 0.5-2.3 gAFDW/m². Piersma et al. (1993) give an overall range of 5-80 gAFDW/m² worldwide with an average of 24 gAFDW/m² for the investigated areas. In general, tropical areas have higher values than found at the Bragantinian peninsula, the lowest are found in Guinea Bissau with 4-5 gAFDW/m². Tropical sites range usually between 0-10 gAFDW/m² in polychaete dominated areas and 10-20 gAFDW/m² if dominated by molluscs or crustaceans, larger figures are an exception (Table 4). Since the biomass results of this study are not measured directly, their value could be doubted. But they are well within the range of the data obtained by Acheampong (2001) by direct biomass measurements at the same study area and can therefore be assumed to be valid. It might be asked, how the birds at the Bragantinian peninsula deal with such a low food stock and if they can fulfil their energetic requirements (chapter 6).

Low abundance and biomasses of the benthic fauna might be a result of the little organic material found in the sediment and of the continuing stress due to the sediment erosion and salinity fluctuations of the pore water. These factors can be expected to be enhanced during the wet season, due to the increased fresh water input and current velocity. Thus, it is possible that during the dry season, which was not investigated in this study, benthic numbers and biomasses on the Bragantinian intertidal are higher than described in this study.

Seasonal trends can be very pronounced in temperate areas like northwest Europe, with lowest biomasses in the northern winter and a peak in midsummer (Beukema 1974). Tropical areas are generally expected to be less seasonal and to offer a more constant food supply (Wolff 1991). The data of the Bragantinian tidal flats is indeed stable if biomasses and abundances are considered on higher benthic taxa. But if the lower taxa are considered, the macrobenthos appears to be extremely variable in abundances as well as in biomasses. All taxa follow individual seasonal trends which appear to be unrelated to each other, an observation also made by de Goeij et al. (2003) in a long term study on the tropical benthic community of Roebuck Bay in Australia.

However, the temporal variability of the benthos is only slight in comparison to its spatial variability. The different locations differ very much from each other and the abundances of the taxa are also not correlated to any of the investigated environmental features. If benthos

organisms are overall abundant, the outstanding spatial variability of the benthos organisms enables the birds to specialize on niches which are most profitable for them. However, if benthos is only scarce birds might not be able to specialize but might have to take whatever they can (chapter 5).

Due to the strong spatial variation no differing faunal zones can be distinguished on the base of abundances. Only with the reduction of variability by the use of ranks instead of original abundances some weak zonations based on benthic assemblages and sediment composition were found, which are still not very consistent in time. Hence, foraging birds presumably cannot use distinct locations, faunistic zones or other environmental clues, like sediment conditions or salinity, as a hint for profitable foraging spots.

In this variable environment, opportunistic avian feeders are presumably in advantage over specialized birds. If they nevertheless focus on only few prey items, they can adopt two different strategies: to specialize on very abundant prey items regardless of energetic content or to select the rare but energetically most profitable organisms. Only few organisms are outstanding in terms of densities or biomass values, most benthic species are low in both. Prey items with high biomasses are the crustacean taxa Callianassidae, *Uca maracoani*, the bivalve *Tagelus plebeius* and the gastropod *Nassarius vibrex*. All of them are found in only very low densities. Large individuals of Callianassidae and *Tagelus plebeius* are found predominantly at >10 cm depth and they all comprise a thick shell and large body size. This means that they can be considered as prey species only by large birds with long bills (insert depth > 10 cm) or very skilful birds which can dig for their prey and handle thick shells. Additionally, large individuals are found only in certain months. In January mostly *Nassarius vibrex* can be found, but in February-April also large individuals of other species are relatively abundant. The few organisms which are found in high densities have extremely low biomass values. They are polychaetes (Nephtyidae, Capitellidae) or crustaceans (Gammaridea, Pinnotheridae). Overall they prefer the top sediment layer and are thus accessible for all bird species. Do the birds indeed adopt one of these techniques, or are also other factors but prey densities and biomasses important for their prey choice (chapter 5)?

Table 4. Number of species, densities and biomasses of the macrozoobenthos and bird densities at different tidal flats obtained by the literature. Given are mean values and ranges in brackets.

Location	Mesh size used	Benthos species numbers	Benthos density [individuals/m ²]*	Benthos biomass [gAFDW]	Bird densities [individuals/ha]	Reference
Banc d'Arguin, Mauretania	0.6mm	132	-	14.5	Jan-March: 41.6	(Altenburg et al. 1982) (Wolff and Smit 1990; Wolff et al. 1993a)
Hichinbrook Channel, Queensland, Australia	0.25, 1mm	202	1,364±1,51 (0-7,550)	-	-	(Dittmann 1995; Dittmann 2002b)
Haughton River estuary, Queensland, Australia	0.25, 0.5, 1mm	96	1,812±4,174, (50-26,150)	-	-	(Dittmann 1995)
Bragança, Brazil	0.5mm	84	137 (Furo Grande) 343 (Canelas)	(0.18-3.38) (0.01-15.79) (mean values)	-	(Acheampong 2001)
Ao Nam Bor, Thailand	0.25, 0.5, 1mm	118	-	-	-	(Reise 1991)
Inhaca Island, Mozambique	1mm	117	2200	6.0	-	(De Boer and Prins 2002)
Pulau Tenga, Malaysia	1.5mm	-	-	November: 31.4; (6.7-69.4)	April: 1.6	(Sasekumar and Chong 1986)
Weg naar Zee, Surinam	1mm			6.45		(Swennen et al. 1982)
Gulf of Nicoya, Costa Rica	0.5mm	79	14,798±6,170 (6,345-25,421)	-	-	(Vargas 1988)
Roebuck Bay, Western Australia	1mm	161	1,287 (40-16,280)	12.46 (0.07-167)	-	(Pepping 1999)
Guinea Bissau	?			4-5	Dec.-Feb: 6.3 (2.6-7.4)	(Zwarts 1985; Zwarts 1988)
Sierra Leone		-	-	-	15.5 (5-28)	(Tye and Tye 1987)
Bragança, Brazil	1mm	55	January (max): 239, (0-677)	Jan: 1.9, (0-25.7)	Jan (max): 22, (0-127)	this study
Dutch Wadden Sea				27	0.4-18.0	(Wolff 1991)

* for macrofauna (0.5-1mm)

4 Migrant meets resident – distribution and structure of the avian community

4.1 Introduction

What appearance has the avian community in the study area and which are the significant environmental factors for the birds distribution?

The coast of Northeast Brazil is known to support high numbers of migratory shorebirds during the winter time of the northern hemisphere. Although not as important as the adjacent coastlines, yet the intertidal of the Bragantinian peninsula accommodates a few thousand shorebirds (Morrison and Ross 1989). The migratory individuals probably belong to populations breeding at the central North American Arctic (Morrison 1984). Beside them, also residential birds live at this habitat, some use the sheltered mangrove area to breed in large colonies of several thousand pairs. Although considerable *numbers* of shorebirds and wading birds depend on this coastal area for their survival, its significance as a feeding habitat has not been investigated in more detail yet. Which *species* use this habitat?

Shorebirds and wading birds use the intertidal areas predominantly as a foraging habitat. Beside the dispersal of food also diverse environmental conditions might effect the foraging and the *distribution* of birds (Burger 1984; Evans and Dugan 1984; Goss-Custard 1984). Initially, studies on the distribution of shorebirds concentrated at temperate areas (Burger et al. 1977; Quammen 1982; Yates et al. 1993a; Botton et al. 1994; Summers et al. 2002). comparatively few were conducted in tropical areas (Zwarts 1988; Ntiamoa-Baidu et al. 1998; De Boer 2002). Also, the habitat use of wading birds was investigated in several studies (Bildstein 1990; Bildstein et al. 1990; Frederick and Bildstein 1992). Which *environmental factors* and *microhabitats* are important for the birds at the Bragantinian peninsula? Can *guilds* be defined, which use the habitat in a specific way? In this chapter the distribution of the avian community is described considering all environmental factors but benthos. The relationship between bird predators and their benthic prey will be investigated separately at the following chapter.

4.2 Results

4.2.1 Taxonomic composition

Overall 19 avian species were identified at the study area (Table 5). Of these, 3 species were counted with less than 10 individuals and they were neglected of most of the investigations (Great Egret, Yellow-crowned Nightheron and Greater Yellowlegs). The 7 residential species (all wading birds and the Collared Plover) held for only 9% of all counted individuals in 2001. The remaining 91% were migratory shorebirds (Scolopacidae and Charadriidae).

Table 5. Bird species found at the study area.

Taxonomy		Species
Herons, egrets and ibises	Ardeida	Great Egret, <i>Ardea alba</i> , (Linnaeus 1758)
		Little Blue Heron, <i>Egretta caerulea</i> (Linnaeus 1758)
		Snowy Egret, <i>Egretta thula</i> (Molina 1782)
		Tricolored Heron, <i>Egretta tricolor</i> (Statius Müller 1776)
		Yellow-crowned Nightheron, <i>Nyctanassa violacea</i> (Linnaeus 1758)
	Threskornithidae	Scarlet Ibis, <i>Eudocimus ruber</i> (Linnaeus 1758)
Plovers	Charadriidae	Collared Plover, <i>Charadrius collaris</i> (Viellot 1818)
		Grey Plover, <i>Pluvialis squatarola</i> (Linnaeus 1758)
		Semipalmated Plover, <i>Charadrius semipalmatus</i> (Bonaparte 1825)
Sandpipers, Snipes etc.	Scolopacidae	Greater Yellowlegs, <i>Tringa melanoleuca</i> (Gmelin 1789)
		Marbled Godwit, <i>Limosa fedoa</i> (Linnaeus 1758)
		Red Knot, <i>Calidris canutus</i> (Linnaeus 1758)
		Ruddy Turnstone, <i>Arenaria interpres</i> (Linnaeus 1758)
		Sanderling, <i>Calidris alba</i> (Pallas 1764)
		Semipalmated Sandpiper, <i>Calidris pusilla</i> (Linnaeus 1766)
		Short-billed Dowitcher, <i>Limnodrimus griseus</i> (Gmelin 1789)
		Spotted Sandpiper, <i>Actitis macularia</i> (Linnaeus 1766)
		Whimbrel, <i>Numenius phaeopus</i> (Linnaeus 1758)
		Willet, <i>Catoptrophorus semipalmatus</i> (Gmelin 1789)



Fig. 21. Herons, egrets, ibises and plovers at the study area.



Fig. 22. Sandpipers at the study area.

A total of 2540 birds were counted during the low tide counts in 2001 of which 6% were contributed by wading birds, 13% by plovers and 82% by sandpipers. Of the sandpipers, the Short-billed Dowitcher and the Semipalmated Sandpiper were the most common, accounting for 22% and 21% of all birds respectively. The most abundant plover was the Semipalmated Plover with 7% of all birds (Fig. 23). The taxonomic compositions of the birds at the first three months and the last three months of the study period differed significantly from each other (Contingency table: $\chi^2=406.979$, $v=15$, $p<0.001$).

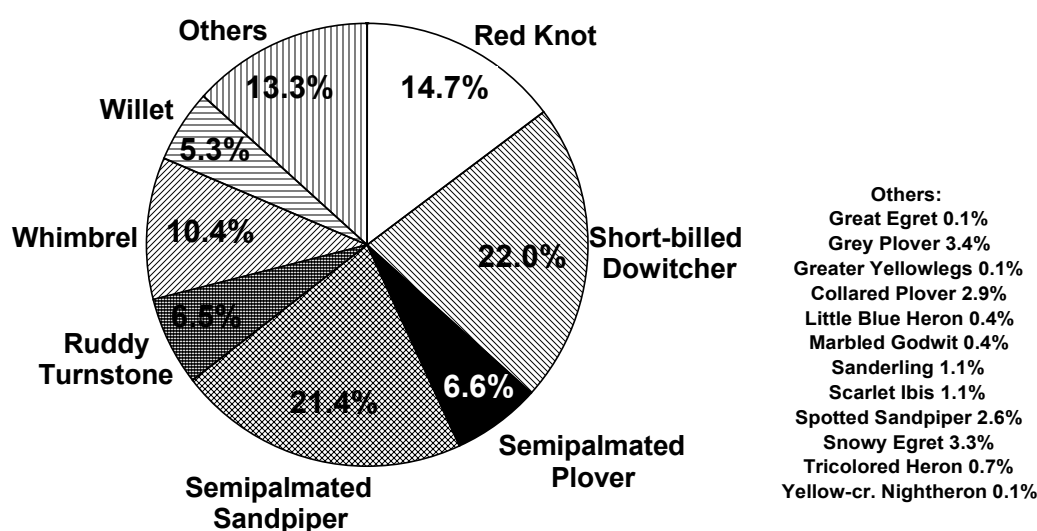


Fig. 23. Taxonomic composition of the birds at the study area. Given is the proportional contribution of the avian species to the total number of individuals found in 2001.

In 2002 the species composition changed significantly in comparison to that of 2001 (Appendix III, Table 36). This was due to significantly lower abundances of Red Knot, Semipalmated Sandpiper, Short-billed Dowitcher and Whimbrel in January of 2002 and to significantly higher abundances of Semipalmated Plover in February of 2002 (Appendix III, Table 37).

4.2.2 Abundances

During the low tide counts, avian abundances ranged between a minimum of 0 and a maximum of 127 birds/ha at the different plots. Ranges of individual bird densities during low tide are given at Appendix III (Table 38). The mean avian density at the study area ranged from a maximum of 22 birds/ha in January to a minimum of 2 birds/ha in May 2001.

Since a majority of the observed birds were migrants, abundances were clearly seasonal dependent. By April most of the migratory birds already departed for their spring migration (Fig. 24, upper left). Thus, the study period was separated in January-March with a strong

influence of migratory species, and April-June, with generally low numbers of mostly residential birds. This differentiation was confirmed by a Kruskal-Wallis Test which detected significant differences between monthly total abundances ($H=47.907$, $p<0.001$). Subsequent Mann-Whitney U-tests showed that the differences occurred only between the first three months and the last three months of the study period (with Bonferroni-correction $\alpha=0.05/15=0.003$; January-May: $z=4.045$, $p<0.001$; January-June: $z=3.526$, $p<0.001$; February-April: $z=4.845$, $p<0.001$; February-May: $z=4.845$, $p<0.001$; February-June: $z=4.478$, $p<0.001$; March-May: $z=3.893$, $p<0.001$; March-June: $z=3.233$, $p=0.001$). While the abundances of some migratory species simply decreased from January until April/May, others showed distinct migration peaks (Fig. 24, upper and lower right). The variable abundances of residential birds suggested also movements in and out the study area (Fig. 24, lower left). The proportional contribution of the residential birds was in the first three months of the year only 5% while it increased to 29 % of all counted individuals after March.

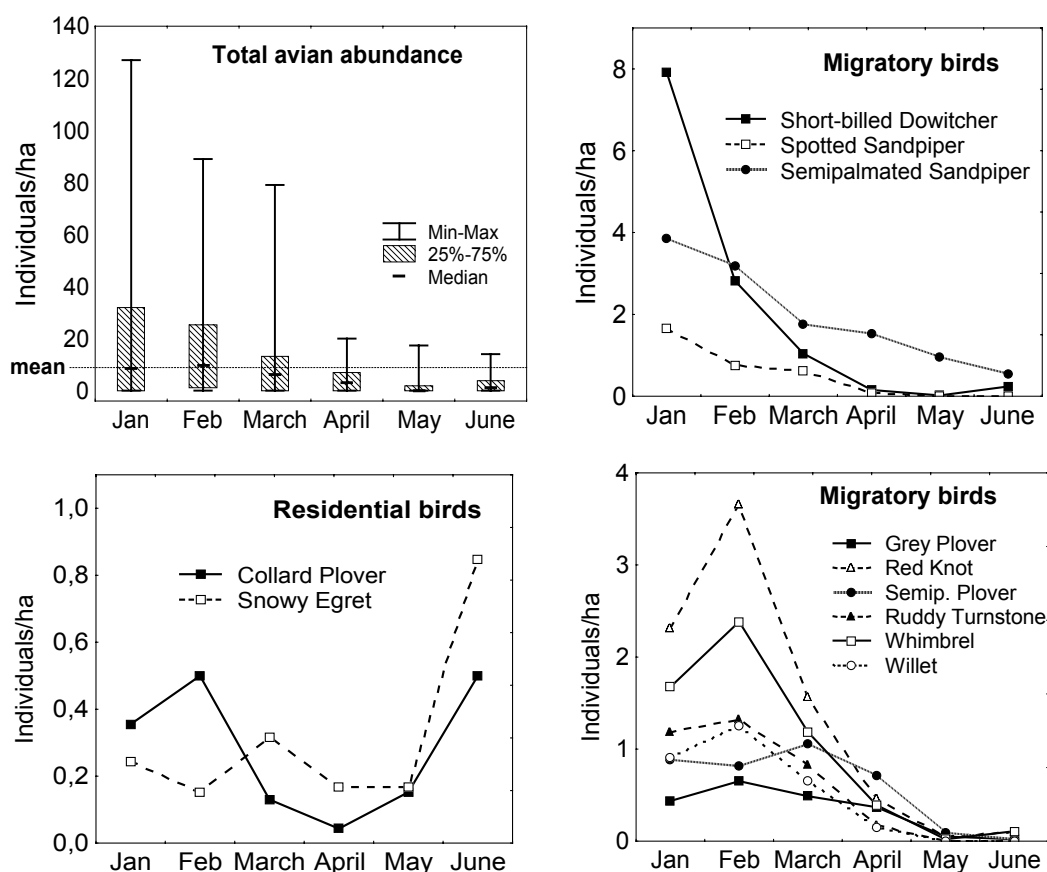


Fig. 24. Phenologies of the total avian community (upper left), of residential birds (lower left) and of migratory birds (upper and lower right) in the study area. Given are the mean individuals/ha found during low tide between January and June 2001.

4.2.3 Spatial distribution

All data concerning the spatial distribution of the birds in 2001 were calibrated by a tidal factor (chapter 2.2.2). In contrast to the low tide counts, they are calculated hypothetical

densities which imply the use of the plots during the time of ebb tide. Tide calibrated densities ranged between 0-738 birds/ha.

Sampling sites

Bird densities differed very much between the open intertidal habitat of the Ilha de Canelas, the mangrove habitat of the Furo Grande and the habitat bordering the mangrove of the Furo do Chato. Although the densities cannot be seen as characteristic for the particular sampling site since the plots were not marked randomly, they still provide an impression of what densities can be found at the area. Some species appeared predominately at the open intertidal (Short-billed Dowitcher, Semipalmated Sandpiper, Red Knot), others occurred additionally at the mangrove channels (Whimbrel, Willet, Ruddy Turnstone). Only the Spotted Sandpiper occurred exclusively at the Furo Grande. All others did not show significant preferences for a particular sampling site (all plovers, Scarlet Ibis, Marbled Godwit, Sanderling).

Table 6. Observed sampling site choices of the birds in the study area. Given are the results of Kruskal-Wallis tests on avian abundances between the plots at the sampling sites (n=25 at Canelas, n=6 at the Furo Grande, n=15 at the Furo do Chato) in 2001. Mann-Whitney U-test identified the differences between the habitats (with Bonferroni-correction).

Species	January			February			March		
	H	p	difference	H	p	difference	H	p	difference
Scarlet Ibis	2.634	0.268		0.840	0.657		2.946	0.229	
Collared Plover	3.888	0.143		5.088	0.079		2.317	0.314	
Grey Plover	10.736	0.005	-	8.681	0.013	fg>fc	1.840	0.399	
Semipalmated Plover	14.190	0.001	c>fc	0.182	0.913		1.185	0.553	
Marbled Godwit	7.870	0.020	-	5.638			-	-	
Red Knot	26.230	<0.001	c>fg, c>fc	30.240	<0.001	c>fg, c>fc	17.252	<0.001	c>fg, c>fc
Ruddy Turnstone	10.454	0.005	-	14.213	0.001	c>fc	3.529	0.171	
Sanderling	3.591	0.166		4.850	0.089		2.056	0.358	
Semipalmated Sandpiper	26.841	<0.001	c>fg, c>fc	11.974	0.003	c>fg	8.774	0.013	c>fg
Short-billed Dowitcher	26.173	<0.001	c>fg, c>fc	20.676	<0.001	c>fg, c>fc	18.994	<0.001	c>fg, c>fc
Spotted Sanpiper	No tidal count available. But bird was seen exclusively at the Furo Grande plots during low tide								
Whimbrel	19.908	<0.001	c>fc, fg>fc	20.729	<0.001	c>fc, fg>fc	4.307	0.116	
Willet	19.226	<0.001	c>fc	24.167	<0.001	c>fc	15.444	0.001	c>fc
Total	31.637	<0.001	c>fc, fg>fc	15.954	<0.001	c>fg, c>fg	6.500	0.039	-

Plots

The spatial distribution of the birds at the plots was – like the benthic distribution - very variable (Fig. 31). While some parts of the study area were mostly vast of birds (Furo do Chato plots 37-46), others comprised comparatively high bird densities (Canelas plots 21 and 23). Plovers and sandpipers often favoured more or less similar areas, but the preferences of herons and egrets were very scattered and dissimilar to the other groups. Although general preferences and avoidances of some plots were observed, they did not last for more than one month.

Environmental characteristics

Spearman Rank Correlations detected no strong correlations between avian abundances and sediment condition, salinity of the pore water, time of emergence or density of burrow openings (Appendix III, Table 39). Though some correlations were significant, none had an R higher than 0.392. Thus, no considerable relationships were detected.

Microhabitats

The characteristic pattern of the avian plot use could be caused by the preference for specific microhabitats, like the association with water or specific water depths. Also, the selection of a probing depth within the sediment can be understood as the use of a specific microhabitat.

Association with water. The birds differed very much in their association with water. Some preferred the dry sand, like the Scarlet Ibis, all plovers, Turnstone, Semipalmated Sandpiper and Sanderling. Others, like the Little Blue Heron, Tricolored Heron, Marbled Godwit and Short-billed Dowitcher, were more often found at watercovered areas. Only the Spotted Sandpiper was mostly associated with the waters edge. All others appeared more or less frequently in all microhabitats (Table 7).

Table 7. Observed associations with water of the birds in the study area. Given are the proportions of all birds observed at dry sand, the waters edge or in the obtained in 2001. All proportions ≥ 50 are bold.

Taxon		Dry sand	Waters edge	Water	n
Herons, egrets and ibises	Great Egret	*	*		3
	Little Blue Heron	20	11	69	11
	Snowy Egret	20	35	45	83
	Tricolored Heron	16	0	84	17
	Yellow-crowned Nightheron	*			3
	Scarlet Ibis	90	7	3	29
Plovers	Collared Plover	86	13	1	74
	Grey Plover	88	11	1	87
	Semipalmated Plover	87	12	1	159
Sandpipers, Snipes etc.	Greater Yellowlegs		*		2
	Marbled Godwit	12	19	69	10
	Red Knot	51	20	29	361
	Ruddy Turnstone	89	7	4	159
	Sanderling	89	7	4	27
	Semipalmated Sandpiper	67	27	6	524
	Short-billed Dowitcher	19	16	65	538
	Spotted Sandpiper	21	79	0	67
	Whimbrel	50	13	37	254
	Willet	30	33	37	130

Water depth. At least some individuals of all species were observed at watercovered areas, only the Spotted Sandpiper completely avoided to walk in the water. There, as well a spatial differentiation according to water depth took place (Fig. 25). This differentiation was clearly depending on the size of the different species, as represented by the leg length obtained from the literature, given at Table 22 (Spearman Rank Correlation $R=0.878$, $p<0.001$).

Probing depth. The probing depth within the sediment differed between the species (Fig. 25). From this, the actual availability of benthic individuals could be calculated by determining the relevant depth for each species (Appendix III, Table 40).

The probing depth was related to the bill size of the different species (Spearman Rank Correlation: $R=0.979$, $p<0.001$).

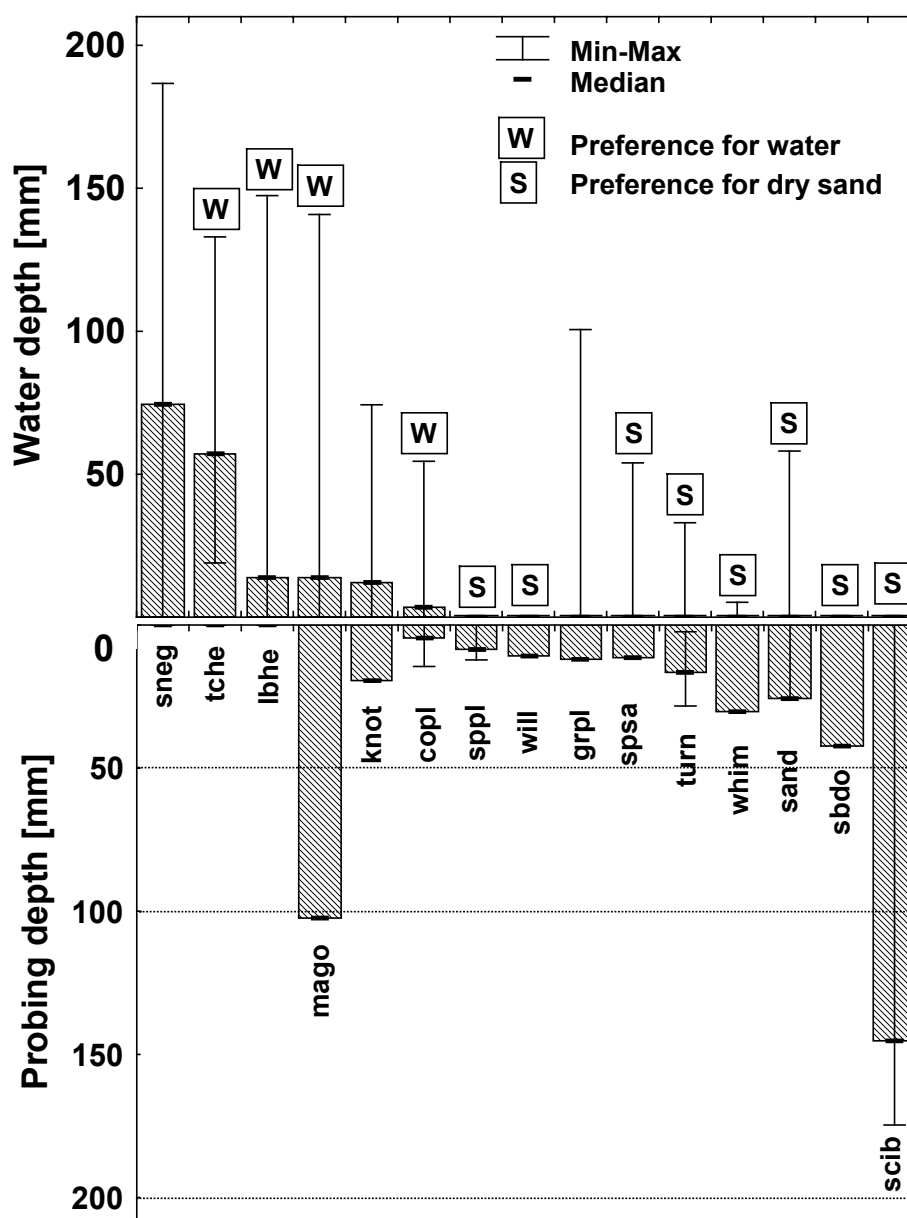


Fig. 25. Observed water- and probing depths of the birds in the study area in 2002. The most common associations with water are given in boxes above the columns (Table 7). Probing depth was calculated as the bill insert depth subtracted by the water depth. Probing depths of herons and egrets are not given since they usually do not probe in the sediment. N of the species ranged between 7 (sand) and 61 (spsa).

4.2.4 Guilds

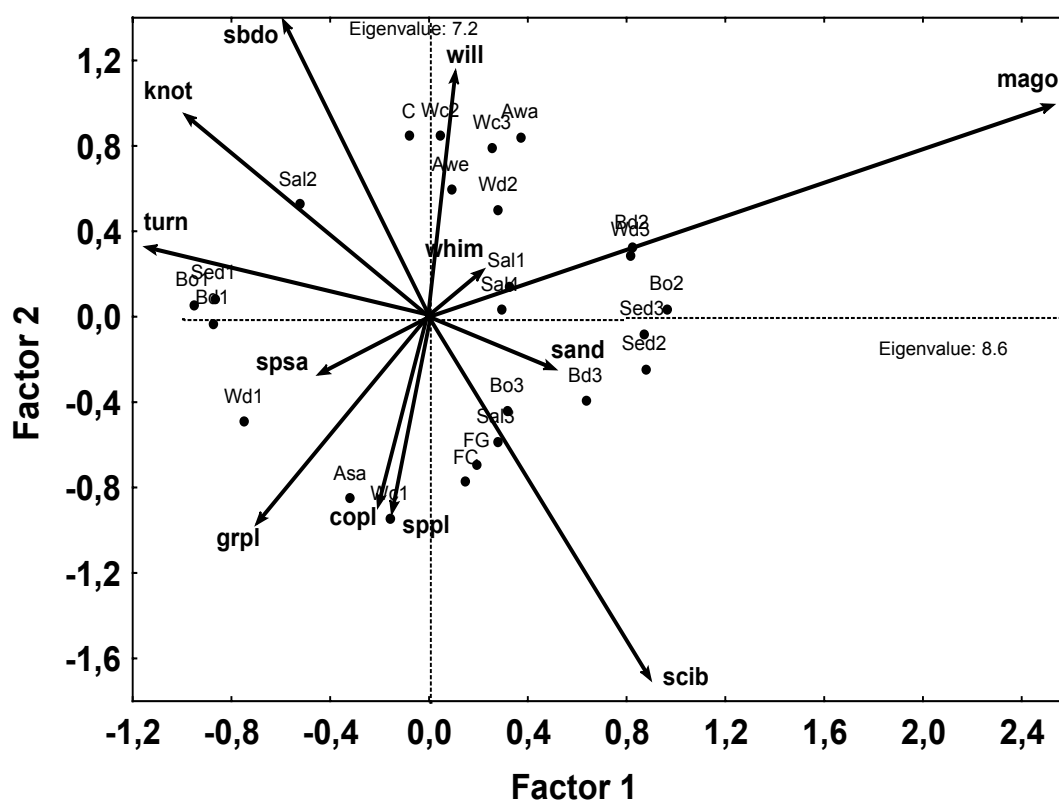
Guilds based on the spatial distribution

When benthic assemblages were investigated in chapter 3, MDS and Cluster analyses based on log-transformed benthic abundance data did not reveal any groups of plots which were similar in their benthic assemblage for more than one month. The same difficulties appeared with the avian assemblages at the plots. Although general preferences or avoidances of some plots can be described, avian abundances in more detail were not stable for more than one month. Thus, guilds based only on spatial distribution were extremely variable.

A Principal Components Analysis on the transformed abundance data of the birds together with environmental data (median grain size of the sediments, salinity and the density of burrow openings at the sediment surface) at the different plots came to the same results. No guild could be identified which was stable for more than one month. As well the environmental variables proved to be of no relevance for the birds. It did not matter if the three sampling sites were investigated separately, the results did not become any clearer.

Guilds based on the microhabitat use

Holmes et al. (1979) used another technique to determine avian guilds with the use of environmental variables (for details on the calculation see chapter 2.3.3). This approach was first conducted on the abundances of the total avian community appearing at the microhabitat categories given in Fig. 26. Only three groups could be distinguished (a) herons, egrets and the Marbled Godwit, b) Scarlet Ibis and Grey Plover and c) all other shorebirds. The difference between wading birds and shorebirds was so large, that all differences within the shorebirds became relatively small and insignificant. Thus, the procedure was repeated with only the shorebirds and the Scarlet Ibis included. A PCA diagram was calculated and the first two axes extracted explained together 63.6% of the variance (Fig. 26).



Category	range	Short form	Category	range	Short form
Sediment grain size [Φ]	2.5-3.0	Sed 1	Burrow openings	0-70	Bo 1
	3.1-3.5	Sed 2		71-140	Bo 2
	>3.5	Sed 3		141-210	Bo 3
Sampling site	Canelas	C	Water coverage of the plots	0-33 %	Wc 1
	Furo Grande	FG		34-66 %	Wc 2
	Furo do Chato	FC		67-100 %	Wc 3
Water depth [cm]	0-65	Wd1	Association with water	Dry sand	Asa
	65-130	Wd2		Waters edge	Awe
	130-195	Wd3		Water	Awa
Foraging depth	0-65	Bd1	Salinity [‰]	0-10	Sal 1
	65-130	Bd2		10.1-20	Sal 2
	130-195	Bd3		20.1-30	Sal 3
				30.1-40	Sal 4

Fig. 26. PCA diagram on microhabitat use of the shorebirds and the Scarlet Ibis. The axes explain together 63.6% of the variance. The microhabitat categories used to determine avian guilds are given in the table below.

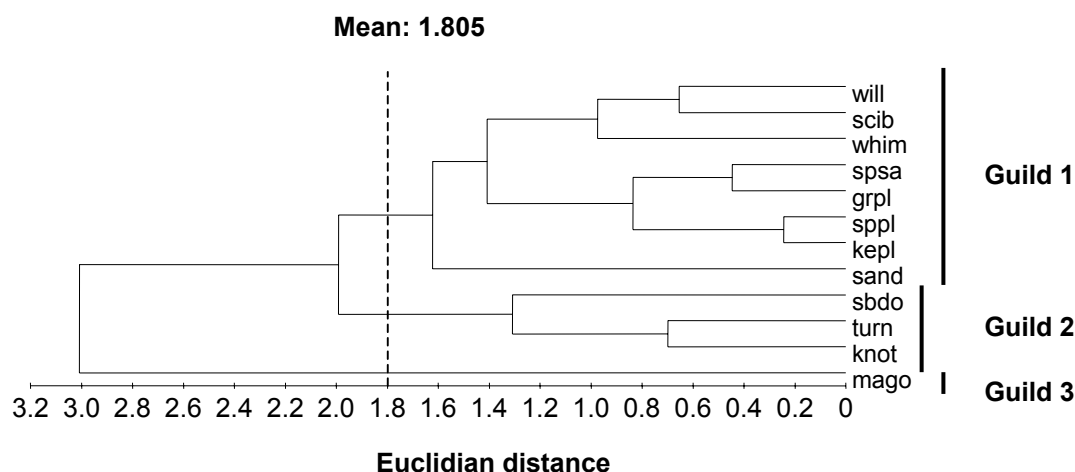


Fig. 27. Dendrogram on the microhabitat use of the shorebird species. The Cluster analysis was performed on Euclidian distances obtained of a PCA diagram.

A Cluster analysis of the Euclidian distances between the species positions in the PCA space identified 3 guilds: (Fig. 27). Together with the PCA diagrams they can be described by their use of microhabitats.

Guild 1: This group was composed of two sub groups. The first one consisted of Whimbrel, Willet and Scarlet Ibis, which were all large birds. Whimbrel and Willet appeared very similar in their microhabitat use. They preferred areas with a high water coverage and foraged often in the water or at the waters edge. The Scarlet Ibis differed from them and – considering the PCA-diagram – it is surprising that this bird was grouped together with Whimbrel and Willet. However, all three of them preferred muddier areas and they used deeper probes. The other subgroup was composed by all plovers and the Semipalmated Sandpiper, which were mostly small individuals. They were found in areas with a low water cover and they preferred dry sand or only very shallow water. The Sanderling seemed to differ from all other birds of that group, its appearance at muddier areas, like proposed by the PCA, was somehow contradicting to the observations.

Guild 2: This group was composed by Ruddy Turnstone, Short-billed Dowitcher and Red Knot. These agile and medium sized shorebirds covered also most of the microhabitats visited by guild 1. Their appear to be characterised by a preference for medium salinities.

Guild 3: Only the Marbled Godwit belonged to this guild. It differed to other birds mainly in the use of deep probes and a distinct preference for muddy areas.

4.3 Discussion

Taxonomic composition

The avian community of the Bragantian tidal flats is dominated by shorebirds which comprised 91% of all observed birds. Almost all shorebirds are migratory and all wading birds are residential. The only residential shorebird is the Collared Plover. As a result, the taxonomic composition of the birds and their densities exposes a strong seasonality. From January to March the community is dominated by high numbers of migratory shorebirds while bird densities are much lower from April to June with a larger proportion of residential birds.

Abundances

During the winter of the northern hemisphere, when migratory shorebirds dominate the tidal flats, avian densities are very high in comparison to other tropical wintering areas. The mean bird density at the study area reached in January-March 22 birds/ha. Quantitative investigations on total bird abundances in tropical tidal flats are rare, but 3 out of the 4 studies given at Table 4 present generally lower bird densities than observed at the Bragantian intertidal. Only the study of Altenburg et al. (1982) found far higher avian abundances at the Banc d'Arguin in Mauritania with 41.6 birds/ha. At the Banc d'Arguin bird numbers were attained by counts of roosting birds, in contrast to the low tide counts of all other studies. According to Yates and Goss-Custard (1991) counts of roosting birds yield commonly to higher numbers than low tide counts, which might be responsible for the extraordinary high numbers at the Banc d'Arguin. However, according to the high shorebird densities at the Bragantian study area, it can be assumed that this part of the coast is an important stop-over- and wintering area for shorebirds in South America, as proposed by Morrison and Ross (1989).

Beside the individual phenologies obtained at the Bragantian peninsula, similar data is also available of the coast of Maranhão, a place a few hundred of kilometers further south-east of Bragança. There, Ferreira Rodrigues (2000 and pers. comm.) investigated in 1991/92 the abundances of shorebirds. When compared with the Bragantian data, some migratory patterns can be proposed. Grey Plover, Short-billed Dowitcher and Whimbrel are species which also winter further south and a part of their population migrates northwards in the first months of the year along the Brazilian coast through both areas. A second part of their population starts migration later, passes through Maranhão and presumably starts from there directly for a non-stop flight over the ocean, skipping the coastal areas further north. Red Knot and Ruddy Turnstone have wintering populations in South Brazil and Argentina (Poole and Gill 2000) and fly directly to the Northern Brazilian coast without stopping at Maranhão. Semipalmated Plovers occur at the Bragantian intertidal only in low abundances. At Maranhão they reach far higher densities and leave the area in spring also without stopping any more at the coast further north. So far, Collared Plovers were assumed to be residential at the Bragantian tidal flats, but they expose a migration peak in February. Thus, they might

be composed of two populations, one migratory, breeding further north and passing through the study area during spring migration, and one residential population which moves in the area in May and June. Unfortunately, no clarifying information about the breeding grounds is available. Snowy Egrets, which have breeding grounds further north (Poole and Gill 2000), show the same pattern. However, to simplify the analysis these species are also further regarded as “residential”.

Although large abundances of herons, egrets and ibises were observed to breed or to roost in the adjacent mangrove areas, only few individuals were observed to forage at the study area. Large movements of these birds during dusk and dawn presume that the wading birds prefer to forage within the mangrove area of the mainland. Their favourite prey, the fish, is very abundant at the mangrove creeks, especially during low tide (Krumme and Saint-Paul 2003). Thus, the birds find within the mangrove probably much more favourable feeding conditions than at the creeks of the open intertidal.

Spatial distribution

The birds differ in their use of the three sampling sites. Many shorebirds avoid to stay close to mangrove vegetation apparently because of the restricted view, which reduces the chance of detecting potential predators in time, as observed in Australia (P. Straw, pers. com.). On the other hand, there is a large amount of medium size crabs (*Uca sp.*) close to the mangrove, which might be a very profitable prey for birds able to harvest on those larger crustaceans. This considerations appear to be reflected in the avian use of the sampling sites: Furo do Chato, the area which provides only small crustaceans but which is close enough to the mangrove to have a raised danger of predation, is generally the least favoured sampling site. Almost all birds used the open intertidal of the Ilha de Canelas. Those birds able to feed on larger crabs also occur at the Furo Grande, presumably to make use of the favourable prey source. Thus, the distribution of the bird community might be partly determined by predator avoidance. However, all plovers, the Scarlet Ibis, the Marbled Godwit and the Sanderling use all areas in the same way. They appear to be unaffected by considerations on predator avoidance or their prey sources compensate for the raised predation risk close to the mangrove sufficiently. For the plovers the large amount of Gammaridea, a small crustacean, at the Furo do Chato would support this idea. However, considerations on this subject have to be treated with caution because of the statistical drawbacks of the analysis.

There are general patterns of avian use or avoidance of plots. While total plovers and sandpipers are moderately variable in their spatial distributions, very distinct individual plot preferences with extreme variability also between months occur on species level. In general, the spatial distribution of bird species cannot be linked with plots or specific locations. Other factors, which are somehow unrelated to the spatial position, must be responsible for avian distribution patterns. If these factors are prey abundances will be investigated in chapter 5.

Abiotic environmental factors are variables which are still partly related to plot location. They might influence the distribution of birds not only indirectly through their impact on the benthic prey organisms, but also directly. Sediment grain sizes can affect the penetrability of the sediment and, thus, the ease to probe for prey. Also, Quammen proposes that similar sizes of sand grains and prey hamper prey detection or prey capture (1982). Many studies found that sediment grain size or substrate type influences the foraging of birds (Myers et al. 1980; Hicklin and Smith 1984; Zwarts 1988; Goss-Custard et al. 1991; Summers et al. 2002). Yates et al. (1993a) proved that benthic prey organisms are so well correlated with grain sizes that they can serve as an important factor to model shorebird distributions, as it was successfully done by Goss-Custard et al. (1991), by Scheiffarth et al. (1996) and by Yates et al. (1993b). However, sediment grain sizes proved to be insignificant for shorebird distributions at Delaware Bay (Botton et al. 1994) and the Berg River estuary (Kalejta and Hockey 1994). Although the physical appearance of the sediment was variable at the Bragantinian peninsula, sediment grain sizes differed not very much. Probably as a consequence, grain sizes were not important for the distribution of shorebirds. Yet, a preferences for wet or dry sand took place, as shown by the avian microhabitat choices.

Klaassen and Ens (1990) propose, even if not found for the well adapted Red Knot, that swallowing of adherent water with the prey and evaporative cooling might increase salt stress of heat stressed birds. Although the environment at the Bragantinian tidal flats did cause heat stress for the birds - indicated by panting, resting in shallow water and lifting of back feathers - the birds did not distribute according to differences in salinity. They might be well adapted to this problem, just like the Knot at the Banc d'Arguin (Klaassen and Ens 1990).

The time of emergence of a foraging habitat does not only indicate the available foraging time for birds at that location (Zwarts et al. 1990a) but also corresponds with a grade of dryness of the sediment. While plots with a long time of emergence generally expose most of this time a desiccated sediment, plots which emerge for only a short time remain close to the waters edge and their sediment stays wet. At the Wadden Sea many birds follow the waters edge as the tide falls and rises (Reise 1985; Scheiffarth and Nehls 1998). Foraging close to the waters edge might be advantageous because of the increased penetrability or an increased prey activity at the wet sand (Pienkowski 1983c; Colwell and Landrum 1993). However, the time of emergence did not influence the distribution of the birds at the Bragantinian tidal flats. A reason might be that numerous tidal creeks cross the intertidal and foraging in the proximity to water is always possible for the birds in the study area.

Although environmental factors had no influence on the birds distribution, the choice of microhabitats differed between the species and microhabitat preferences can be distinguished. This differentiation was at least in part determined by physiological characteristics of the birds. The water depth selected by the birds is correlated with leg length, a relationship also described by Ntiamoa-Baidu et al. (1998). Herons and egrets are

bound to deep water, they are large enough to explore this microhabitat and their dominant prey (fish) is found there. A second group, composed of Marbled Godwit, Red Knot and Short-billed Dowitcher, is also found mainly at water covered areas, using more or less deep probes in the sediment. They are medium or large sized shorebirds which forage mostly tactile (chapter 6). Thus they are large enough to be able to forage in reasonably deep water and they can make advantage of the soft wet sand. The third and largest group of birds is predominantly associated with dry sand. Some of those birds use at least occasionally areas covered by water (Willet, Grey Plover, Semipalmated Sandpiper, Ruddy Turnstone and Whimbrel). They expose either predominantly tactile behaviour, which might be favoured by wet sediment (Semipalmated Sandpiper), or they show a very variable and opportunistic behaviour (chapter 6.2.4). The microhabitat use of birds with flexible behaviours might be determined to a lesser extent by technical problems of the foraging behaviour but by prey characteristics (Turpie and Hockey 1997). The other species avoided water strictly (Collared Plover, Semipalmated Plover and Sanderling). Light reflections and refractions might hamper these mostly visually foraging birds and as a result they might avoid areas covered by water. Since they generally do not probe deeply in the sediment, they are not dependent on moist sand. The Scarlet Ibis is quite exceptional in its use of microhabitats with the complete avoidance of water and extremely deep probes. It belongs also to the opportunistic birds but is able to use also the deep and profitable sediment layers due to its large bill.

The size of the bill determines the probing depth and therefore the harvestable prey fraction (Recher 1966; Piersma et al. 1993; Zwarts and Wanink 1993). Most species can only make use of the prey in the first 5 cm depth. Only the Scarlet Ibis uses a depth up to 20 cm, the Marbled Godwit probes up to 10 cm. Most birds probe as deep as possible, merely Whimbrels and Willets use unusually shallow probes which might be related to their prey choice.

Microhabitat preferences are consistent with preferences of birds reported elsewhere (Poole and Gill 2000 and references therein). Recher (1966) also investigated the birds association with water, water depths- and probing depths preferences of wintering shorebirds at the central coast of California and birds apparently preferred similar microhabitats as in Brazil. At New Jersey Burger et al. (1977) also found comparable habitat preferences. The authors described that large birds prefer an algae covered muddy zone while the small shorebirds are mostly found at the dry sand. Since at the Bragantinian peninsula the small shorebirds are highly visual foraging shorebirds, they prefer as well dry sand presumably because of their foraging technique, which requires no deep probing. And since the large shorebirds forage mostly tactile they prefer the softer sediments in the water. Not surprisingly, the foraging habitat of herons and egrets is always described as more or less deep water (Bildstein 1990; Frederick and Bildstein 1992).

Guilds

As the strong variability of avian plot preferences predicted, a guild structure based merely on the spatial distribution of the birds is short living and variable. The including of environmental factors as sediment characteristics, pore water salinity, time of emergence or number of burrow openings at the sediment surface in the PCA does not help to determine stable avian guilds. Quite the reverse, this environmental factors attain an own factor, unrelated to the avian distributions. That means either, that the factor which differentiates the bird community was not measured, that the wrong spatial scale was chosen to detect separations or that the birds are completely randomly distributed. The last point can be ruled out, since already the inspection of the figures reveal distributional patterns (Fig.31).

Some studies determined microhabitat preferences of birds to be important for their distribution (Recher 1966; Burger et al. 1977). When microhabitat preferences were used to determine guild structure, some more distinct formations occurred. Wading birds and shorebirds were distinct groups, as could be expected before. But also within the shorebirds three guilds could be defined and the microhabitat preferences described before were in part reflected in this structure. The first guild is composed by a group of large birds , which preferred muddy areas, the presence of water and deep probes, and a second group of smaller birds, preferring dry and sandy areas and only shallow probes. This guild is distinctly separated from guild 2, a group of medium sized birds favouring intermediate salinities. This could be a result of a special prey preference, all three birds feed to a larger part on bivalves. However, since no detailed data on prey taxa is available and nothing is known about salinity preferences of the prey organisms, this remains speculative. Only the Marbled Godwit belongs to the last guild. With its deep probes and its preference for muddier areas, it favours apparently a different microhabitat compared to all other birds.

The microhabitat distinctions used in the analysis proved to be valuable to define different groups of birds by their microhabitat use. Salinity, sediment grain size and water requirements were the best separating variables.

To summarize, at the Bragantinian tidal flats two groups of birds occur: migratory shorebirds in northern winter time and residential wading birds mostly in the summer. Hence, the differentiation between migrants and residents is not only manifested in their migratory habits, but also in their devotion to different taxonomic and ecological groups. This is also manifested in a distinct separation in microhabitat use. The shorebirds can be distinguished further in groups of birds preferring specific salinities, sediment grain sizes and the presence or absence of water. This differentiation can partly be explained by shorebird size and maybe also by prey preferences, a question addressed in chapter 5.

5 Foraging at tropical tidal flats – birds in relation to the benthic community

5.1 Introduction

What prey is eaten by the birds, why did they choose it and do the benthic resources determine the birds' spatial distribution?

Birds require energy in the form of food for several purposes: self-maintenance, flying to and from their feeding grounds and foraging. For breeding birds the costs of reproduction add to this and migrants need to accumulate fuel reserves prior to migration. But shorebirds and wading birds feeding at intertidal areas face the constraint that their feeding grounds are only temporarily available during low tide, so the foraging time is limited. Thus, birds might be restricted in their energy intake and they are therefore generally expected to maximize their food intake rate.

Not all of the benthic organisms present on a tidal flat are accessible and ingestible for the birds. Zwarts and Wanink (1993) and Piersma et al. (1993) draw special attention to the so called "*harvestable fraction*" of prey, the fraction which occurs in sediment depths accessible by probing, which shows sizes adequate for handling and which is also profitable for the birds. In contrast to these studies, here, harvestability refers only to accessibility (probing depth) and ingestibility (prey size), since special emphasis is given to profitability in a separate section. How rich is the effective food stock available for the birds at the Bragantinian peninsula?

Which of the potential prey items are actually chosen by the birds? The *observed diet* of the birds will be described in detail. But prey items can often be distinguished only in broad categories, during focal observations. To get a more detailed impression of the variety of prey items ingested, droppings were searched for the remains of prey taxa. Also, Charnovs (1976) concept for the calculations of profitabilities and optimal diet was used to determine which harvestable prey taxa should be included in the diet to maximize the energetic gain.

The term "*profitability*" was first used by MacArthur and Pianka (1966) to articulate the theory of optimal foraging. Any ingested prey item has a cost for the predator in terms of searching- and handling time, and a benefit expressed as its energetic- and nutritional value. The net value is termed profitability. It is defined as the energetic value of a prey item divided by the sum of handling time and searching time (MacArthur and Pianka 1966; Pyke et al. 1977). Predators, which optimize their feeding efficiency, are expected to choose the most profitable prey (Sutherland 1982). With help of behavioural data (handling- and searching time of prey), the profitability of harvestable benthic taxa will be determined individually for all bird species. Since searching time was not determined directly during focal observations, it was calculated

with the assumption that it is inversely proportional to the density of prey organisms, thus prey density is taken in account (chapter 2.2.2).

MacArthur and Pianka (1966) used profitability to develop a model for the determination of the *optimal diet* of a predator, which was transferred to a more mathematical form by Charnov (1976). It predicts that a predator should only include those prey types in its diet, which provide an equal or larger energy gain (AFDW/handling time) than the mean energy gain by searching and feeding of already included prey items (AFDW/handling+searching time) (chapter 2.2.2).

Because of its central meaning for birds, prey is considered to be the most important factor for the birds' *distribution* (O'Connor 1981; Evans and Dugan 1984; Goss-Custard 1984; Puttick 1984). Is the avian distribution in the study area related to the distribution of the prey organisms? Holling (1959) proposed that increasing prey densities accelerate the rate of feeding up to an asymptotic level. Since foraging is most beneficial in areas with high prey densities, predators could be expected to accumulate in those patches (Hassel and May 1974; Charnov 1976). However, Fretwell and Lucas (1970) point out that predators will not distribute solely according to prey densities since competition will act against accumulations of predators in profitable patches. The distribution resulting from these two processes acting together is called the "ideal free distribution".

Initially, the influence of benthic distribution on their avian predators were investigated in temperate regions (Recher 1966; Wolff 1969; Pienkowski 1983a; Smit and Wolff 1983; Goss-Custard et al. 1991; Colwell and Landrum 1993; Zwarts and Wanink 1993). Only recently, also shorebirds (Zwarts 1988; McNeil et al. 1995; De Boer 2002) and wading birds (Miranda and Collazo 1997; Smith 1997; Olmos et al. 2001) in the tropics were subjects of those types of studies.

To compare the avian spatial distribution with that of the benthic organisms at the Bragantian peninsula, different statistical methods were applied. While Correlation analysis and Multiple Regressions are able to investigate the relationship between one avian variable (total birds or only one bird species) and one or more benthic species, Multivariate analysis (Multidimensional Scaling (MDS) or Canonical Correspondence analysis (CCA)) are capable of investigating these relationships simultaneously for all bird species.

Since the primary prey of wading birds, the fish, was not investigated for its energetic content and its spatial distribution, this group of birds had to be ignored in most considerations of this chapter.

5.2 Results

5.2.1 *Harvestable prey fraction*

The prey within the sediment can be divided into fractions of certain depth- and size classes. These fractions constitute different amounts of biomass, depending on the number and weight of items belonging to these fractions. Biomass rich depth/size fractions of bivalves were located at <5 cm depth and >10 cm depth and they included only species of > 3 cm length (Fig. 28). Some bird species could not benefit from those fractions since they fed only on smaller bivalves (Semipalmated Plover, Sanderling, Semipalmated Sandpiper and Collared Plover). Other species were able to prey on that size fraction but could only penetrate the upper 5 cm depth (Grey Plover, Red Knot, Willet, Whimbrel and Short-billed Dowitcher). Only the Scarlet Ibis was able to use the entire size and depth range and could therefore benefit from all advantageous depth/size fractions (Fig. 28).

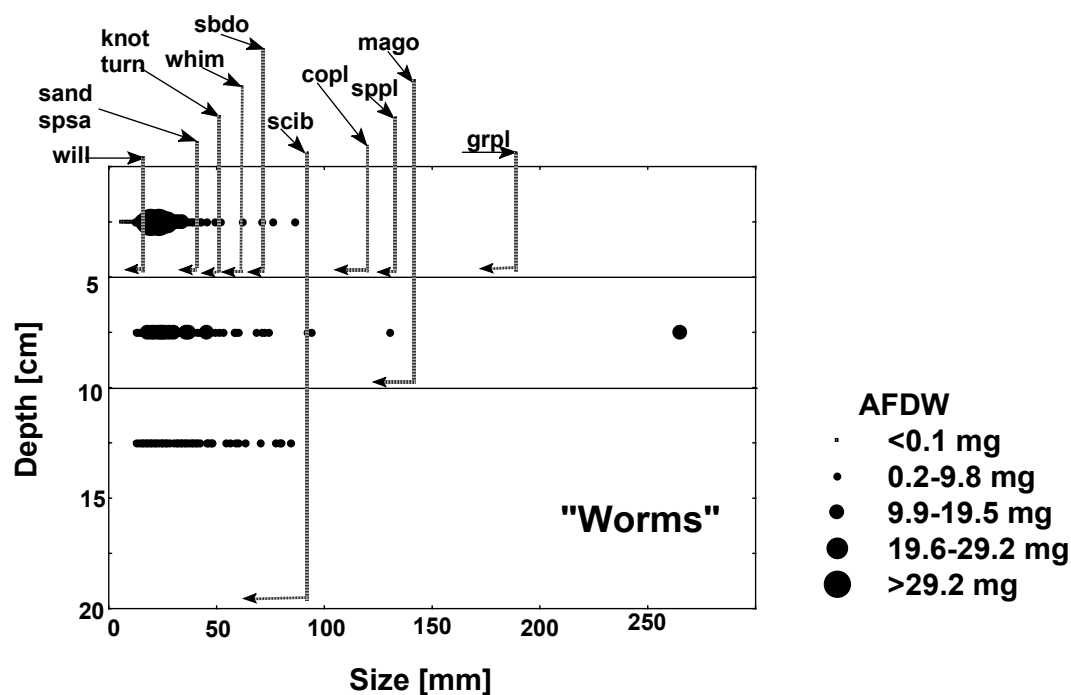
Highest AFDW of crustaceans were found in depths >10 cm and sizes of >3 cm (Fig. 28). This prey fraction was available only for Scarlet Ibises, all other birds fed only on small crustaceans.

“Worms” were found with highest AFDWs in the upper 5 cm of the sediment and a size of 2-3 cm. They were accessible to all species. Only the Willet appeared to be restricted to “worms” <2 cm (Fig. 28).

The mean harvestable biomasses available for each bird species were generally very low (Table 8) and decreased over time. Yet, the range shows that the intertidal provided spots for most birds with very high harvestable biomass values, at least in the first months of the year. For only few species (Semipalmated Plover, Marbled Godwit, Sanderling and Semipalmated Sandpiper) there seemed to be no location at all with considerable amounts of harvestable biomasses.

Table 8. Harvestable biomass available to the birds in the study area. Given are the biomasses per plot with their mean and range per month [gAFDW/m²] in 2001.

Taxon	January	February	March	April	May	June
Scarlet Ibis	1.5 (0-24.1)	1.9 (0-25.6)	2.2 (0-25.6)	1.3 (0-25.6)	0.3 (0-8)	1.1 (0-25.6)
Collared Plover	0.2 (0-3.2)	0.1 (0-1.8)	0.4 (0-13.3)	0.2 (0-2.8)	0.1 (0-1.2)	0.1 (0-1.2)
Grey Plover	0.9 (0-11.3)	0.5 (0-8.4)	0.5 (0-13.3)	0.3 (0-4.6)	0.1 (0-1.7)	0.1 (0-1.2)
Semipalmated Plover	<0.1 (0-1.1)	<0.1 (0-1)	<0.1 (0-0.1)	<0.1 (0-0.7)	<0.1 (0-0.6)	0.1 (0-1.2)
Marbled Godwit	<0.1 (0-0.1)	<0.1 (0-0.1)	<0.1 (0-0.2)	<0.1 (0-0.1)	<0.1 (0-0.1)	<0.1 (0-0.2)
Red Knot	0.7 (0-11.3)	0.4 (0-8.4)	0.1 (0-3.1)	0.2 (0-4.6)	0.2 (0-8)	<0.1 (0-0.4)
Ruddy Turnstone	0.7 (0-11.3)	0.4 (0-8.4)	0.1 (0-3.1)	0.2 (0-4.6)	0.2 (0-8)	<0.1 (0-0.4)
Sanderling	<0.1 (0-0.2)	<0.1 (0-0.1)	<0.1 (0-0.2)	<0.1 (0-<0.1)	<0.1 (0-<0.1)	<0.1 (0-<0.1)
Semipalmated Sandpiper	<0.1 (0-0.1)	<0.1 (0-0.2)	<0.1 (0-0.1)	<0.1 (0-0.1)	<0.1 (0-0.1)	<0.1 (0-0.1)
Short-billed Dowitcher	0.8 (0-11.3)	0.5 (0-8.4)	0.2 (0-5.6)	0.3 (0-4.6)	0.2 (0-8.1)	<0.1 (0-0.4)
Whimbrel	0.8 (0-11.3)	0.5 (0-8.4)	0.5 (0-13.2)	0.3 (0-4.6)	0.2 (0-8)	0.1 (0-1.2)
Willet	0.8 (0-11.3)	0.5 (0-8.4)	0.5 (0-12.8)	0.3 (0-4.6)	0.2 (0-8.1)	<0.1 (0-1.1)



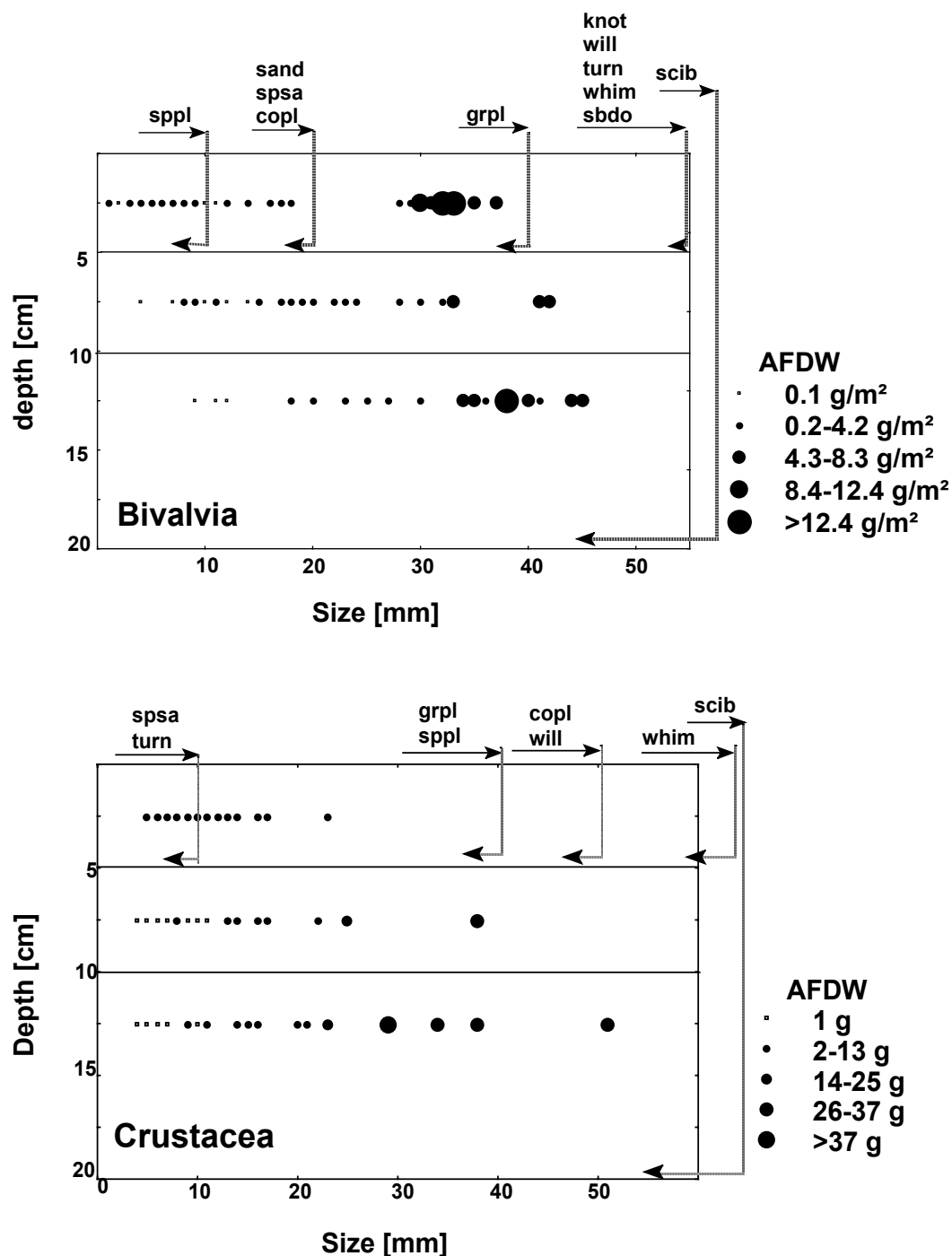


Fig. 28. Size-depth occurrence of the benthos organisms. The size of the dots referring to a certain size/depth class gives the sum of AFDWs found during all benthic investigations 2001/2002. The dotted lines for the individual bird species indicate the searching depth and maximal size of prey chosen during the focal observations. The prey fraction to the left of the lines is the harvestable prey fraction for the species. Minimal sizes were not considered in the diagram since they mostly reached only few mm and all birds were observed to feed on tiny prey items that were not identifiable. An explanation of the short forms of the bird names is given in the Abbreviation list. The diagram was inspired by those given by Piersma et al. (1993).

5.2.2 Diet

Observed prey

During the focal observations in 2002 prey items were identified by sight. Prey groups could be differentiated broadly into mussels, crustaceans, fish, snails and “worms” (Table 9). On two occasions Tricolored Herons were observed to snap for dragonflies passing by. At another incident a Little Blue Heron was feeding on discarded fish which was deposited on the beach by local fishermen. Unfortunately, in many instances identification of the prey was impossible due to the small size of the items or the speed of feeding. Those items were labelled as “unknown”.

As could be expected, a large proportion of the prey of herons and egrets was composed of fish (Table 9). Scarlet Ibises and Willets showed a preference for crustaceans within their identified prey items, the Scarlet Ibis combined them with bivalves. The Marbled Godwit and all plovers showed a more or less distinct preference for “worms” while the Grey Plover added mussels and crustaceans as well. The other sandpipers favoured a combination of mussels and “worms”, sometimes supplemented by crustaceans and snails. Only the Red Knot showed a preference for snails combined with some bivalves (Table 9).

Table 9. Proportional prey composition for the birds observed 2002 in the study area. N is the number of observed prey items.

Species	Prey								n
	bivalve	snail	crustacean	“Worm”	fish	insect	discard	unknown	
Little Blue Heron	0	0	5	5	35	0	0	55	20
Snowy Egret	0	0	1	0	42	0	1	56	79
Tricolored Heron	0	0	3	0	78	2	0	17	64
Scarlet Ibis	16	3	23	11	1	0	0	46	92
Collared Plover	4	0	2	42	0	0	0	52	163
Grey Plover	12	1	14	27	0	0	0	46	104
Semipalmated Plover	1	0	0	70	0	0	0	29	269
Marbled Godwit	0	2	0	41	0	0	0	56	41
Red Knot	13	19	0	1	0	0	0	68	96
Ruddy Turnstone	39	0	4	4	0	0	0	52	46
Sanderling	11	4	0	11	0	0	0	75	28
Short-billed Dowitcher	13	4	0	9	0	0	0	74	152
Semipalmated Sandpiper	11	0	1	9	0	0	0	79	130
Whimbrel	27	4	11	5	0	0	0	53	75
Willet	10	5	16	2	0	0	0	68	62

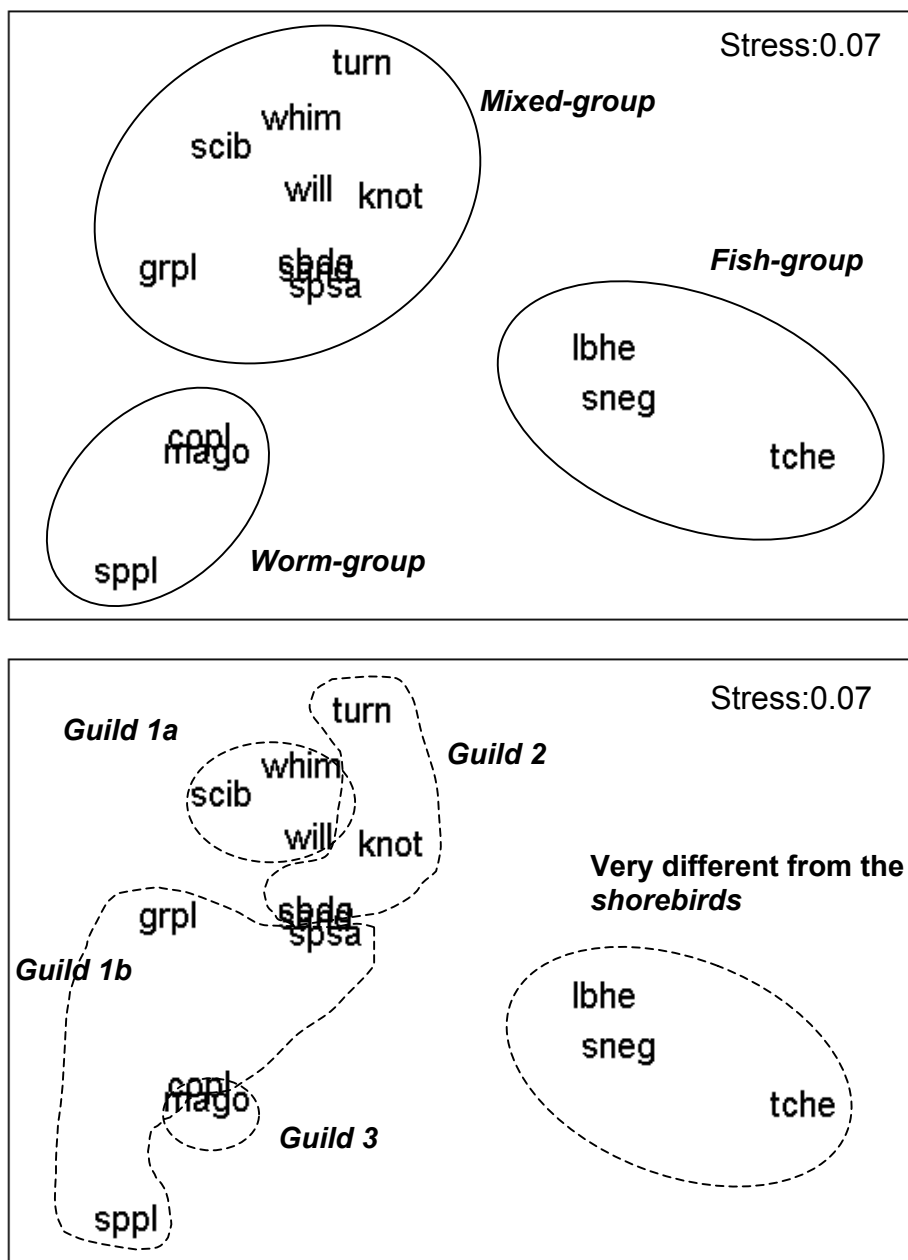


Fig. 29. Similarities of the birds diets (top) and microhabitat uses (bottom). Shown are two identical MDS-plots calculated on the observed prey proportions with Schoeners Similarity Index. At the top, three groups with relatively similar prey are marked with circles. At the bottom, the guilds based on similar microhabitat use (chapter 4.2.4) are marked with dotted lines.

Similarities in the choice of prey organisms, termed the “dietary overlap”, were calculated by the formula given by Schoener (1970) (Fig. 29). Three groups could be distinguished according to their diet: the “Fish-group” was composed of herons and egrets with a large proportion of fish prey. The “Worm-group” was composed of the “worm” preferring Collared Plover, the Marbled Godwit and the Semipalmated Plover. And the third and largest “Mixed-group” consisted of all birds which favoured a diet of different combinations of prey taxa (Fig. 29). When the guilds based on microhabitat use, as defined in chapter 4.2.4, are indicated in the same diagram, it becomes apparent that diet is related to the use of microhabitats.

Although the guilds do not match exactly with the groups of dietary preferences, they do, however, show a certain amount of overlap.

More detailed information on ingested prey taxa was provided by the investigations of the collected droppings. Additionally, the calculation of optimal diets gave insight into the most likely consumed prey items.

Droppings

Through the collection of droppings, some prey taxa actually ingested could be identified (Table 10, Appendix IV Table 41). But since only some benthic organisms are comprised of recognizable body parts in the droppings, the list cannot be considered as complete. To obtain a more comprehensive list of prey taxa, an optimal diet was calculated under the assumption that birds tend to optimise their dietary preferences.

Profitability and optimal diet

Profitabilities were calculated as AFDW gain per second foraging (for details on the calculations see chapter 2.2.2). Profitabilities could be simply compared between prey items, but they do not provide information on which of this prey is attractive enough to be included in the birds diet. Hence, calculations were done according to Pyke et al. (1977) to evaluate a (theoretical) optimal diet (Table 10). Since no size preferences for gastropods were available, they could not be included in the calculations for profitabilities or optimal diets.

Although bivalves and crustaceans generally provided more biomass per prey item (chapter 3.2.4), polychaetes were also profitable in some cases merely due to their high densities, which resulted in short searching times. The optimal diet of some bird species included only few prey items (Red Knot, Sanderling, Whimbrel, Willet) (Table 10). The prey items for those optimally specialized birds were some bivalves, often *Tellina radiata* and *Protothaca pectorina*, sometimes supplemented by polychaetes (Sanderling) or crustaceans (Willet). Other bird species should always have been generalists according to their calculated optimal diet (Marbled Godwit, Ruddy Turnstone, Semipalmated Sandpiper). They should have included many types of bivalves, crustaceans and polychaetes in their diet (Table 10). The optimal diet of the remaining species switched between these strategies (Scarlet Ibis, Collared Plover, Semipalmated Plover, Short-billed Dowitcher).

		Ruddy Turnstone						Sanderling						Short-b. Dowitcher						Semip. Sandp.						Whimbrel						Willet					
Taxon	Months:	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Sipunculidae	Sipunculidae																																				
Nemertinea	Nemertinea	X	X	X	X		X									X			X	X	X	X	X	X	X												
Bivalvia	<i>Anomalocardia brasiliana</i>		X											X	X											X	X					X	X				
	<i>Divaricella quadrisulcata</i>																			X												X		X			
	<i>Lucina pectinata</i>															X	X	X			X	X	X	X								X		X			
	<i>Protothaca pectorina</i>				X	X	X							X		X	X	X					X			X		X	X					X	X		
	<i>Tagelus plebeius</i>				X		X		X	X						X		X			X	X	X					X		X				X		X	
	<i>Tellina lineata</i>																																				
	<i>Tellina radiata</i>		X	X	X		X		X	X	X	X	X		X	X	X	X	X		X	X	X	X	X	X	X	X	X	X				X		X	
Crustacea	Callianassidae					X	X																												X		
	<i>Callinectes sp.</i>					X																															
	Decapoda																																		X		X
	<i>Eurytium limosum</i>																					X															
	Gammaridea	X	X				X	X													X	X	X														
	Hippolytidae						X																														
	Idotheidae	X		X																		X	X	X													
	Mysidae		X	X			X																X											X		X	
	Pinnotheridae	X	X	X			X														X	X			X	X											
<i>Uca maracoani</i>	X	X		X																				X	X							X					
Polychaeta	Capitellidae	X	X	X		X					X	X			X				X	X	X		X	X					X								
	Eulepethidae																																				
	Glyceridae	X		X											X						X		X														
	Goniadidae		X	X	X										X						X	X	X	X													
	Lumbrineridae	X																			X																
	Magelonidae	X		X	X										X						X		X	X													
	Nephtyidae	X	X	X	X		X			X	X	X			X		X		X	X	X	X	X	X	X			X									
	Nereidae	X	X	X	X	X	X		X					X		X		X		X	X	X	X	X	X			X									
	Onuphidae																																				
	Orbiniidae		X																			X															
	Phyllodocidae				X																			X													
	Pilargiidae												X																								
	PilargiidaeB	X	X		X																	X	X		X	X											
	Saccocirridae																																				
	Spionidae																																				

Prey size

The prey sizes observed ranged between 18.5 cm (fish) and about 1 mm (bivalvia) (Table 11).

Table 11. Prey sizes chosen by the birds in the study area in 2002. Sizes are given in mm.

Species	Bivalvia	Crustacea	“Worm”	Fish	<i>n</i>
Little Blue Heron		22	148	15-185	20
Snowy Egret		16		8-81	79
Tricolored Heron		29-48		10-67	64
Scarlet Ibis	15-58	15-58	29-87	29	92
Collared Plover	1-10	3-44	4-116		163
Grey Plover	3-36	3-39	9-180		104
Semipalmated Plover	5	10	2-122		269
Marbled Godwit			10-133		41
Red Knot	14-40		43		96
Ruddy Turnstone	12-59	5-7	19-47		46
Sanderling	8-15		13-38		28
Short-billed Dowitcher	6-63		11-68		152
Semipalmated Sandpiper	4-10	4	2-39		130
Whimbrel	9-52	17-61	35-52		75
Willet	5-44	11-49	11		62

The sizes of chosen bivalves and crustaceans were correlated with bill sizes of the shorebirds. “Worm” sizes showed no significant relationship (Appendix IV, Table 45) (Fig. 30).

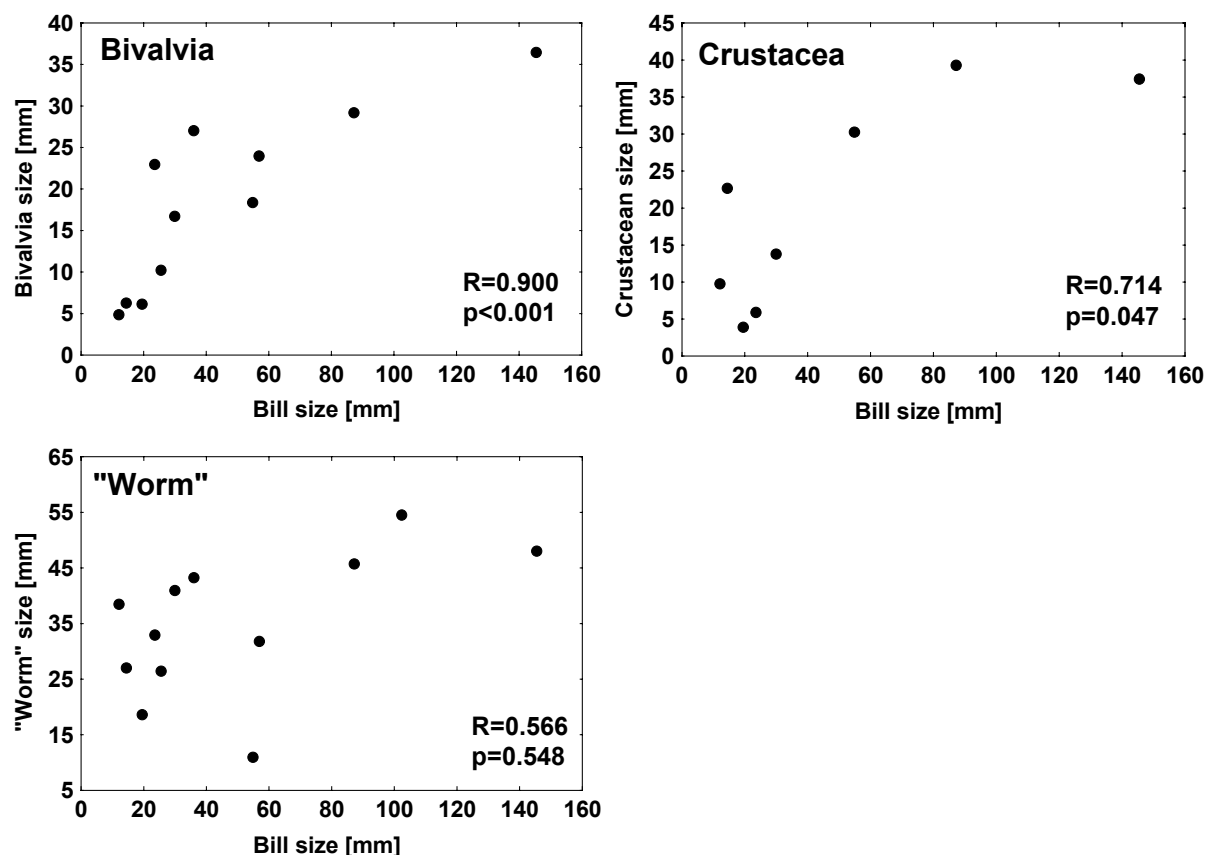
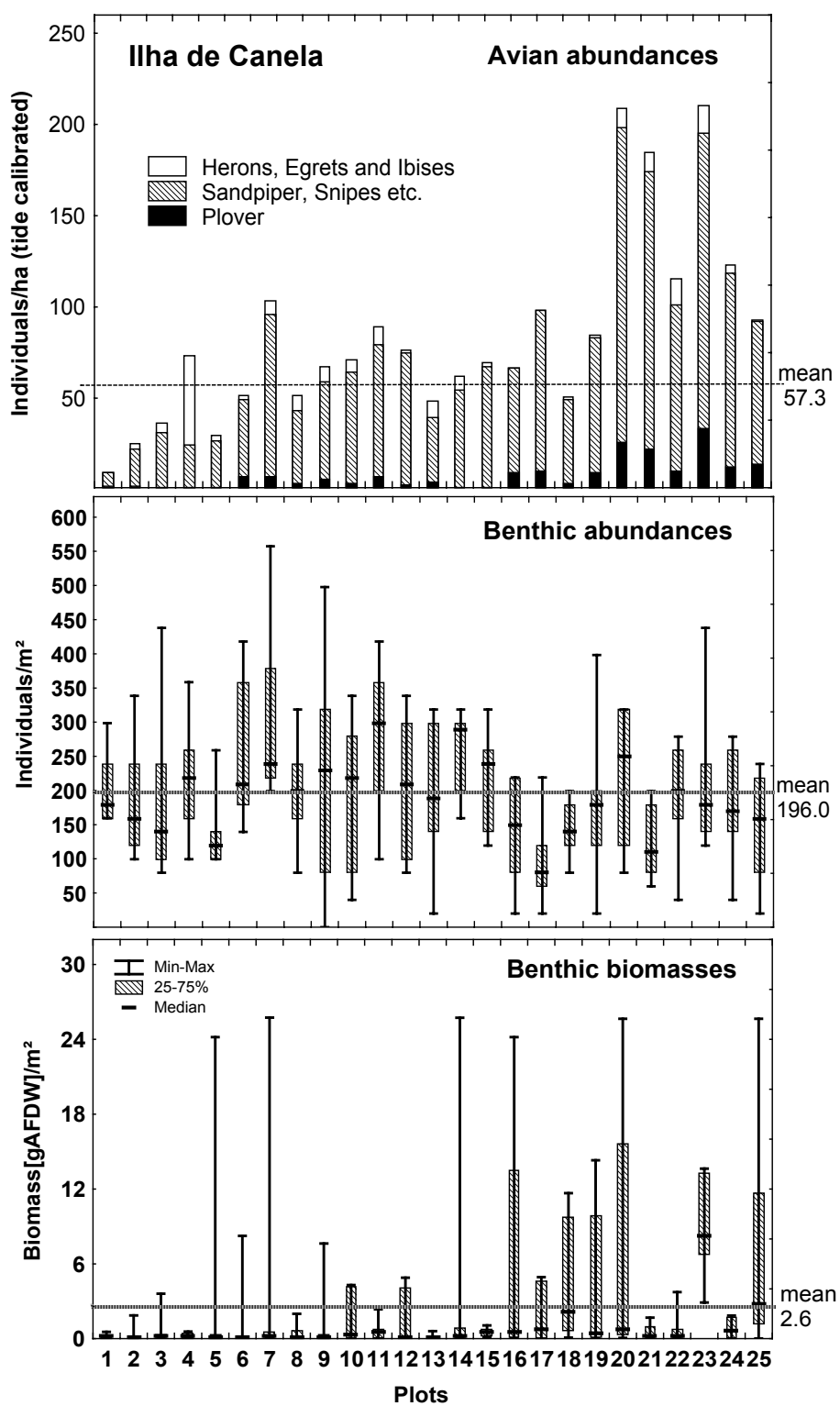
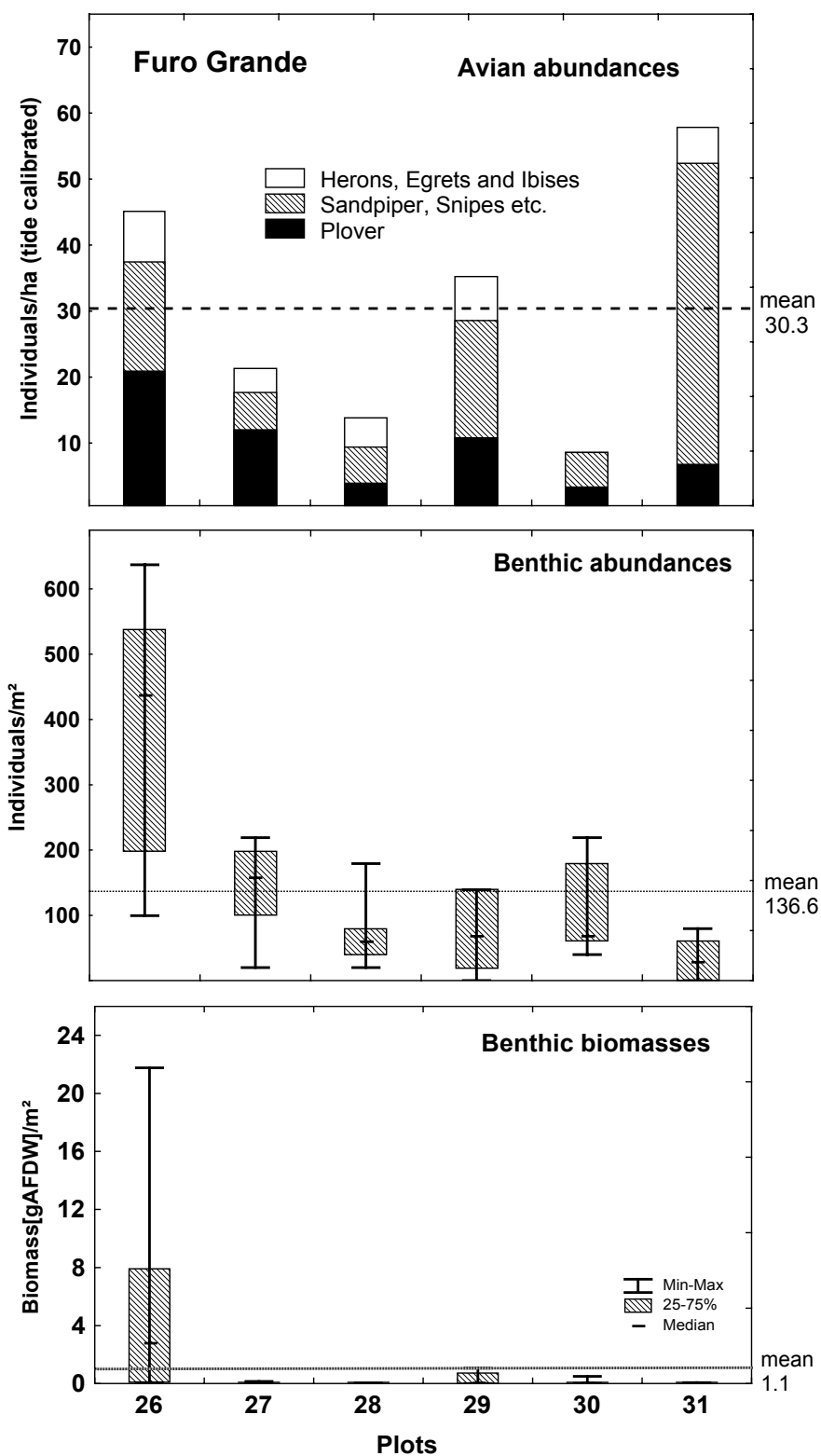


Fig. 30. Significant correlations (Spearman Rank Correlation Analysis) between shorebird bill sizes and mean prey sizes. Each data point corresponds to the mean bill size/prey size relation of a bird species. Bill sizes were obtained from the literature (Appendix I, Table 22) and mean prey sizes were calculated from the data collected during the focal observations in 2002.

5.2.3 Distribution of birds in relation to macrobenthos

When avian abundances and benthic abundances and -biomasses were plotted together, no immediately apparent relationships became evident (Fig 31). Although areas of higher or lower avian abundance appeared, no clear association with benthos organisms was noticeable. Since it was not clear whether birds would react to benthos all in the same fashion or differently, according to species, whether prey of interest would include all benthic organisms, faunistic zones, benthic groups or benthic taxa, whether the abundances, the biomass or the mean profitability of the prey are crucial, a series of statistical tests was conducted to evaluate all these different possibilities and combinations. The results of these tests were compared with each other to find the model that best fits the pattern of the Bragantinian birds and their prey organisms.





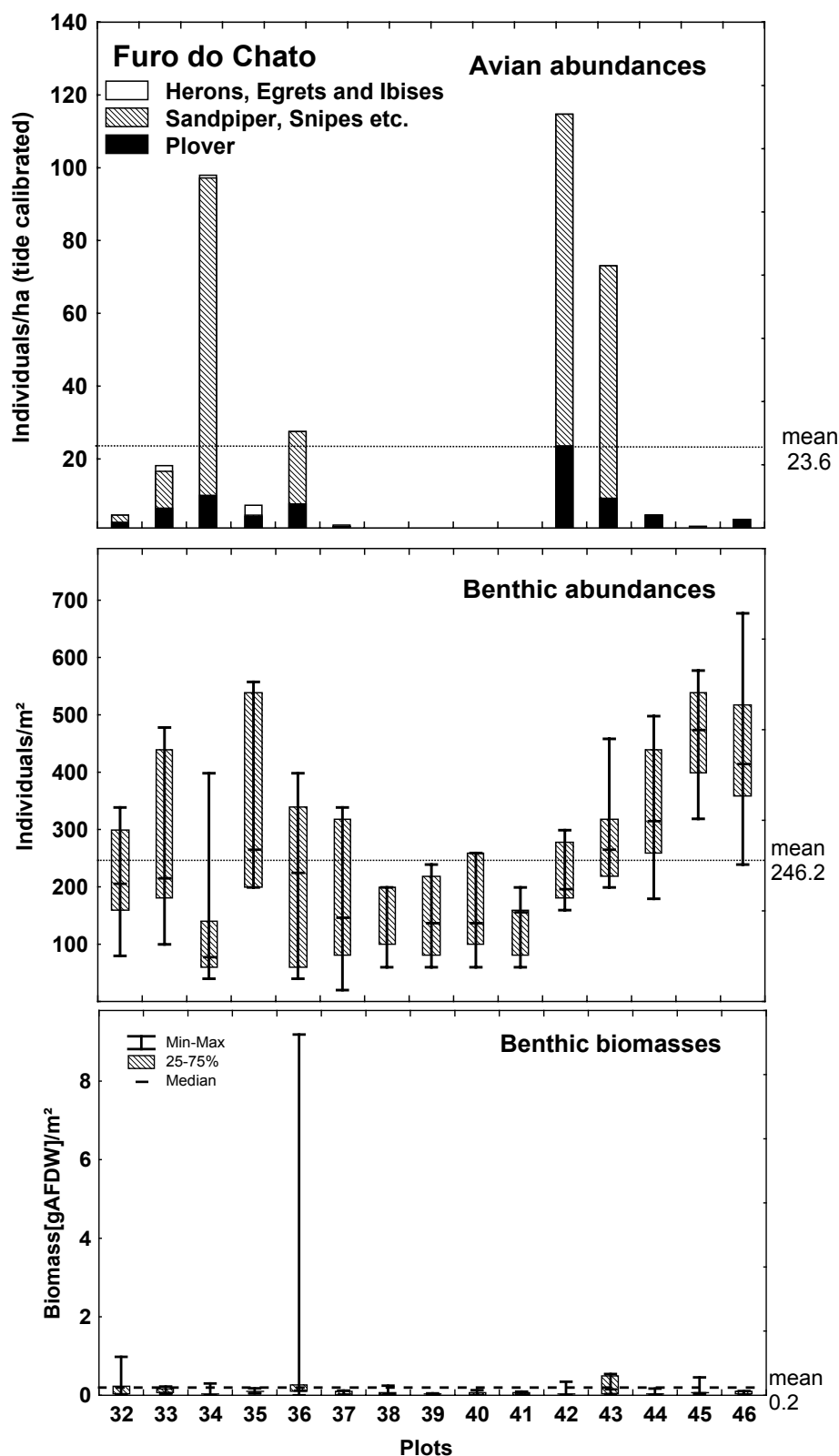


Fig. 31. Mean avian abundances (tide calibrated), benthic abundances and benthic biomasses in the plots of the Ilha de Canelas, Furo Grande and Furo do Chato. Given are the mean avian abundances and median, minimum and maximum of benthic abundances and biomasses during January-June 2001.

Spearman rank correlations and Multiple regressions

To test if bird abundances were correlated with the appearance of the overall benthic community, Spearman Rank Correlations between abundance of individual avian species and total harvestable benthic abundance, total harvestable benthic biomass and mean benthic profitability per plot and month were conducted. The highest R reached 0.715 (between Scarlet Ibis and benthic abundances) but generally R was very low (only 3 out of 120 tests reached an R higher than 0.5). Thus, correlations were in general ineffective in detecting considerable relationships (Appendix IV, Table 42).

Instead of pooling all benthic taxa, Multiple Regression analyses were done with either individual benthic taxa or higher benthic groups as dependent variables. Each test was done with log transformed total benthic abundances and total benthic biomasses in each plot, and a comparison between the R^2 revealed the convenience of the different variables. Since birds generally do not distribute linearly along gradients, quadratic terms of the variables were also included in the analysis (ter Braak and Verdonschot 1995). The adjusted R^2 values ranged between <0.01 and 0.70, but only 5 out of 240 tests yielded in an R^2 value larger than 0.5 (Appendix IV, Table 43). The use of benthic taxa resulted generally in higher R^2 values than the use of taxonomically higher benthic groups and benthic abundances were more successful than using biomasses. It proved that some bird species responded at few months to abundances. Nevertheless, R^2 was very low in most cases and Multiple Regressions could generally not be used to reveal the relationship between avian and benthic spatial distributions.

Faunistic zones

An MDS plot was calculated for the avian assemblages in the different plots to reveal if they could be separated in subgroups. No differentiation according to the use of faunistic zones as defined in chapter 3.2.4 emerged (Fig. 32).

On the contrary, the avian communities found in the different faunistic zones were quite similar. Only few plots within faunistic zones exposed differing avian communities but those differentiations were apparently not related to the benthic assemblages. When bird species were investigated individually, some were equally abundant in all faunistic zones while others preferred specific areas (Appendix IV, Table 44 and Fig. 41). The zones 3 and 4 were the most preferred areas, zone 5 was mostly avoided by the birds. None of the bird species was distinctly bound to a particular zone. Although there is a certain effect of the faunistic zones on the birds' distribution, this pattern is not very distinct and cannot singularly explain the distribution of the birds.

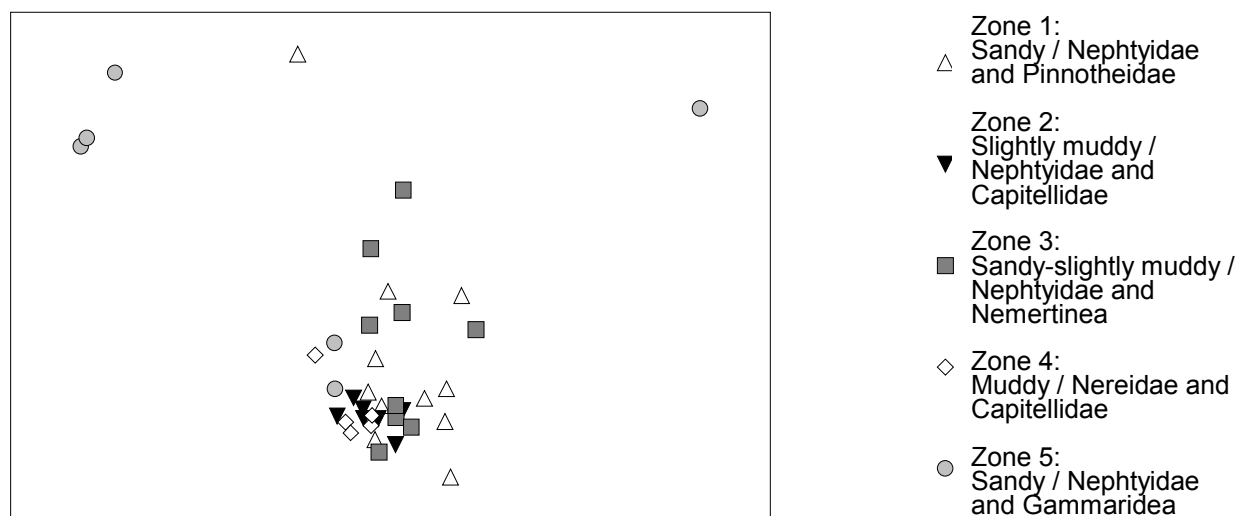


Fig. 32. Avian composition in the benthic zones. Given is a MDS plot calculated with mean avian compositions in the plots in 2001 (tide calibrated). The corresponding faunistic zones of the plots are indicated by symbols.

Canonical Correspondence analysis

Canonical Correspondence analyses was also applied several times with modified variables in search of the best fit model. Avian abundances were included as “all species”, “only plovers”, “only sandpipers”, “only birds that forage within the upper 5 cm” of the sediment or “up to 20 cm depth”. The benthic variables were altered between “taxonomic level”, “higher taxonomic level” and even rougher differentiations (Groups1 and Groups 2, see Appendix IX, Table 46). They were all applied with abundance and biomasse. As in the Multiple Regression analysis, it proved that the more detailed the included variables, the better was the model (measured by the sum of eigenvalues). Transformations did not improve the model. Eigenvalues of the single axis never exceeded 0.40, i.e. they could not explain more than 40% of the variables variance (Appendix IV, Table 46). To exemplify this, a diagram of the best CCA is given (Fig. 33). Of all CCAs conducted, this is the only one with eigenvalues high enough to provide a meaningful diagram. The diagram shows that in January the bird community splits into two groups. Spotted Sandpiper, Semipalmated Sandpiper and Snowy Egret are assembled in one group, and all other birds in the other. The Collared Plover is the only bird that distributes very differently from all others. This differentiation is clearly associated with plot preferences. While the birds of the first group preferred plots close to the beach of the Ilha de Canelas, the Collared Plover appeared primarily in plots of the Furo do Chato. All other birds were distributed in the remaining plots. Also, relationships between the birds’ distribution and some benthic organisms became apparent (Collared Plover and Gammaridae; the first group and Pinnotheridae). However, when compared to the

observations made in the plots, the diagram did not provide a good picture of reality. The Spotted Sandpiper only appeared in the plots of the Furo Grande, which was not reflected very well by the diagram. According to Jongmann et al. (1987), eigenvalues below 0.5 are weak, thus, the model is most likely not able to explain the situation very well. In addition, most environmental factors are indicated by relatively short arrows, i.e. their explanatory value is quite low. Finally, the CCA was also not able to find distinctions between most bird species, which are grouped together tightly. Overall, it is not quite clear if the shown diagram characterizes the situation reasonably, but all other CCAs, which resulted in far lower eigenvalues, certainly do not. Hence, the CCA also failed to reveal a clear picture of the bird distribution in relation to the benthic distribution.

5.3 Discussion

Shorebirds can only feed in intertidal areas when these are exposed during low tide. Due to this limitation they might be food limited and one would expect the birds to choose their prey carefully in order to focus on the most profitable organisms and spots on the tidal flats. This optimisation is subject of the “optimal foraging theory” as developed by Krebs (1978). To understand which spots are most attractive for the birds and if they distribute according to this, it must be evaluated first, which of the prey species present are harvestable (accessible and ingestible) for the birds.

Harvestability

The harvestable prey fraction differs greatly from the total prey present and it is also different for all species. The majority of all benthic individuals found in the Bragantinian tidal flats are polychaetes (Fig. 13). Most of them are harvestable by all birds, but they do not provide much biomass. Crustaceans and bivalves have comparatively large individual AFDWs, but the large individuals are deeply burrowed and not accessible for most birds. The most rewarding depth/size classes are available for only few large birds. Thus, most birds, especially the small species, are excluded from a large fraction of the food stock and have to rely on “worms” present in only low biomasses.

The importance of the harvestable biomass fraction for the value of a feeding site is also stressed by Piersma et al. (1993) when comparing the intertidal of the Wadden Sea with that of the tropical Banc d’Arguin. Although the total benthic biomass at the Wadden Sea is much higher than that of the Banc d’Arguin (19.7g/m² and 4.8 g/m² respectively), both areas comprise a comparable amount of harvestable biomass for Red Knots (Wadden Sea: 2.96 g/m², Banc d’Arguin: 3.4 g/m²). Together with the lower cost of living in the tropics (Klaassen et al. 1990), life is energetically much more advantageous for the Red Knot at the Banc d’Arguin than at the Wadden Sea.

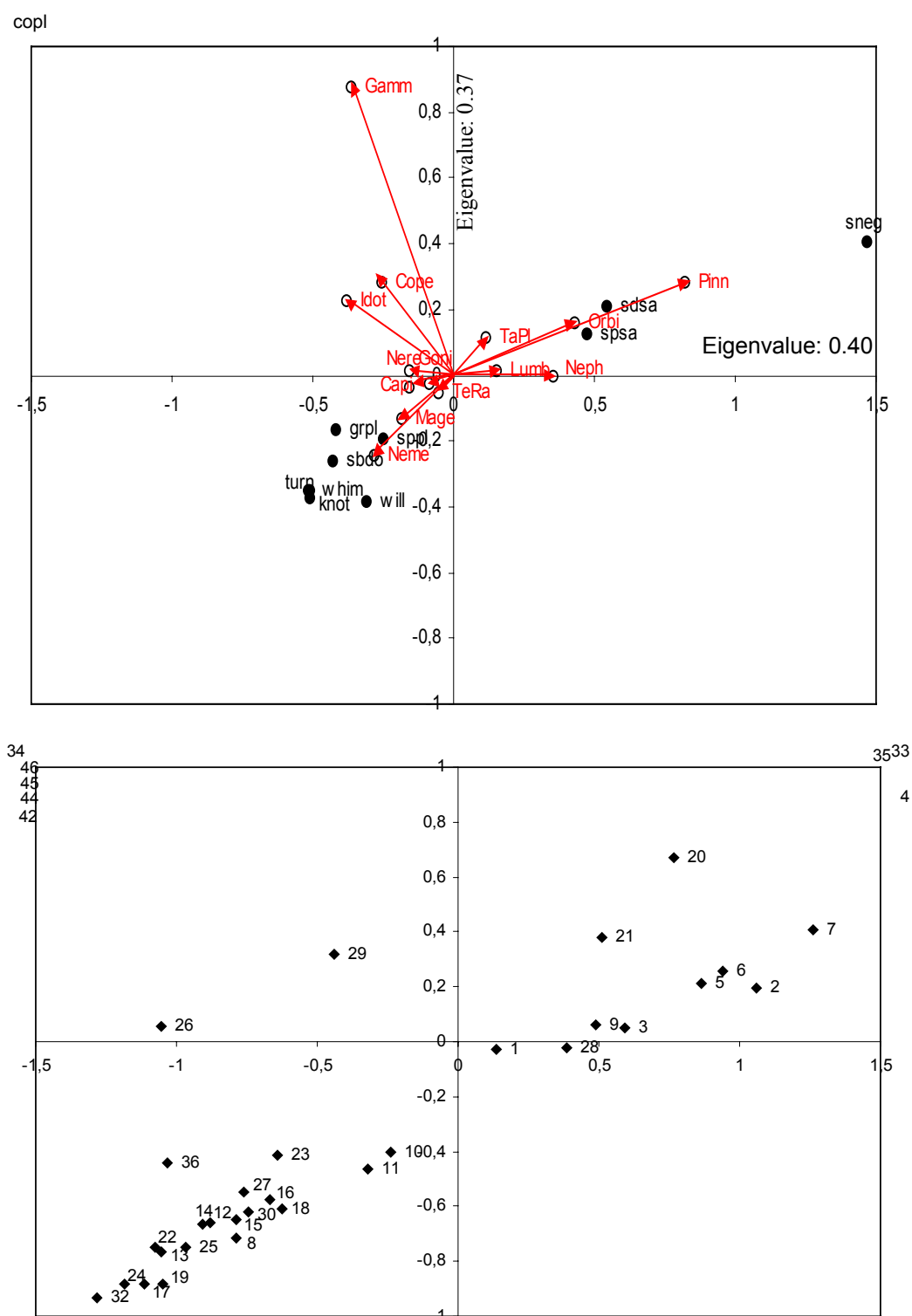


Fig. 33. Diagram of a CCA calculated on bird- and benthic abundances on the plots in January 2001. For a better understanding the diagram is given twice: on top, with the bird variables (points) and the benthos variables (arrows), and at the bottom, with the sites indicated as points. Bird numbers were tide calibrated and the benthos was included on a lower taxonomic level. The sum of all eigenvalues is 1.18.

Chapter 3 shows that mean benthic abundances and biomasses of the intertidal at the Bragantinian peninsula were low in comparison to other areas, presumably as a result of the environmental variability of the study area. But in contrast to the Banc d'Arguin, the harvestable fraction of the biomass was at low level as well, the mean harvestable biomasses for individual bird species only reached values between <0.1 and 2.2 gAFDW/m^2 . However, when the range of the values is considered, there are still spots with a very high harvestable biomass for most birds, at least in the first months of the year. This might raise the need for the birds to search for profitable spots in the intertidal.

Diets

The observed diets include generally a large variety of prey items. All shorebirds feed on “worms”, most of them prey also on bivalves and/or snails and few as well on crustaceans. Because of this dietary variety, only a broad differentiation in a fish-eating group (herons and egrets), a “worm”-eating group, and a mixed-diet group is possible, no further specializations on certain prey groups are apparent. The results of the dropping analysis showed that also within each main prey group a variety of prey items were consumed. Recognized prey types do not differ from previously recorded prey at other wintering areas, as summarized by Poole and Gill (2000) or Skagen and Oman (1996). Since many prey taxa do not provide body parts recognizable in droppings, the diversity of the diet might be even larger. In agreement with this, the calculated optimal diet of many bird species consists of a large variety of favourable prey items. This might offer an explanation for the broad diets observed during focal observations and the analysis of droppings.

Optimal diets

Optimal diets provide only a calculated list of favourable prey items for each bird species, they do not give any information about actually ingested prey organisms. However, they might be a good estimate of what might have been eaten preferably, especially since the variability of the organisms in terms of body sizes, vertical and horizontal movements – as described in detail in chapter 3.2.4 – is taken into account. Remains of the items which are part of the optimal diet, are indeed often found in the droppings, hence, it is possible that most birds do in fact optimise their foraging.

When prey was classified as potentially attractive due to high biomasses (*Uca maracoani*, *Tagelus plebeius* and *Nassarius vibrex*) or high abundances (Nephytidae, Capitellidae, Gammaridae and Pinnotheirdae) (Fig. 15), only few items appeared to be of interest for the birds. But when the harvestability and the time needed to search and to handle this prey for the individual avian species is also considered, as was done with the calculation of an optimal diet, the emerging picture of attractive prey is very different. In most cases a far larger set of profitable prey becomes apparent. Thus, it is generally of large importance not only to consider abundances and biomasses of possible prey items, but also to include the accessibility and the cost of feeding on them in order to understand the prey choice of birds.

According to the optimal diets some birds should be concentrating only on few items (somewhat arbitrarily determined as <5 taxa; Red Knot, Sanderling, Whimbrel and Willet), while other species should prey on many items (>5 taxa; Marbled Godwit, Ruddy Turnstone, Semipalmated Sandpiper) and in some cases they should switch from month to month between specialization and generalization (Scarlet Ibis, all plovers and Short-billed Dowitcher). If optimal diets were specialized, they always focused on bivalves and crustaceans. Only in May and June polychaetes became important, too. The attractiveness of bivalves and crustaceans is due to their high biomass values per prey item. During May and June, bivalves become rare (Fig. 14) and polychaetes therefore relatively more attractive.

A specialization of the optimal diet on bivalves and crustaceans is at least partly related to the capability to feed on large prey items. Of the seven species which feed on bivalves larger than 3 cm, five have a relatively specialized optimal diet, only two are mostly generalists. In contrast, of the 5 species which can only prey on bivalves smaller than 3 cm, only one species has a specialized optimal diet, all others have more generalized optimal diets. Bill size proves to be significant for the size of prey ingested, a relationship already identified in numerous previous studies (Holmes and Pitelka 1968; Goss-Custard et al. 1977a; Liffield 1984; Weber and Haig 1997). This is presumably a result of the increased ability to reach deeper burrowed prey and to handle and swallow larger organisms. The shortened handling time increases the profitability of prey. But while this holds true for bivalve- and crustacean prey at the Bragantian peninsula, the size of “worm-“ prey did not depend on bill size of the predators. Presumably large “worms” do not raise the handling difficulties as much as hard-shelled or many-legged prey. Hence, bill size proves to be significant for the determination of the harvestable prey fraction, which is in turn responsible for the ability to prey and specialize on profitable prey items.

The benthic taxa included in the optimal diets also reflect the ability of the birds to prey on certain prey sizes. The bivalve *Tellina radiata* occurred in the optimal diets of almost all birds. While *Protothaca pectorina* was common for those birds which could feed also on larger bivalves (Grey Plover, Red Knot, Willet, Ruddy Turnstone and Whimbrel), *Lucina pectinata* occurred mostly in the optimal diet of birds feeding on smaller bivalves (Sanderling, Semipalmated Sandpiper, Collared Plover and Semipalmated Plover). Specialization on crustaceans only occurred in the optimal diets of the Scarlet Ibis, the large sandpipers Whimbrel and Willet, and all plovers. They are split in two groups: the Scarlet Ibis and the large sandpipers, which are able to handle large crustaceans, focused on Decapoda and *Uca maracoani*. All plovers included additionally a variety of small crustaceans. They might have been important for them because of their mobility: they are easily detectable for the plovers hunting by visibility (Turpie and Hockey 1997). Also, the temporal and spatial variability of Callianassidae, *Uca maracoani* and *Tagelus plebeius*, as discussed in detail in chapter 3, is reflected in the calculated optimal diets.

Although specialization occurred within the optimal diet, the focus was mostly on groups of prey, and very broad optimal diets were common. This is a consequence of relatively long searching times at the Bragantinian intertidal with its sparse macrobenthic densities (chapter 3.2.4). Searching times are very time-consuming in comparison to the handling times. Thus, birds could not afford to reject even small prey items and had to maximize their energetic input through a large diet width. The conclusion of chapter 3, that opportunistically feeding birds have an advantage over highly specialized birds in highly variable environments, is supported by the observed diets, the analysis of droppings, and by the theory underlying the concept of optimal diets for the majority of birds.

Diet and the distribution of birds in relation to macrobenthos

In the last decades many studies have focused on the distribution of shorebirds in relation to their prey. Some studies compared bird distributions to the zonation of benthic organisms by sight with variable success (Wolff 1969) or with the help of dendrograms, which found clear associations (Meire and Kuyken 1984). Many attempts were made to find correlations between bird distributions and benthic densities. Although some authors found strong relationships (Bryant 1979; Colwell and Landrum 1993; Yates et al. 1993a), others failed to find a correlation (Botton et al. 1994). Many results were not clear: in some investigations only weak relationships were found (Goss-Custard 1970; Wilson Jr. 1990) and Wilson suggested that any intertidal area exceeding a critical threshold value of prey is acceptable for the birds. Some studies altered the variables to find the critical factors: Kalejta and Hockey (1994) found that one avian species is associated with prey densities while another corresponds to prey biomasses. Goss-Custard et al. (1977b) improved correlations between Redshank and prey by combining additional prey species with the most important prey item and used in some cases prey species, and in other cases much higher taxonomic groups.

The attempt to define the spatial relationship between birds and their prey was also made at the Bragantinian peninsula. Diverse statistical techniques were applied, but all of them were not able to display and to explain a sufficient amount of the inherent variability. Although different attributes of the prey were investigated – abundance, biomass and profitability – no clear picture emerged. After all, this result is not very surprising, since the birds do not focus on only one or two prey items, but forage mostly on a large variety of benthic taxa. This leads to a very complex pattern of relationships between birds and their prey and the descriptive abilities of Multivariate Analysis are probably too restricted to exhibit this in a sufficiently precise matter. Thus, there might be doubts if these models are applicable at all in situations where predators are not reasonably specialized. However, even for the more specialized birds of this study, no clearer picture appeared. To my knowledge, no other attempt to link environmental factors to shorebird distributions was made so far in the tropics, but there are several examples for temperate regions (Goss-Custard et al. 1991; Scheiffarth et al. 1996; Burger et al. 1997).

Niche overlap

Niche separation can take place on different levels: through the segregation of habitats (geographical, between habitats etc.), through a vertical segregation, through a segregation in time (daily, seasonal), or through a differentiation of diet and feeding behaviours. All these levels were investigated in this study.

Temporal segregation clearly splits the avian community of the Bragantiner peninsula in the groups of migrants and residents, with migrants occurring predominantly from January until April, and raised numbers of residents in June.

A separation by habitat took place at least partly. When the use of the three sampling areas was investigated, the Spotted Sandpiper only appeared in the plots inside the mangrove (Furo Grande), while Red Knot, Sanderling, Short-billed Dowitcher and Marbled Godwit were only found in the open intertidal of the Ilha de Canelas (Appendix III, Table 38). However, most birds had a very variable distribution and clear habitat segregations based on the smaller scaled plots did not appear. Environmental factors, although known to influence prey availability (Goss-Custard 1984), cannot be linked to the distribution of the birds (Appendix III, Table 39).

However, a segregation by microhabitats was observed. The avian community is roughly split in a group of wading birds and a group of all other, mostly migratory, birds. This last group can be distinguished further in three different groups of shorebirds, according to their salinity and sediment preferences or the presence or absence of water at the feeding site.

Although the diets of the birds showed large overlaps, they can be distinguished in a fish-eating group (residential herons and egrets), a “worm”-eating group and a large group with a mixed diet (both mostly migratory shorebirds). This differentiation is more or less consistent with the groups differentiated by microhabitat use. This might be due to a combination of habitat preferences of preferred prey organisms and foraging techniques which explore only a certain microhabitat. For example, the fish-prey of the wading birds is found exclusively in deeper water, and the pecking of the plovers aided by their vision can only reach prey in the upper centimetre of the sediment, mostly occupied by “worms”. Skagen and Oman showed that shorebirds in general exhibit a considerable dietary breadth and their prey choice is very flexible (1996).

Overall, the avian community is split into residential herons and egrets and migratory shorebirds. This separation is manifested by time, by the use of microhabitats and diet and it is a result of the different ecological roles these groups occupy in the system. As a consequence, residential birds do not tend to fill the niches which are occupied by the migrants during the winter time, when those leave the area in spring. The space used by them apparently remains, for the most part, abandoned during their absence. An exception to

this pattern are the Scarlet Ibis and the Collared Plover, both are (largely) residential. They use the same resources as the migratory shorebirds and do not have a special status.

Beyond this obvious segregation, less distinct niches defined by microhabitat characteristics - partly related with diet - can be distinguished among the shorebirds. The association with water and the probing depths are such attributes and they are at least partly linked to physical characteristics such as leg- and bill size. However, most birds occupy very broad niches and display a variable resource use.

To understand the lack of clear niche differentiations at the Bragantinian peninsula, the general ideas of niche formation have to be considered. Two contradictory processes are thought to affect niche differentiation (Begon et al. 1998): when only one species is considered, niche breadth is a result of resource abundance. High prey abundances are beneficial for specializations and low abundances promote broad niches (Zwarts and Wanink 1993). But under the competitive pressure of additive species – which also limits a resource – niche differentiation is enhanced (Cody 1974). The actual state of niche differentiation within an ecosystem is a result of both processes (Wiens 1992). Whether one or the other process is dominating depends on the resource abundance and the requirements of the involved species.

At the Bragantinian peninsula the food stock for the birds is very restricted as will be shown in chapter 6. It is assumed that the resource limitation is so strong, that the consequences of competition become insignificant. All birds are forced to forage opportunistically since a restriction on few prey organisms might lead to food shortages. This constraint might be less marked on large birds which are able to prey on more profitable organisms than smaller species.

6 Avian consumption and foraging behaviour

6.1 Introduction

How much do the birds consume at the study site and what does this mean for the avian community and for the benthos?

The proportional avian consumption of the total benthic production is an indicator for the efficiency of the energy transfer between the benthic production and the shorebird predators. Compared with the primary and secondary production found in terrestrial ecosystems and the respective proportion consumed by birds, the energy transfer is generally very high at tidal flats. It reaches between 15-25% of the standing stock at temperate areas (in Great Britain a bit higher) and far higher values in tropical areas, for example 82.7% at the Banc d'Arguin and up to 135% in this study (Table 19) (Baird et al. 1985; Meire et al. 1994). Thus, consumption is an important process in some tidal flats. The consumption rate of an organism – the biomass consumed during a defined period of time - can be considered from the perspective of the predator and the perspective of the prey. Both viewpoints will be explored in this chapter.

For the avian predators, an observed consumption rate determines if their energetic requirements can be fulfilled within a specific area. It shows if they can survive in the area over a longer time period. Are the birds able to gather sufficient energy in the available time for foraging and is there enough food to support all birds? Do they alter their behaviour according to the situation? To find out if birds are food limited, many studies compare the total consumption by birds with the food stock under investigation (Schneider 1981; Schneider 1985; Sherry and Holmes 1996). But the avian consumption at stop-over- and wintering sites does not only determine the survival in these areas, it might also affect the future fitness during the subsequent breeding season. Some studies found a tight relationship between energy stores accumulated up to departure from the final staging site en route to the nesting grounds and subsequent reproductive success (Pfister et al. 1998; Drent et al. 2003). Thus, the ease to gain weight at wintering areas and stop-over sites is of importance for the robustness of birds during migration and it is also responsible for their overall fitness. Birds can be distinguished in “income breeders” (individuals which fuel reproductive expenditure by simultaneous feeding) and “capital breeders” (individuals which rely on energy gained earlier, and stored prior to use). Capital breeders pay a number of energetic costs for their stored resources. But during unpredictable food conditions, food/time limitations and risky foraging conditions at the breeding grounds, capital breeding also offers many benefits (Jönsson 1997). However, capital breeders are probably especially vulnerable to food shortages during migration to their breeding grounds, since they are particularly dependent on their stored energy reserves. Also, a delayed migratory departure, for

example as a result of a prolonged fattening period in areas with a poor food stock, might decrease the individual fitness, since reproductive prospects decline with advancing laying dates (Drent et al. 2003).

From the perspective of prey it should be considered, if the predation pressure is able to control and possibly deplete the prey community. In temperate latitudes, predation is seen as the fundamental process regulating the benthic fauna in the intertidal (Baird et al. 1985; Reise 1985). In the tropics the situation is not clear, as investigations are scarce due to taxonomic problems, limited support facilities and the small number of scientists working in those regions (Vargas 1988). There are two common techniques to investigate if birds influence or even deplete the benthic community. The first is the comparison of the standing food stock and the birds consumption as directly observed or calculated from their Basal Metabolic Rates. The second one is an experimental approach with exclosures or inclosures of predators. Both techniques were applied in this study. It will be investigated if shorebird predation alters the numbers of benthic species or the composition of the benthic community, and if this effect occurs only in certain depth horizons or size classes of the prey.

Arntz (1981) and Ólafson et al. (1994) reviewed a large selection of experiments on the exclusion or inclusion of epibenthic predators. Arntz found that the outcome could range from effects on the entire benthic community (densities, diversity or dominance structure), to only single benthic species or to no effect at all. Ólafson et al. stated that at least in shallow-water and unvegetated habitats, epibenthic consumers control the infauna abundances.

The observation and interpretation of avian behaviour (time budgets, intake rates) is necessary for the calculation of consumption rates, hence this chapter will start with an investigation of the avian time budgets. But behavioural expressions like territoriality and the different foraging techniques are also indicators of the foraging strategies applied by the birds, as response to the environmental conditions experienced. This will therefore be considered at the end of the chapter.

6.2 Results

6.2.1 *Time budgets*

The time the birds spent during daylight at the intertidal was used for different activities, like feeding, resting, locomotion and aggressive encounters. For practical reasons, behavioural data will be distinguished only into “foraging” and “all other activities”. Plovers, Herons and Egrets spent only little time foraging (16-46%), while most sandpipers and the Scarlet Ibis required much more time (49-83%) for this. Only the Spotted Sandpiper differed conspicuously with only 14% of observed individuals foraging (Table 12). The proportion of

time spent feeding was significantly lower for plovers ($n=3$) than for sandpipers ($n=9$) (Mann-Whitney U-test: $U=0$, $Z=-2.449$, $p=0.014$).

Table 12. Activities of the birds in the study area. Given are the proportions of the activities of all individuals observed during focal observations in 2001. Species with <10 individuals were only indicated by “*” in the different categories.

Taxonomic grouping	species	foraging	Other activities	n
Hérons, Egrets and Ibises	Great Egret		*	3
	Little Blue Heron	46	54	11
	Snowy Egret	35	65	83
	Tricolored Heron	16	84	17
	Yellow-crowned Nightheron		*	3
	Scarlet Ibis	83	17	29
Plovers	Collared Plover	45	55	74
	Grey Plover	22	78	87
	Semipalmated Plover	23	77	159
Sandpipers, Snipes etc.	Greater Yellowlegs	*		2
	Marbled Godwit	88	12	10
	Red Knot	88	12	361
	Ruddy Turnstone	70	30	159
	Sanderling	70	30	27
	Semipalmated Sandpiper	93	7	524
	Short-billed Dowitcher	91	9	538
	Spottet Sandpiper	14	86	67
	Whimbrel	49	51	254
	Willet	67	32	130

A Spearman Rank Correlation analysis detected no significant relationships between time spent foraging and avian size indicators (tarsus length ($R=-0.055$, $p=0.873$) and mean weight of the birds ($R=0.295$, $P=0.352$)). Bill size did also not correlate with time spent foraging ($R=0.333$, $p=0.290$). However, the prey intake rates were positively correlated with bird weight ($R=0.125$, $p=0.004$).

Most avian species did not alter the time spent feeding between months. Contingency tables showed that only Semipalmated Plovers, Semipalmated Sandpipers and Whimbrels modified their times spent foraging between months (Table 13, Fig. 34).

Kruskal-Wallis tests revealed that some birds increased their intake rates in certain months significantly (Red Knot, Semipalmated Sandpiper and Short-billed Dowitcher). Peak intake rates were always observed in February (Table 13).

Presence and activities of the birds fluctuated also over the course of ebb tide. All plovers were present in high numbers when tide began to recede. Later on, some individuals moved away, presumably to newly emerged areas. The plovers remaining in the area kept more or less constant numbers, with a stable proportion feeding (Fig. 35). Short-billed Dowitcher, Whimbrel, Willet and Spotted Sandpiper became increasingly abundant with maximum numbers present and feeding at low tide in the study area. All other sandpipers and the wading birds occupied the study area only at the beginning of ebb tide (Sanderling) or passed through the area 1-3 hours before low tide, to spend low tide at other locations (Fig. 35).

Table 13. Temporal development of avian foraging times and intake rates in the study area. Given are the results of Contingency tables on the total numbers of foraging/not foraging birds between months in 2001 and of Kruskal-Wallis Tests on intake rates between the months in 2002. Only months with >10 individuals were included.

Species	time foraging (Contingency table)				intake rates (Kruskal-Wallis Test)		
	df	χ^2	p	Peak month	H	p	Peak month
Snowy Egret	2	9,162	0,103		-	-	
Scarlet Ibis	-	-	-		2.330	0.507	
Collared Plover	2	8,953	0,111		2.632	0.452	
Grey Plover	3	9,319	0,097		3.796	0.284	
Semipalmated Plover	3	22,998	<0.001*	Feb	2.604	0.626	
Red Knot	3	10,891	0,054		9.857	0.007*	Feb
Ruddy Turnstone	2	1,466	0,917		1.613	0.240	
Semipalmated Sandpiper	5	17,912	0,003*	May/June	16.551	0.002*	Feb
Short-billed Dowitcher	3	5,427	0,366		16.409	0.003*	Feb
Spotted Sandpiper	2	0,133	1		-	-	
Whimbrel	3	14,597	0,012*	April	1.763	0.779	
Willet	2	3,116	0,682		1.051	0.591	

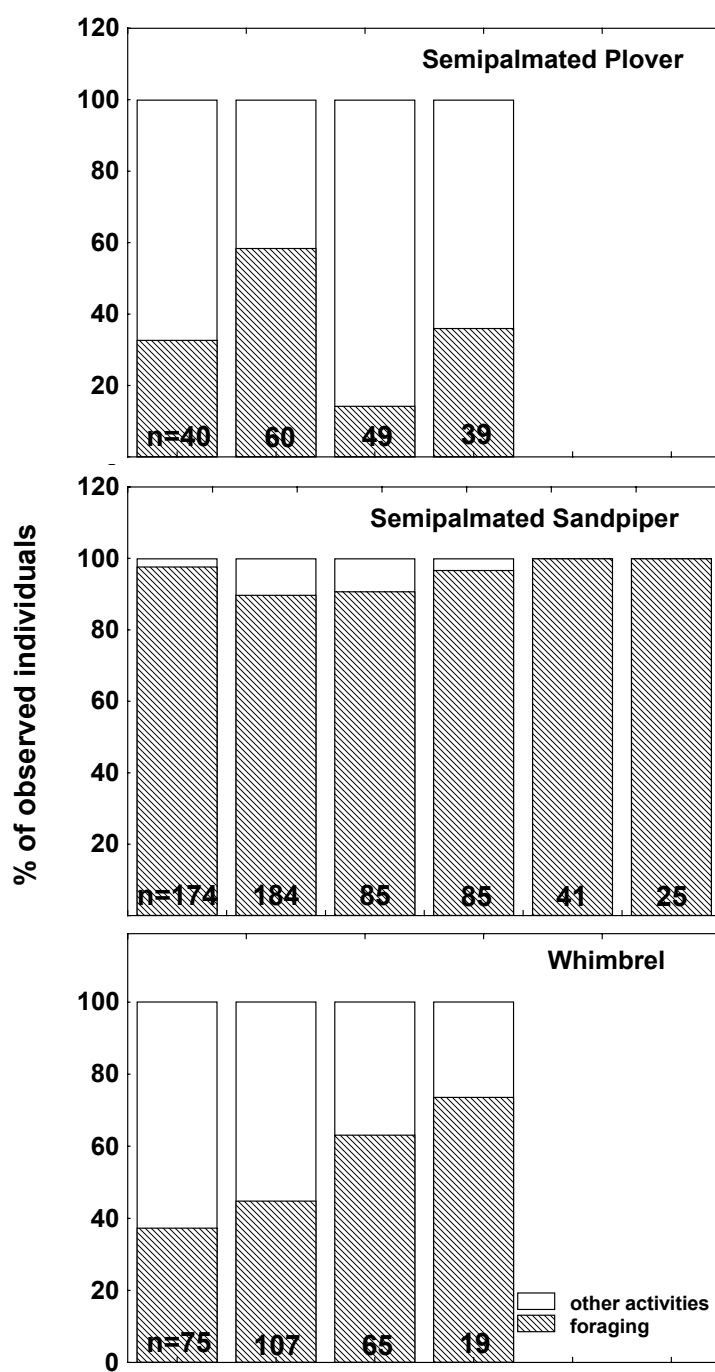


Fig. 34. Significant changes in the proportions of foraging individuals observed in 2001. N is given at the bottom of the columns. Only months with >10 observations were included.

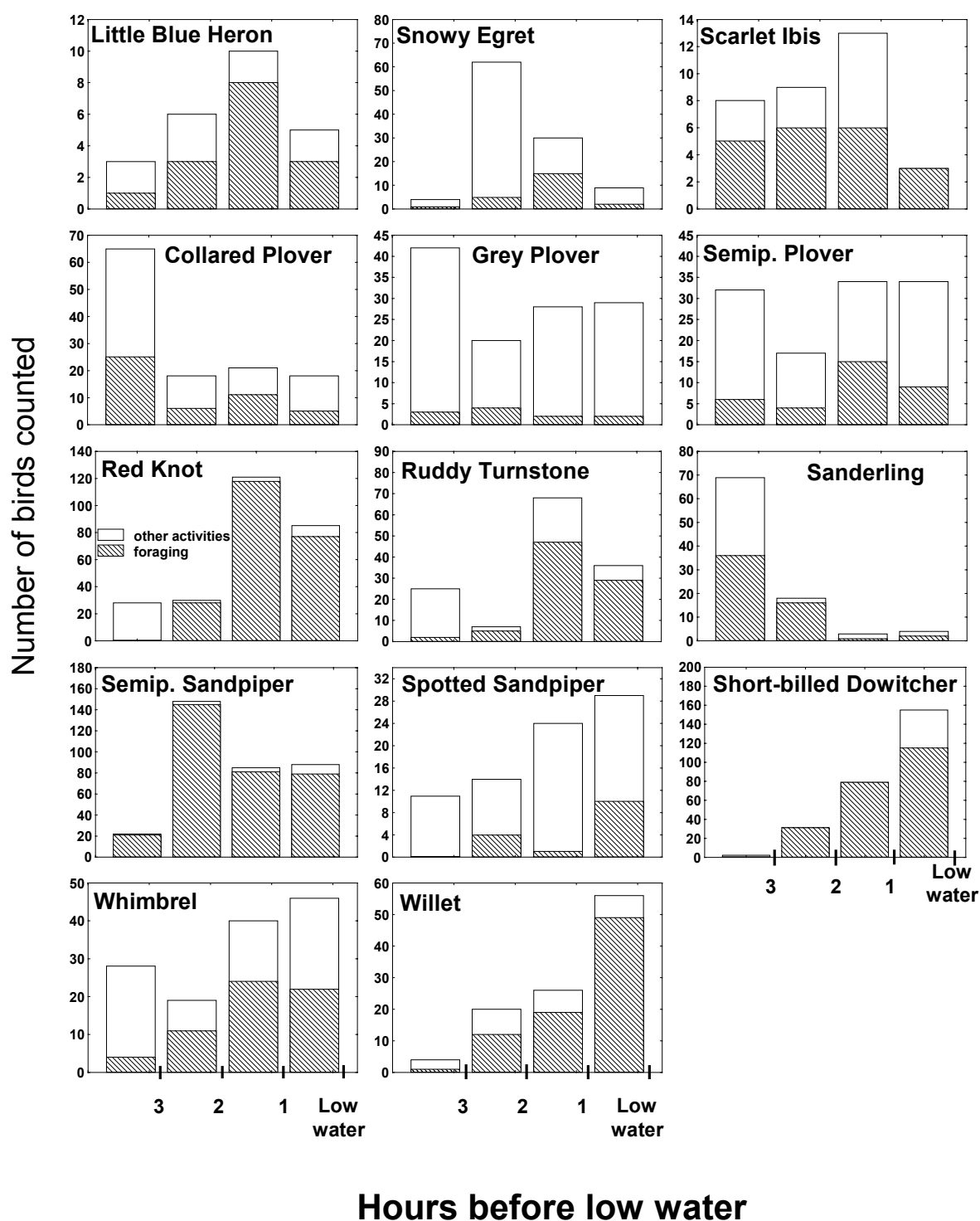


Fig. 35. Time budgets over the course of ebb tide. The graphs are based on all individuals recorded during tidal counts at all plots in 2001.

6.2.2 Calculated consumption

The mean consumption rates of the total avian community ranged between $793 \text{ gAFDW} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$ in February and $51 \text{ gAFDW} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$ in May. The strongest predation

pressure during January-March 2001 was exerted by Knot, Short-billed Dowitcher and Whimbrels and the least by Scarlet Ibis, Collared- and Semipalmated Plover, Marbled Godwit and Sanderling (Fig. 36).

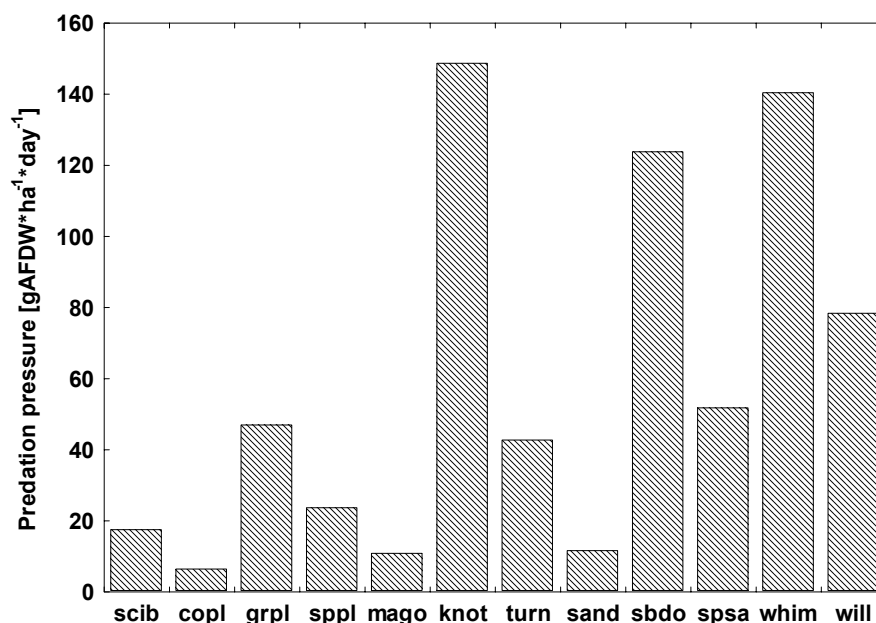


Fig. 36. Mean predation pressure on the study area by the different avian species between January and March 2001.

When a maximal possible consumption per day was calculated on the basis of known foraging times and energy intake rates, it appeared that half of the avian species obtained their required food easily in less than 5 hours (Scarlet Ibis, Collared Plover, Ruddy Turnstone, Short-billed Dowitcher, Whimbrel and Willet) (Table 14). Two species could only fulfil their energetic requirements when feeding most of the time (Grey Plover and Red Knot). All other birds would need far more than 100 hours (!) per day to obtain enough energy (Table 14).

When the total avian AFDW-consumption per month was expressed as proportion of the standing 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%. The consumption rates yielded a theoretical need of over 100% of the standing stock in January and February (Table 15).

Table 14. Calculated gross food intake (GFI) in comparison with the observed consumption/day at Canelas in 2001. The GFI is the essential food value per day necessary for a bird to survive. The maximal possible consumption during daytime at the study area was calculated by multiplication of the maximal exposure time of the flats during the day (299 min at Canelas) with the proportion of time spent feeding and the mean consumption during feeding time observed at the study area. The last column gives the calculated necessary time foraging to fulfil the energetic needs when foraging with the intake rates observed at the study area. It was calculated by dividing the GFI [gAFDW/day] through the mean consumption during feeding time [gAFDW/d].

Species	Weight [kg]	GFI [gAFDW/day]	n	Mean consumption during feeding time [gAFDW/min]	Mean proportional time spend feeding at the tidal flats [%]	Max possible consumption during daytime at Canelas [gAFDW/day]	Necessary time foraging to fulfill the energetic requirements [h]
Scarlet Ibis	0.514	29.30	53	0.71±1.50	83	177.08	0.83
Collared Plover	0.026	3.33	57	0.03±0.20	45	4.01	4.13
Grey Plover	0.180	13.64	46	0.05±0.18	22	3.28	20.70
Semipalmated Plover	0.047	5.12	55	<0.01±<0.01	23	0.08	328.74
Marbled Godwit	0.285	19.06	9	<0.01±<0.01	88	0.27	350.40
Red Knot	0.135	11.06	48	0.01±0.04	88	3.45	15.99
Ruddy Turnstone	0.084	7.82	39	0.04±0.18	70	7.94	4.91
Sanderling	0.040	4.56	7	<0.01±<0.01	70	0.17	137.25
Semipalmated Sandpiper	0.021	2.85	61	<0.01±<0.01	93	0.05	288.23
Short-billed Dowitcher	0.090	8.23	56	0.08±0.60	91	22.43	1.83
Whimbrel	0.310	20.27	54	0.30±1.11	49	44.45	2.27
Willet	0.200	14.73	50	0.16±0.64	67	32.36	2.27

Table 15. Consumption by birds of the standing food stock in the study area. Per month, a mean benthic standing stock (biomass) was determined and compared with a consumption rate/month (consumption rate per day x number of days at the month).

Month	Benthos standing stock gAFDW/m ²	Consumption per month	
		gAFDW/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

These general figures were refined by calculating the relative predation pressure in each plot and on each benthic group separately. Relative predation pressure is defined as the consumption divided by the standing stock. Thus a relative predation pressure below 1 would indicate that the standing stock is larger than the predation, and a relative predation pressure exceeding 1 shows that consumption is higher than the food supply (Zwarts 1988). It appears that median relative predation pressures are extremely high, especially on bivalves and “worms” in the first three months of the year (Fig. 37). Some plots experience maximum predation pressures as high as >10.000 times the values reached by the standing stock. Also, quartiles show that a consumption many times higher than the food stock occurs regularly. Moreover, the values are still underestimated, since plots with a certain avian consumption but a measured zero standing stock had to be excluded from the calculations (chapter 2.2.2).

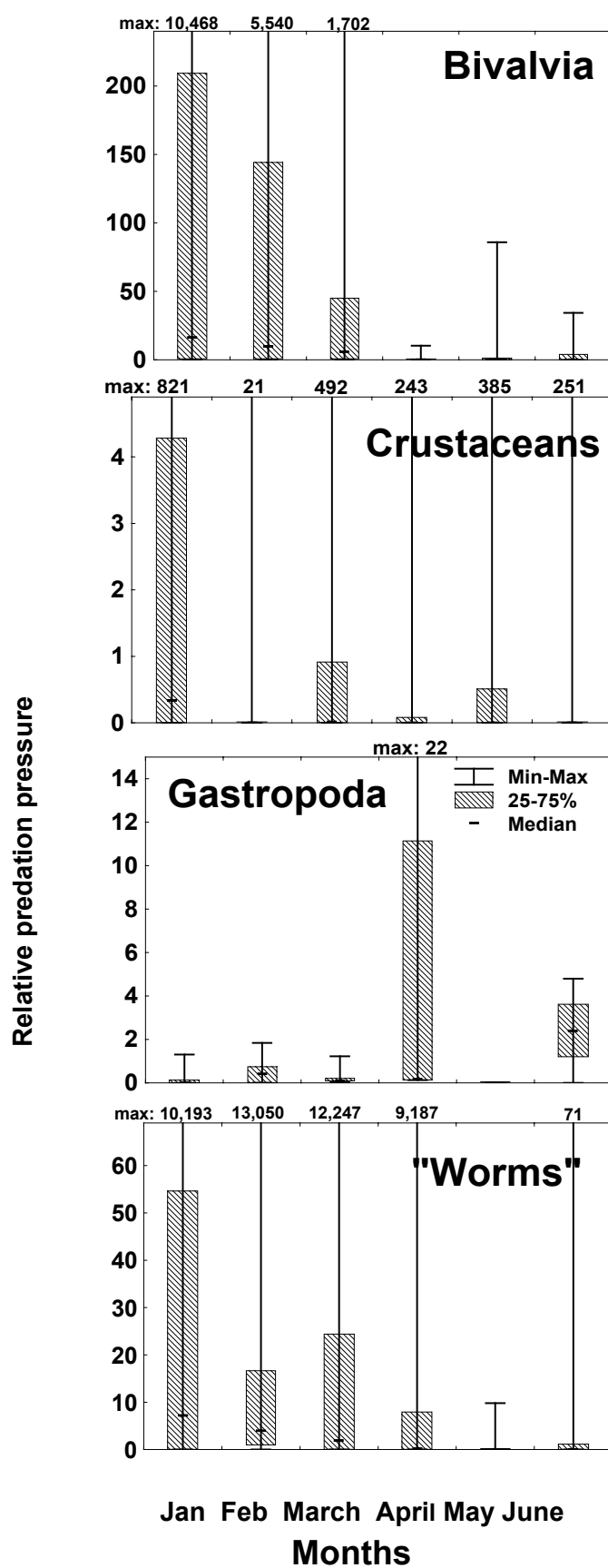


Fig. 37. Relative predation pressure per month. Given are relative predation pressure values of all 46 plots from January-June 2001. The maximum value is given above the column if whiskers were extraordinary high. Predation pressure was calculated as given in chapter 2.2.2.

6.2.3 Exclosures

In exclosure experiments a potential main predator is excluded from an area for a certain time. By observing the effect on the prey community during this time, the influence of the predator on its prey can be evaluated. During the exclosure experiment at the Bragantinian peninsula all samples were dominated by Polychaeta and Crustaceans with 46% and 32% respectively of all individuals found. This was very similar over the entire study area, with 59% Polychaeta and 26% Crustaceans. All taxa found in the treatment areas are listed in Appendix V Table 47.

The median grain-sizes of the sediment varied between 2.77-2.83 Φ . Although low compared to the other samples obtained in the estuary (2.76-4.41 Φ), this span includes the grain-sizes of the majority of investigated pots in 2001. Generally, the grain-sizes did not differ significantly between treatments. Only in January the controls showed a significantly larger median grain-size than the procedural controls (Kruskal-Wallis test: $H=7.515$, $p=0.023$; Mann-Whitney U-test (c-pc): $U=5.000$, $Z=2.492$, $p=0.013$). In contrast, the salinity differed significantly every month between the treatments, even though the values itself were quite similar. However, these differences appeared irrelevant in comparison to the high monthly variation in salinity that the entire study area was exposed to (Fig. 9).

The bird numbers at the two plots close to the exclosure area hosted between 0 and 33 birds/ha, a range well within the densities reported for the entire study area.

Differences between the treatments

The variability in overall abundances was very large. Most trophic groups (suspension feeders, carnivores and omnivores) and taxa (Nephtyidae (Polychaeta), Pinnotheridae (Crustacea) and *Tellina radiata* (Bivalvia)) did not show any significant difference between the treatments. The only significant distinctions appeared in February and April (Kruskal-Wallis test and Mann-Whitney U-test with Bonferroni-correction, Table 16). In February, the trophic group of deposit feeders and polychaetes showed significantly increased numbers in the controls in comparison to the procedural controls, but not to the exclosures. In April, the total benthic community, deposit feeders, Polychaeta, and the Capitellidae had distinctly raised abundances in the procedural controls in contrast to the 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 (Fig. 38). To assess how Capitellidae, a deposit feeding polychaete, effected the outcome of the tests, all Kruskal-Wallis- and Mann-Whitney U-tests were repeated excluding all Capitellidae (Table 16).

It appears that Capitellidae were largely responsible for some effects, such as the overall effect on the benthic community in April (exclosure-procedural control), the effect on the deposit feeder in April, and the effect on the Polychaeta (control-procedural control) in April and February. Other effects, like the one on the deposit feeders in February and on the Polychaeta

in April (exclosures-procedural controls), lasted also without Capitellidae and were caused by a combination of organisms which showed no significant differing abundances on their own. Investigation of the raw data reveals, that the effect in February was due to the combination of high numbers of Polychaete taxa and an increase of Callianassidae in the controls and a decrease of Callianassidae in the Procedural controls. Hence, it is an effect of compilation of non-significant variations within abundances of three different deposit feeding taxa.

The effect in April is due to a combination of various taxa. The high numbers inside the procedural controls are due to rising abundances of Capitellidae, Orbiniidae (both deposit feeders) and Pilargiidae (carnivor), while the low numbers inside the exclosures are due to decreases in Pilargiidae and Goniadidae (both carnivores), Nereidae (omnivor) and Capitellidae (deposit feeder).

Vertical distribution

To investigate if the benthic taxa of certain depth regions respond particularly strong to the exclusion of birds, a monthly Kruskal-Wallis test was done between the treatments separately for each depth horizon. Significant differences between the treatments were only found within the depth of 0-5 cm, indicating that only the surface living animals were affected by the birds' predation pressure. The overall benthic abundance was significantly greater in the procedural control than in the exclosures (Fig. 39). The trophic groups showed no significant difference in abundances. Of the taxonomic groups, only the Polychaeta had significant results, as in February they became significantly less abundant in the procedural controls than in the controls, and in April they became more abundant in the procedural controls than in the exclosures (Fig. 39).

Of the lower benthic taxa only the Pinnotheridae were abundant enough to warrant investigation of their vertical distribution, but no significant differences were found.

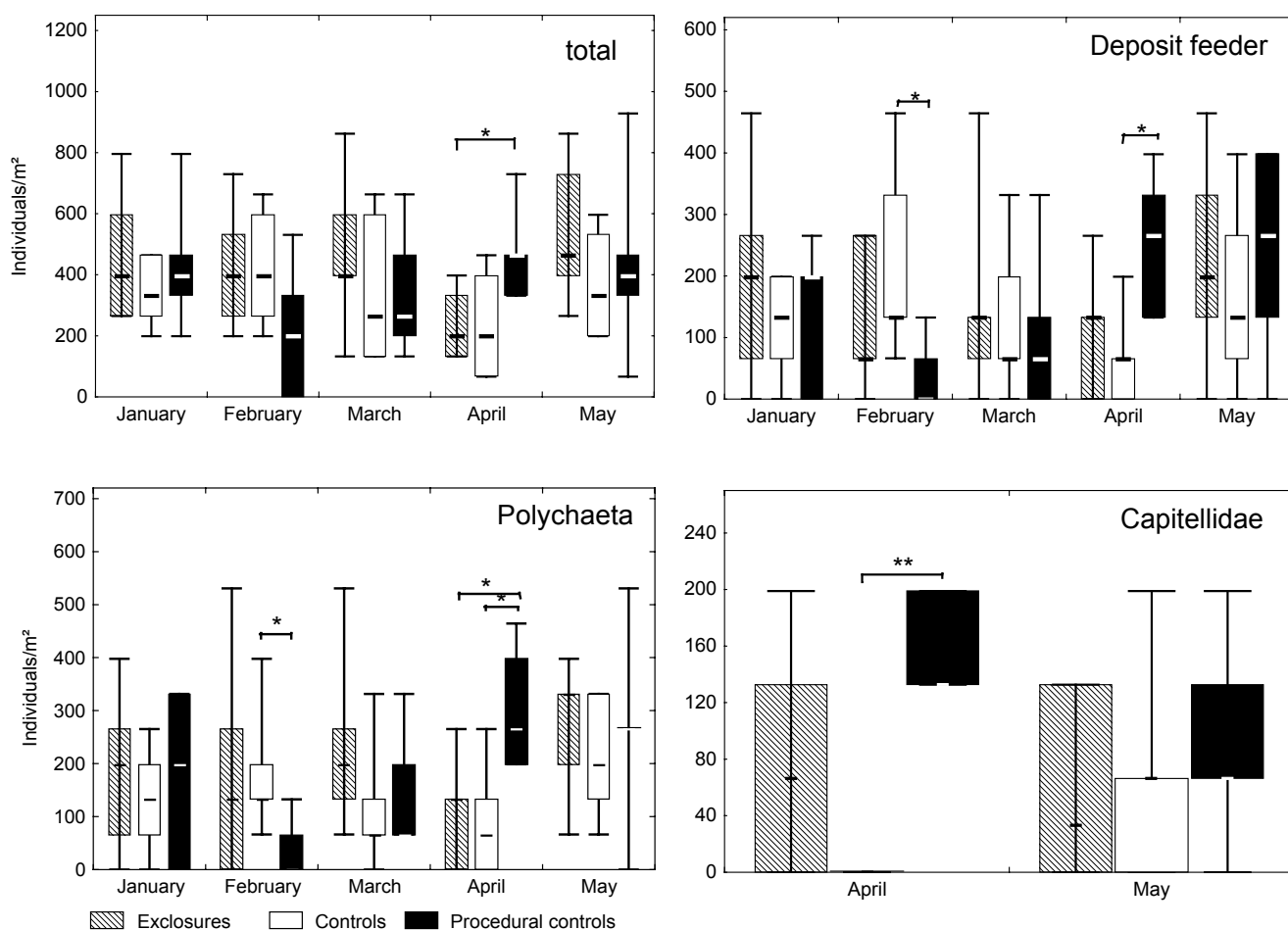


Fig. 38. Abundances of the benthic community, deposit feeders, Polychaeta and Capitellidae in the treatment areas of the enclosure experiment. Given are the medians, quartiles and ranges of the numbers of individuals per square within each treatment. Capitellidae only had sufficient numbers for the Analysis in April and May.

Table 16. Comparison of the enclosure-effects including and excluding Capitellidae. Given are the results of Mann-Whitney U-tests between the treatments.

Effect	With/without Capitellidae	total		Deposit feeder		Polychaeta	
		Z	p	Z	p	Z	p
February: c-pc	+ Capitellidae	n.s.	n.s.	2.683	0.007	2.683	0.007
	- Capitellidae	n.s.	n.s.	2.492	0.013	n.s.	n.s.
April: c-pc	+ Capitellidae	n.s.	n.s.	-2.875	0.004	-2.747	0.006
	- Capitellidae	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
April: ex-pc	+ Capitellidae	-2.556	0.011	n.s.	n.s.	-2.747	0.006
	- Capitellidae	n.s.	n.s.	n.s.	n.s.	-2.747	0.006

c-pc = test between controls and procedural controls

ex-pc = test between enclosures and procedural controls

n.s.= non significant

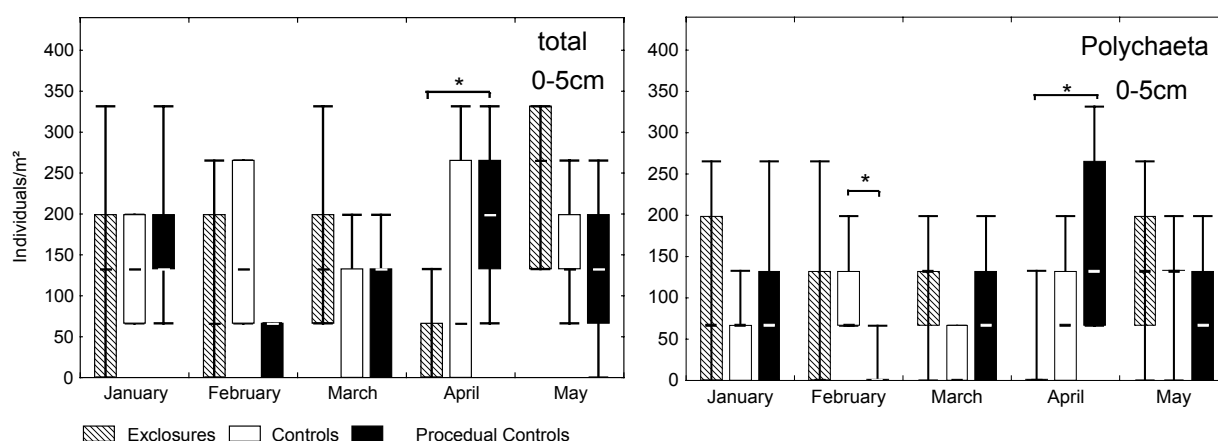


Fig. 39. Abundances of the benthic community and of Polychaeta in the top 5 cm of the treatments. Given are the medians, quartiles and ranges of the numbers of individuals per square within each treatment.

Size

To investigate if the birds predation pressure acts selectively on certain size classes of prey, the sizes of the benthic taxa in the different treatments were compared. The only taxonomic groups abundant enough for the investigation were *Tellina radiata* in January and February, Pinnotheridae between January and May and Nephtyidae in May. None of those showed significant differences between the treatments (Appendix V Table 48).

6.2.4 Behaviour

Descriptions of the foraging behaviour

The foraging behaviours of birds at the Bragantian mudflats will be shortly described in the following. Many of the terms are used in the sense of Kushlan (1978).

Little Blue Herons are primarily solitary foragers. Most individuals occurred in the tidal creeks and ponds, displaying standing, walking, running, hopping, and open wing feeding. Some individuals were observed to feed also on muddy substrate where their behaviour was different. It was reduced to standing and slow walking. When they fed at muddy parts of the study area, with only little pools of water, they were observed to sneak up on their prey and to stare at the sediment surface for a long time before they stroked. There, they were found to eat very large prey, like eel-like fish (30 cm) or flatfish. Vocalization was very rare.

Snowy egrets exposed a variety of foraging behaviours and postures: standing with bill pointing downwards, crouched postures, walking, running, open wing feeding, food stirring, hopping and short flights. Although they often fed solitary, seemed to prefer gregarious foraging, and were often attracted by other herons, especially when these were obviously successful hunters. Vocalisation was often part of the foraging behaviour.

Tricolored Herons exposed the same foraging behaviours as Snowy egrets (walking, running, open wing feeding, food stirring, hopping and short flights) but -unlike them- they were hardly ever standing still or watched a spot motionless. They also ran more crouched and their behaviour appeared more hectic. They fed solitary, as well as together with Snowy Egrets. Vocalisation occurred very often.

Scarlet Ibises were feeding mostly in little dispersed groups or pairs. They preferred small watery holes for probing. Some visual preselection was carried out while they walked and probed randomly. If they detected signs of prey at the sediment surface, they sometimes started to run and jammed their beak violently into the sand, twisting and turning it to reach the item. They were always ready to rob prey from other birds, mostly from Whimbrels, Willets or other Scarlet ibises. Also very large prey items, like flatfish, were eaten. They were very sensitive to disturbances.

The *Collared Plover* displayed feeding territories. They were feeding solitary, defending their territories against conspecifics or Semipalmated Plovers. They were using a run-stop-run-technique like the Semipalmated Plovers, but unlike them, their behaviour appeared hectic, with rapid movements, quick walking and infrequent stops of different durations. The rapid pecks mostly only scraped the surface.

Grey Plovers were foraging solitary with a highly visual run-stop-run technique. Only in May did they seem to congregate in little groups of up to 7 birds. Before attacking, they often watched a suspect spot with the head turned to one side to get a better view with just one eye, or stopped to focus motionless on a possible prey until the moment of attack. They also paid attention to other birds near by, trying to rob detected prey. They always stayed above the tide line, close to the mangrove or on the sandy parts of the estuary.

Semipalmated Plovers foraged mostly solitary or in pairs within feeding territories. Aggressive encounters were observed mostly with conspecifics and Collared Plovers. Like them, they foraged visually in a run-stop-run manner, frequently pecking on the sediment surface. If large "worms" were caught, they often stood tip-toed, leaning backwards to be able to pull the "worm" slowly out of the ground. Feeding was often extremely quick, apparently sucking the "worm" like a spaghetti in the beak within split seconds.

Often it was not clear if the caught "worm" was eaten at all. These instances could be due to the following reasons: 1) the "worm" escaped into the sediment, 2) the bird rejected the "worm" or 3) the "worm" was eaten so quickly that it could not be detected.

The first point was rejected due to the generally large size of these "worms" which will delay their retreat. The rejection of prey could occur if some of the "worms" were not edible or tasty for the birds. But it seems unlikely that the birds pulled the whole "worm" out of the sediment before they decided not to eat it. The last possibility seemed most probable, since the speed of

feeding was incredibly high and the distance to the observed birds often large. Hence, those “worms” were counted as eaten in the analysis.

Marbled Godwits adopted a mixture of visual and tactile foraging techniques. They inspected the ground for promising spots to probe. They used their long bills to probe deep into the ground, sometimes persistently punching around in a single hole for a while. They foraged mostly solitary.

Red Knots were highly gregarious, often found together with Short-billed Dowitchers. Only seldom they were observed foraging solitary. They adapted a technique that included visual and tactile foraging: while walking they surveyed the ground for promising spots and would probe there. The visual component was more or less pronounced, presumably depending on the environmental conditions and/or the preferences of the bird. Like many Turnstones some individuals were specialized in searching for little lumps of plant material laying on the surface to explore them for prey.

Ruddy Turnstones were solitary feeders with high site fidelity. Sites were often occupied by pairs, yet they did not have defined territorial boundaries. Their preferred muddy areas close to the mangrove. They were searching for their prey visually, running quickly long ways, digging at promising spots, probing in lumps of plant material or turning around small objects like shells or leaves. They were often investigating a single object for a long time until they succeeded or continued searching. They were also paying a lot of attention to other birds and were always ready to rob prey.

Sanderlings adopted a visual and tactile foraging technique. Using the run-stop-run manner, they were watching the ground and pecked only seldomly for prey. They were highly solitary and covered a large area while searching for prey. They were found only at sandy locations.

Semipalmated Sandpipers were gregarious feeders, often found in large groups, together with conspecifics or plovers. They were feeding predominantly tactile. Two techniques could be observed:

- a) primarily tactile probing into the sand, with little visual preselection
- b) in very soft and watery mud they occasionally used forward ploughing and head swinging on the surface without any obvious visual component. The success of this behaviour could not be estimated since no bill movements or gulps could be observed. Maybe this behaviour was adopted to filter smaller prey items out of the mud, without noticeable swallowing movements.

Like most other small shorebirds, they were not shy at all and observers could approach very close until they displayed signs of disturbance.

Short-billed Dowitcher were highly gregarious birds which hardly looked up when feeding. They always stayed in dense groups, probing very quickly in soft mud while walking slowly. Since they often foraged in water, successful probes were hard to detect. They preferred soft mud or water as substrates and were rarely seen on dry sand. On sand, they adapted their feeding behaviour to more visual preselection before probing and foraging was far more slow.

Willetts were feeding predominatly solitary. While walking around, they probed into the sediment only when they detected something at the surface. Like Scarlet Ibises, they preferred probing in little lumps of plant material or little watery ponds. Frequently their prey was robbed by Scarlet Ibises.

Whimbrels displayed much of the same behaviour as Willets. They searched for food solitary and probed only if something was detected at the sediment surface. They often turned their bill when probing in the sand like Scarlet Ibises. But unlike them, they paid much more attention to other birds and were ready to rob prey quite forcefully. Although they had no territories, they did not allow other birds to approach and fought frequently when birds were coming too close.

Visual and tactile foraging

Shorebirds are often differentiated according to their visual or tactile foraging behaviour. Plovers, herons and egrets expose a highly visual foraging behaviour while that of the Short-billed Dowitchers is predominantly tactile. However, the behaviour of most sandpipers and the Scarlet Ibis was a mixture of both (Table 17).

Table 17. Bird species arranged according to the more visual or more tactile elements of their behaviour.

visual	both		tactile
	More visual	More tactile	
Collared Plover	Sanderling	Red Knot	Short-billed Dowitcher
Grey Plover	Willet	Marbled Godwit	
Little Blue Heron		Semipalmated Sandpiper	
Snowy Egret		Whimbrel	
Tricolored Heron		Scarlet Ibis	
Semipalmated Plover			
Ruddy Turnstone			

A Kruskal-Wallis test showed that shorebirds which were observed to forage visually, shorebirds observed to forage tactile, and shorebirds combining both techniques differed significantly in the number of prey organisms obtained during the three minutes of focal observations ($H=15.684$, $p<0.001$). Visually foraging birds caught significantly more prey items (mean: 2.6 prey items) than birds with a mixed technique (mean: 1.7 prey items) (Mann-Whitney U-test with Bonferroni correction ($\alpha=0.017$): $U=14223.5$, $Z=3.681$, $p<0.001$). But while the number of prey items differed significantly, the biomass actually ingested during the

observations did not ($H=2.678$, $p=0.262$). The weights of the birds comprising the groups with these different foraging techniques - representative of bird sizes – differed only slightly from each other (Kruskal-Wallis test: $H=6.125$, $p=0.047$; Mann-Whitneys U-test found no significantly differing pairs).

Spacing behaviour: aggregation and territoriality

Aggregations of birds were widespread and 41% of the birds investigated during focal observations were associated with other birds. While plovers and several sandpipers were observed to forage mostly solitary, Red Knot, Short-billed Dowitcher, Semipalmated Sandpiper and the Snowy Egret were found mostly in flocks (Table 18).

Table 18. Observed group associations of the birds in the study area. Given are the proportions of all individuals observed during focal observations in 2002. Species clearly preferred for associations are bold.

Species	n	gregarious	solitary	Associated with...
Little Blue Heron	20	20%	80%	tche, scib, sneg
Snowy Egret	33	76%	24%	sneg , tche, lbhe, grpl
Tricolored Heron	29	41%	59%	sneg , lbhe
Scarlet Ibis	53	53%	47%	scib , spsa, sbdo, whim, grpl, will
Collared Plover	57	21%	79%	spsa, copl, sand, turn
Grey Plover	46	17%	83%	grpl, turn, whim, will
Semipalmated Plover	55	11%	89%	copl
Marbled Godwit	9	33%	67%	whim
Red Knot	48	71%	29%	knot , sbdo, spsa
Ruddy Turnstone	39	26%	74%	turn , whim, grpl, knot, spsa
Sanderling	7	43%	57%	spsa, copl
Short-billed Dowitcher	56	64%	36%	sbdo , spsa, lbhe, copl, sand, sneg, grpl, will
Semipalmated Sandpiper	61	64%	36%	spsa , sbdo, copl, will
Whimbrel	54	30%	70%	whim , scib, will, sbdo, tche
Willet	50	36%	64%	will , whim, sbdo, sneg

The association with other birds generally did not influence the prey intake rate or the biomass ingested for most birds (Appendix V, Table 49). Only the Tricolored Heron appeared to catch more prey when foraging in groups, while the Semipalmated Plover was more successful when foraging solitary. But again, the amount of ingested biomass was not influenced.

Territoriality was only observed in pairs of Semipalmated- and Collared Plovers. These territorial birds experienced a significantly higher prey abundance at the location of their appearance than the gregarious feeding birds or the birds neither displaying territoriality nor gregarious feeding (Kruskal-Wallis Test: $H=459.906$, $p<0.001$; Mann-Whitney U-test with Bonferroni-correction ($\alpha=0.017$): (territorial-gregarious): $U=100,956.0$, $Z=17.590$, $p>0.001$; (territorial-nothing): $U=234,384.5$, $Z=-20.110$, $p<0.001$; (gregarious-nothing): n.s).

Aggression was rarely observed, and of the 617 birds investigated only 21 were involved in aggressive encounters. Of these, only 6 instances were related to territorial- or individual distance defence, and they included only Collared-, Semipalmated Plover and Short-billed Dowitcher, individuals with strict territorial or gregarious behaviour. 15 encounters were attempts of prey robbing, involving mainly the Ruddy Turnstone, together with larger birds like Whimbrel, Willet, Grey Plover, Scarlet Ibis or egrets.

6.3 Discussion

In chapter 3 it was shown that the food supply of the birds at the Bragantinian peninsula is very low in comparison to other tropical intertidal foraging areas. The harvestable fraction shows also quite low amounts for the birds. Nevertheless, the avian community is comparatively abundant. Thus, predation pressure might be high for the benthos and the birds might consume significant parts of it.

Time budgets

The calculation of time budgets is necessary to determine daily consumption rates for the birds. It is also often understood as an indicator of the effort to obtain enough food per day. However, the time foraging is restricted by the tide and - as proposed by Zwarts and Dirksen (1990) - by a "hidden feeding time", a resting or preening pause of the large birds presumably necessary for digestion.

The time spent foraging differed very much between the birds at the Bragantinian intertidal. While plovers and wading birds spent only little time to obtain their food, the sandpipers were observed to forage most of the time. Only the Spotted Sandpiper seemed to be an exception, with only 14% of their time spend foraging. Since this was the only sandpiper found exclusively at the study area at the Furo Grande, its available foraging area might be very different and probably not comparable to that of all other sandpipers.

Several authors found that the proportion of time spend feeding is negatively correlated with body mass (Pienkowski 1981; Engelmoer et al. 1984; Zwarts et al. 1990b; Fasola and Canova 1993; Ntiamoa-Baidu et al. 1998). This pattern has been attributed to the relative decrease in energy expenditure with increasing body size. Also, it might be partly due to the "hidden feeding time" necessary for digestion (Zwarts et al. 1990b). At the Bragantinian peninsula this relationship could not be confirmed. Foraging time appeared to be better related to foraging style, as proposed by Pienkowski (1981), with plovers exhibiting significantly lower proportions of time spend feeding than sandpipers. The visually foraging plovers might be able to scan a defined area more rapidly for food than probing sandpipers, which makes it also necessary to be more mobile and to walk between patches of prey. This could result in a higher proportion of movement, a non-feeding behaviour in this study. However, walking and standing actually belongs to the foraging behaviour of plovers. Herons and egrets spent only little time foraging

when present on the tidal flats. Their primary foraging area was most likely the mangrove forest, since the mangrove creeks contain large amounts of fish, especially during low tide (Krumme and Saint-Paul 2003).

Several authors proposed that shorebirds will increase their feeding time prior migration to be able to accumulate some fat reserves (Zwarts et al. 1990b; Rompré and McNeil 1994; Turpie 1995). Zwarts et al. (1990b) described that large species increased their energetic intake during the premigration period by increased feeding time at the Banc d'Arguin, while small birds, which already fed maximal time during the day, could only increase energy intake by feeding faster. At the Bragantinian peninsula, both tactics occurred. Of the 5 species which were quite capable of obtaining their required energy in only a short time, two increased their foraging effort noticeably: the large Whimbrel with increased foraging time, and the smaller Short-billed Dowitcher with increased intake rates. Of the 4 abundant species which had problems of obtaining enough energy in reasonable time, three increased their efforts, the Semipalmated Plover by an increased foraging time, the Red Knot by an increased intake rate, and the Semipalmated Sandpiper with both. Since the increased intake rates occur especially in February, it seems likely that they are related to migratory departure. However, unlike the results of the study at the Banc d'Arguin, no clear association with the size of birds (and their required foraging time) was apparent. It also remains unclear why, for example, the Grey Plover does not exhibit this behaviour and if the increased effort helps to satisfy the needs when the low food supply is bared in mind.

The species also differ in their presence over the time period of ebb tide. The primarily territorial plovers occupy the area more or less constantly. Some individuals, presumably those not holding territories in the study area, appear only at the beginning of ebb tide. Most sandpipers and wading birds stay in the study area only for limited time. They spend low tide either foraging at other – probably more profitable - parts of the intertidal or not foraging at all. Since many species appear to have difficulties in obtaining enough food, the latter possibility is unlikely. These other locations might contain more prey items, or prey items might be better available or detectable. For example, wet sand close to the waters edge might be easier to penetrate (Myers 1984), an aspect particularly important for probing birds (Pienkowski 1981), or prey items might show more surface activity in wet than in the hardened dry sand (Evans and Dugan 1984). Wading birds presumably forage predominantly at the creeks within the mangrove. Only Whimbrel, Willet and Short-billed Dowitcher chose the study area from all locations available at low tide. These birds might be less dependent on the penetrability of the sand because of their large size which enables them to dig in the sand more forcefully (Whimbrel and Willet) or because they usually fed in creeks and pools (Short-billed Dowitcher). They also need the least time to obtain their necessary daily food intake when foraging as observed in the study area.

Consumption from the birds perspective

Consumption vs. energetic requirements. Most birds foraging in the tidal flat of the Bragantian peninsula are able to gain enough energy in only a few hours or at least when feeding day and night, when using the foraging technique and the prey items observed in this study. However, four species apparently cannot satisfy their daily needs when foraging like observed during sampling: Semipalmated Plover, Marbled Godwit, Sanderling and Semipalmated Sandpiper. This inability is apparently not linked to a visual or tactile foraging technique or to territorial or gregarious feeding, as suggested by a study in Ghana (Ntiemoa-Baidu et al. 1998). These species have in common that they were observed to feed only on "worms" or very small prey, profitable large bivalves and crustaceans were not part of their diet (Table 11). As a consequence, the harvestable benthic biomass, as well as the energetic intake rate was very low for these birds (Table 8). Hence, they must obtain much higher energy intake rates elsewhere or they forage more efficiently at times not observed during the sampling within the study area. Sanderlings and some Semipalmated Sandpipers were observed, like many other species, to spend low tide away from the study area. Thus, they might use this time to forage at more attractive intertidal spots in other places which may be the predominant sources of their required energy. But many of the Semipalmated Sandpipers and most of the territorial Semipalmated Plovers do not leave the study area. Hence, they might gain much of their required energy at times not observed during the sampling, possibly during the night, providing that either their foraging technique is much more efficient or that prey availability is much higher during the night.

Nocturnal foraging has been described for many birds in the literature (McNeil and Robert 1988; Robert and McNeil 1989; Robert et al. 1989a; 1989b; McNeil et al. 1995; Dodd and Colwell 1998; Poole and Gill 2000; Sitters et al. 2001). There is much debate if nocturnal feeding is needed to supplement the diurnal foraging, or if it is the preferred foraging time (see McNeil et al. 1992 for review). However, the necessity of nocturnal foraging to fulfill energetic requirements was also assumed in other studies (for plover Pienkowski 1983b; for Semipalmated Sandpiper McCurdy et al. 1997). If birds forage at night at the Bragantian peninsula is unknown. But it is likely for at least a number of species, which must actually attain the majority of their daily energy intake at night, since they acquire only extremely little energy by day. Several authors showed that prey activity can be accelerated during the night (Pienkowski 1983b; Pienkowski 1983c; McNeil et al. 1995). In Venezuela, swimming organisms (isopods, amphipods and shrimps) and organisms at the sediment surface (isopods, amphipods and polychaetes) were clearly more active during the night (McNeil et al. 1995). If this also holds true for the benthic fauna at the Bragantian intertidal, the birds might have enough opportunity to satisfy their energetic needs. Additionally, Morrier and McNeil (1991) propose that nocturnal foraging might be especially advantageous in the tropics, since the high daily temperatures could be avoided. They lead to an enhanced drying of the sediment surface. However, more detailed investigations on nocturnal foraging are needed at the study area to evaluate its relevance in the northeast of Brazil.

Consumption vs. food stock. The above discussion does not take into account if the required prey is present at the Bragantinian tidal flats at all. Although food may not be a limiting factor in many coastal areas (Fasola 1994), some studies found surprisingly high consumption rates (in this study a consumption of 135% of the standing stock in January). Meire (1994) states that benthic food supplies are limiting for the avian community when birds consume the same amount or more than can be replaced by production or immigration. Unfortunately, little is known about annual production/mean biomass (P/B) ratios in tropical environments (Longhurst and Pauly 1987) and no data on this is available for the benthos in the north of Brazil. Hence, comparisons had to be done on the standing stock. According to a review of Kalejta and Hockey (1999), annual P/B ratios might range between 1 and 5 and they are positively correlated with mean ambient temperature. Tropical benthic communities are composed of a particularly large proportion of very small organisms (Dittmann 1995; Dittmann 2002b), which generally expose short life-cycles and lead to high P/B ratios (Wolff and Smit 1990). But even if a very high yearly P/B ratio would be assumed for the benthic community of the Bragantinian intertidal – like 5 or 6, as proposed for the Banc d'Arguin (Wolff and Smit 1990) – consumption would most likely reach or even exceed production in January and February.

Additionally, the relative predation pressure on individual benthic groups showed that in many plots birds cannot fulfil their energetic needs in the way they were observed to feed. They could not find enough biomass of the organisms they were observed to prey on, even though size classes and depth distributions of the benthos organisms were not taken into account. This would further restrict the available prey biomass (Piersma 1987). Thus, a food limitation for the birds can be expected. However, to verify this assumption, more detailed investigations on avian consumption during a complete annual cycle and on production rates of the benthic community are needed.

It has to be pointed out that according to Zwarts et al. (1990a) small waders might feed to a large extent on prey which would slip through the 1 mm sieve used in this study. Thus, the predation pressure - the ratio between avian consumption and benthic food stock - might actually be lower than that calculated in this investigation. Nevertheless, it cannot be expected that this difference might outweigh the expected food constraint.

Some authors argue that birds in the tropics might be able to consume a far larger proportion of the yearly production than in temperate regions, since the climatic situation and benthic production is more stable and predictable (Wolff and Smit 1990; Wolff 1991; Hockey et al. 1992). In contrast, de Goeij et al. (2003) showed that the tropical benthic community at Roebuck Bay is extremely variable, due to highly seasonal recruitment of benthic animals which takes place year around and do not correspond to each other. They conclude that this tropical intertidal is even less dependable than the Wadden Sea. At the Bragantinian peninsula a similar variability was observed, yet, overall abundances and biomasses were quite stable. Hence, it can be concluded that bird species, which are specialized on only few benthic organisms do indeed have to face a strong variability of their food stock and the intertidal can

support only few of these birds. On the other hand, birds which feed opportunistically on a broad variety of prey items might find extraordinarily stable food resources. These individuals might be able to make use of a large proportion of the benthic production. This supports the idea that only very opportunistic species can occur in this environment in large numbers. And indeed, in chapter 5 it was concluded that most birds at the study site are probably quite opportunistic in their food acquisition.

So far, all calculations only involved the satisfaction of the cost for living. But beside that, fat stocks have to be deposited to buffer short-term food shortages and a post-migratory diet and the building of fat reserves should enable the birds to reach at least their next stop-over sites (Puttick 1979; Zwarts et al. 1990b; Morrier and McNeil 1991). Thus, the energetic needs, especially prior to migration, might be actually even higher than considered so far

It is not known how long the birds stay at the Bragantinian intertidal. Since this location is a major stop over site, most of the observed birds might spend only little time at this area and move on to other, more favourable locations. If other areas might provide the essential food stock, the food availability might not be important at all for the birds,. But the situation is probably severe for the longer residing wintering individuals. However, it is not known how abundant prey is before January, but it could be assumed that benthic individuals are more abundant during that time due to less environmental disturbances (chapter 3).

Consumption from the prey's perspective

Exclosures. In various caging experiments shorebirds and other epibenthic predators proved to be capable of seriously depleting densities of a particular benthic prey at sediment shores (Goss-Custard 1977a; Schneider and Harrington 1981; Woodin 1981; Bell and Woodin 1984; Mercier and McNeil 1994). Few investigations report no avian impact on the prey organisms (Raffaelli and Milne 1987; Vargas 1988; Kalejta 1993), but the publication of such negative results might be underrepresented (Raffaelli and Moller 2000).

In this study, no strong impact of the avian community on the benthic infauna was measurable. Benthic abundances were very variable within and between the treatments. Significant effects were restricted to a few taxa and most of them were produced by the variable abundances of some taxa which compiled in certain months. Only the increase of Capitellidae in April in the procedural controls was not such an artefact. In fact, Capitellidae also increased inside the exclosures at the same time, but this was masked by simultaneous decrease of other taxa. Why did the abundance of Capitellidae rises inside the cages and procedural controls, but not in the controls? Cages and poles could have resulted in a reduced foraging efficiency for birds through disturbance. In that case, abundances of Capitellidae would have been limited by shorebird predation in April. Alternatively, aiding effects of the experimental construction (cages and poles), "cage artefacts", might have produced the experimental result (Hulberg and Oliver 1980; Quammen 1984b; Ólafsson et al. 1994). Altered sediment conditions and increased larvae settlement due to a limited disturbance between the poles can be ruled out,

since grain sizes and sizes of benthic individuals were similar between the treatments. An increased organic matter settlement might have been a possible explanation, since this factor was not controlled for in the investigation. Because the substrate would then be of higher nutritional value for the deposit feeding Capitellidae, their numbers might increase as a result. The life history of this organism could be responsible for the restricted time frame of the effect.

However, no satisfactory explanation can be given so far for the appearing effect on Capitellidae in April by the investigated factors. Overall, the benthic community appears rather unaffected by the consumption of shorebirds.

Some authors point out that the benthic community is not only modified by epibenthic predation, but also by predation, competition or promotional effects among the benthic organisms (Reise 1983; Commito and Shrader 1985; Reise 1985; Wilson Jr. 1989; Kneib 1991; Gurevitch et al. 2000). Hence, predation might be capable of changing the benthic community in a complex manner. In the present investigation the benthic community did not change in a strong fashion after six month of experimental treatments. Neither were the uppermost ranks of benthic organisms in the community altered, nor did a cluster analysis reveal differences between the communities in the treatment areas. Therefore a strong impact of the avian community on the benthic community within the investigated time frame can be ruled out. Van der Meer et al. (2000) state that enclosure experiments which aim to assess the impact of predation on the benthic community should exceed at least the generation time of the prey species. A modification of the benthic community in the long run cannot be rejected, since this would not have been detected by the experimental set up. In addition, Wilson (1989) and Mercier and McNeil (1994) stress the impact of seasonal variables. During the avian fall migration, with a differing impact of predators and another stage of reproduction or settlement of the benthic prey, the experiment might have lead to a different result.

Zwarts and Wanink (1989) point out that the predation pressure on shallow- living benthic species is much higher than on deep burrowing species. At the Bragantiner mudflats, 68% of all benthic animals live in the top sediment layer and the harvestable fraction of most birds is restricted to those individuals (chapter 5.2.1). Consequently, the few observed experimental effects appeared only in the top 5 cm of the sediment. The birds' impact might not reach deeper sediment levels. Surface differentiations, like increased organic contents might influence only the top sediment layers and possible effects in the deeper sediment regions are harder to detect due to the low numbers of benthic organisms.

Predation might also effect only certain size classes of the prey as shown by Richards et al. (1999) with *Carcinus maenas* depleting only large size bivalves. Size selective predation or changed recruitment numbers could cause this. In this study, only three taxa were abundant enough to test for size specific effects. They were not altered in their size classes between the treatments, but these organisms did generally not show large size ranges. However, there is no evidence for size selective predation so far.

Calculated consumption.

The calculated daily consumption per ha was high, though comparable with other areas (Table 19). Since the food stock available at the Bragantinian tidal flats was low in comparison to the other areas (Table 4), the consumed proportion of prey was extraordinarily large. If the birds would indeed satisfy their energetic requirements at the study site alone, they would have diminished the entire benthos community within a few weeks. If the avian preferences for particular benthic taxa would also have been considered, the benthos might have been depleted even earlier. But the benthos community did not disappear and the exclosure experiment showed that the avian impact on the infauna was negligible. Some authors suggest that prey reduction could be masked by high production rates (Duffy et al. 1981; Kalejta 1993). Even a very high production of the benthic community, as could be assumed for a tropical community like this, would probably not be able to buffer or to mask the reduction. Also, during the exclosure experiment no size differences were detected between the benthic organisms at the different treatments, thus it is unlikely that the eaten organisms were simply replaced by the next generation. Consequently, the observed avian community cannot forage exclusively in the study area but has to exploit other food sources as well. The benthic animals in the study area are thus able to exist in low densities without being depleted. However, since no data is available on benthic densities during winter time or of the time when the birds arrived in the area, it cannot be concluded that the birds have no depleting affect on their prey. It can only be stated that during the investigated time frame there was no marked effect.

Table 19. Avian consumption of benthic organisms at differnd tropical and temperate tidal flats as obtained by the literature.

Location	consumption	% of total production	% of standing stock	reference
Banc d'Arguin, Mauritania	11.5 gAFDW*m ⁻² *a ⁻¹	42.6%	82.7%	(Wolff and Smit 1990; Wolff 1991)0)
Inhaca Bay, Mozambique	2.1 gAFDW*m ⁻² *a ⁻¹ (45 gAFDW/ ha ⁻¹ *d ⁻¹ in winter)			(De Boer and Longamane 1996)
Bragança, Brazil	0-11.1 gAFDW*m⁻²*month⁻¹		15.2-134.6% per month	this study
Sylt-Rømø wadden sea, Germany	8.7 gAFDW*m ⁻² *a ⁻¹ (only intertidal)		15-25%	(Scheiffarth and Nehls 1997)
Oosterschelde estuary, Netherlands	11.5-13.2 gAFDW*m ⁻² *a ⁻¹		13-23%	(Meire et al. 1994)
Berg River estuary, South Africa	26.7 gAFDW*m ⁻² *a ⁻¹	26%		(Kalejta 1992; Kalejta 1993)
	4.4 gAFDW in three months by Curl. Sandpiper		77% of initial biomass of nereids by Curlew Sandpiper	
	0.4 gAFDW in three months by Grey Plover		7% of initial biomass of nereids by Grey Plover	
Ythan estuary, Great Britain	17.3 gAFDW*m ⁻² *a ⁻¹	36.5%		(Baird and Milne 1981)
Tees estuary, Great Britain	14.7 gAFDW*m ⁻² *a ⁻¹	44%		(Baird et al. 1985)
Wash, Great Britain	3.95-8.1 gAFDW*m ⁻² in 4 months (*), 1,3-1,8 gAFDW*m ⁻² in 2 months		14-34% in their main feeding areas, 2-21% elsewhere	(Goss-Custard 1977a)

(*) kilo joules had to be calculated into gAFDW (1gAFDW=25 kJ) according to (Higgins and Thiel 1988)

Behaviour

The behaviour of the different avian species was in most cases consistent with behavioural descriptions of these birds in other areas (Kushlan 1978; Poole and Gill 2000). Only Willets seem to expose fewer behavioural modes than usual. In contrast, the Little Blue Heron showed a far more diverse foraging behaviour at the Bragantinian peninsula with running, hopping and open-wing-feeding. The highly variable behaviour of herons and egrets indicates that prey items are rare at the study site and only obtainable by flushing (Kushlan 1981). Finally, the head-swinging foraging technique of the Semipalmated Sandpiper was also not found elsewhere. It is presumably an adaptation to foraging in liquid mud.

Visual vs. tactile foraging. Baker and Baker (1973) showed that different foraging methods lead to different rates of feeding and locomotion. Some studies also stress the idea that visual foraging plovers have more difficulties to satisfy their energetic requirements because their surface living prey is more influenced by temperature fluctuations than the infauna (Pienkowski 1981; Pienkowski et al. 1984). In the tropics, surface living prey organisms might be additionally disturbed by the strong salinity fluctuations (rain, hypersaline pools) or the quick drying of the sediment surface, which might hamper surface activity of benthic prey. The decision of the Bragantinian birds to forage visually, tactile or with a mixture of both, did indeed influence the prey intake rate, but the biomass ingestion was constant. The foraging technique represents different ways of obtaining food and probably maximizes the biomass intake rate according to the birds' capacities. However, it does not provide an energetic advantage if the behaviour itself does not differ in its energetic expenditure.

Spacing behaviour. Territoriality and aggregations are both spacing behaviours which occur primarily in patchy environments or environments with a scarce or medium food supply to increase the net energy intake rate (Recher and Recher 1969; Hall et al. 1990). Both behaviours include costs, as well as benefits and it might be assumed that they will be only adaptive if benefits exceed costs (Hall et al. 1990).

Aggregation improves predator avoidance and splits the predation risk among the flock members. The effect on the foraging efficiency of birds is complicated and sometimes contradictory. Flocking increases the likelihood of foraging at beneficial areas, since the observation of other birds can help to avoid locations with low food abundances (Hall et al. 1990). On the other hand, it might lead to depressed feeding rates since some prey organisms were shown to react negatively to predator presence (Goss-Custard 1980).

At the Bragantinian peninsula most bird species forage occasionally in congregations, only Snowy Egret, Red Knot, Short-billed Dowitcher and Semipalmated Sandpiper prefer flocking permanently. The sandpipers forage mostly tactile, and can thus enjoy the benefits of gregarious feeding (predator defence, eased detection of profitable spots), possibly without suffering under decreased prey availability, since they generally do not rely on visual cues

(Prater 1972; Hall et al. 1990). Snowy Egrets use a highly variable flushing technique in order to rouse up potential prey organisms and social foraging presumably improves this technique (Bennett and Smithson 2001). Herons and egrets are shown to increase their capture rate and their capture efficiency and to decrease the energy expenditure and the variance of the capture efficiency when foraging in mixed flocks (Master et al. 1993).

The benefit of territoriality, the other spacing behaviour, is the resource control in the defended area, though the cost is the energetic expenditure of territorial defence. Territories are only profitable at locations with medium food densities, since the costs of defending the territory will exceed the benefits if prey is too scarce, while territorial defence might not be longer possible if prey is too abundant (Myers 1984; Hall et al. 1990). Also, the benefit will level off with increasing prey availabilities, since intake rates and prey densities presumably have an asymptotic relationship (Hollings disc equation, Holling 1959).

Territoriality occurs only in Collared- and Semipalmated Plovers at the intertidal of the Bragantinian peninsula, therefore they are the two most solitary feeding birds. They are small and prey predominately on "worms". Since they forage highly visually, flocking behaviour would not be advantageous for them because of their reliance on surface activity of prey (Pienkowski 1981). Territoriality is probably most rewarding for them since they need to ensure high intake rates of an intermediately abundant prey item and congregations of other birds probably disturb their visual foraging technique. However, Semipalmated Plovers apparently do not form winter territories in Venezuela (Smit and Nol 2000). Unfortunately no information about the abundance of prey is given in that publication.

The group of birds exposing neither territorial nor gregarious behaviour includes shorebird species which show, according to the literature, territorial behaviour in other studies (McNeil and Rompré 1995; Turpie 1995; Burton and Evans 1997; Tripp and Collazo 1997; Poole and Gill 2000). Why don't they defend territories at the intertidal of the Bragantinian peninsula? These bird species are of mostly medium or large size and they forage with visual as well as tactile elements. Because of their size they are able to prey on crustaceans and bivalves, which are most profitable for them. But this prey is scarce and only available in significantly lower numbers than the prey of the territorial plovers. The birds probably have to explore a large area to find enough prey items to satisfy their daily needs. Thus, territories might not be advantageous, since the defence of such large areas would lead to large expenses. Therefore, it is more favourable for them to feed opportunistically and cover large intertidal areas. This is supported by the observed aggressive encounters. Although these encounters are rare, they involve mainly birds from this group and their aim is in most cases opportunistic prey robbing, and only rarely territorial defence.

Aggressive encounters, as they occur during territorial or individual distance defense, increase with increased patchiness of the environment and increased bird densities, because these conditions lead to a decreasing foraging space (Myers 1984; Wilson Jr. 1990).

Although both factors coincide at the intertidal of the Bragantinian peninsula, only few encounters were observed. Aggressive encounters, which might require a high energetic expenditure, are presumably not beneficial when prey organisms are generally as small as observed in the study area. Prey robbing is only profitable when extraordinarily large organisms are involved and might thus be feasible only for large birds.

It appears that the birds at the Bragantinian peninsula forage in the way which is probably most rewarding for them considering their size and – related to that – the prey fraction available to them. Although the optimised foraging techniques lead to different prey intake rates, biomass ingestion rates do not differ between foraging behaviours.

The intertidal of the Bragantinian peninsula

Overall, the picture emerges that the study area at the Bragantinian peninsula is a variable and rather poor area. The avian community observed in the area is not able to gain enough energy from this part of the intertidal and probably forages predominantly at other locations on this part of the coast. One alternative would be to forage within the roosting areas of the mangrove forest, although this idea is generally rejected in studies on shorebirds in the tropics (Evans 1976; Piersma et al. 1993). In Panama, Butler et al. (1997) recorded highest bird densities on mudflats adjacent to mangroves, presumably due to the high food availability associated with mangrove forests. Higher parts of the forest often remain exposed even during high tide and are thus available as foraging areas. A rich benthic fauna lives in the sediments there, dominated by polychaetes. Guimarães Figueira (2002) found macrobenthic densities of 858 individuals per m² inside the mangrove forest and close to the Furo Grande plots of this study. This density is still not very high in comparison to densities of some intertidal areas given in the literature, but exceeds the densities found in this study (Table 4). Unfortunately, no biomass data is available for the area inside the mangrove forest. However, the mean number of birds found at Furo Grande inside the mangrove was far lower than that found at the open intertidal of the Ilha de Canelas (30.3 and 57.3 individuals/ha respectively). Hence, most shorebirds seem to avoid this area, maybe as a result of predator avoidance. Furthermore, the plots at the Furo Grande do not contain a distinctly different benthic community (Fig. 17), though the diversity of the benthic taxa is lower than that obtained at the open intertidal of the Ilha de Canelas (Appendix II, Table 29). The birds might not find their favourite prey taxa within the mangrove, but only in the open intertidal.

Besides feeding in the mangrove forest, birds could also use other locations in the open intertidal. The sediment of the Bragantinian intertidal contains at some places extraordinary amounts of sand when compared to the other coastal areas of that region, which contain high levels of muddy sediments (Muehe and Neves 1995). As a result, the benthic community might differ in comparison to other locations on the coast. Morrison and Ross (1989) found in their investigations along the coast of South America that most of the avian

species showed a clumped dispersion and the intertidal around the Bragantinian peninsula held comparatively low numbers of shorebirds (2500-6000 shorebirds in the western intertidal, 700-1500 individuals in the eastern intertidal of the peninsula). Only 100 km further east or 50 km further west, far larger concentrations of shorebirds were found. It is possible that those areas provide a more abundant food stock. Birds using the poor intertidal at the Bragantinian peninsula might represent subdominant individuals, which are displaced from richer tidal flats by dominating individuals. Such competitive situations might easily occur on this part of the South American coast, since overall bird densities are high and foraging time in intertidal habitats is limited by the tidal movements of the water. While birds in temperate zones might use also salt marshes and fields for foraging when the tidal flats are inundated, this is not possible in the tropics, since mangroves fringe the intertidal. However, this remains a speculation until the more preferred tidal areas have also been investigated.

7 References

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11 Appendices

11.1 Appendix I: Methods

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Plots	January			February			March			April			May			June		
	X ²	p	v	X ²	p	v	X ²	p	v	X ²	p	v	X ²	p	v	X ²	p	v
1-5	257.333	<0.001	20	784.556	<0.001	36	1001.719	<0.001	32	160.064	<0.001	12	555.739	<0.001	16	250.976	<0.001	12
6-10	858.982	<0.001	24	274.339	<0.001	16	296.905	<0.001	27	560.573	<0.001	20	1069.882	<0.001	28	904.051	<0.001	20
11-15	842.652	<0.001	32	647.767	<0.001	20	314.507	<0.001	16	831.875	<0.001	24	549.931	<0.001	20	850.481	<0.001	16
16-19	206.069	<0.001	9	214.033	<0.001	9	318.140	<0.001	15	180.138	<0.001	4	293.465	<0.001	9	612.260	<0.001	18
20-23	435.531	<0.001	12	842.497	<0.001	18	345.616	<0.001	12	199.100	<0.001	12	129.851	<0.001	9	207.954	<0.001	12
24-25	146.670	<0.001	6	74.663	<0.001	4	52.637	0.036	4	61.616	0.005	4	-	-	-	44.244	0.163	1
26-25	657.215	<0.001	8	477.840	<0.001	8	747.939	<0.001	8	413.185	<0.001	4	391.000	<0.001	6	170.231	<0.001	8
29-31	59.730	0.008	2	314.827	<0.001	8	85.171	<0.001	2	31.856	0.666	2	122.778	<0.001	2	396.430	<0.001	10
32-36	1468.396	<0.001	28	524.297	<0.001	16	469.077	<0.001	16	484.684	<0.001	12	1677.694	<0.001	24	1144.197	<0.001	12
37-41	463.110	<0.001	12	649.307	<0.001	20	323.827	<0.001	12	439.811	<0.001	12	186.496	<0.001	12	429.022	<0.001	12
42-46	383.966	<0.001	16	329.815	<0.001	12	491.982	<0.001	12	185.059	<0.001	6	1044.936	<0.001	16	693.353	<0.001	12
Ex	517.548	<0.001	25	397.127	<0.001	18	765.962	<0.001	36	489.934	<0.001	24	620.918	<0.001	30	440.303	<0.001	30
C	721.585	<0.001	36	349.716	<0.001	20	966.741	<0.001	30	1013.198	<0.001	36	864.094	<0.001	36	599.202	<0.001	30
Pc	1001.943	<0.001	42	191.807	<0.001	16	591.539	<0.001	25	505.068	<0.001	30	1004.116	<0.001	30	751.526	<0.001	35

Table 21. Mean avian steps/min determined by recorded sequences on video tape in 2002..

species	Mean steps/min	Standard deviation	n
Grey Plover	382.3	89.7	8
Collared Plover	440.4	111.4	7
Red Knot	305.9	77.5	8
Semipalmated Plover	481.5	160.0	7
Semipalmated Sandpiper	286.1	41.2	14
Ruddy Turnstone	310.2	80.5	7

Table 22. Biometric data obtained from the literature. The biometric data were found in three different publications. It was taken care to take data of adult birds from South America or migrants with pathways down the east American coast, if possible. If the source differentiated between males and females a mean was calculated since in this study no such segregation took place. As no data on leg length could be found in the literature a doubled tarsus lengths were taken.

Species		Bill [mm]	Tarsus [mm]	Weight [kg]	Publication
Hérons, egrets and ibises	Little Blue Heron	74.2	92.2	No data	1)
	Snowy Egret	81.0	93.4	No data	3)
	Tricolored Heron	96.0	95.0	No data	2)
	Scarlet Ibis	145.6	No data	0.514	1), 3)
Plover	Collared Plover	14.5	25.1	0.026	1), 3)
	Grey Plover	30.0	45.0	0.180	1), 3)
	Semipalmated Plover	12.2	22.1	0.047	1), 3)
Sandpiper, Snipes etc.	Marbled Godwit	102.6	70.4	0.285	1), 3)
	Red Knot	36.1	31.0	0.135	2), 3)
	Ruddy Turnstone	23.6	26.3	0.084	2), 3)
	Sanderling	25.5	25.8	0.040	3), 3)
	Semipalmated Sandpiper	19.5	20.7	0.021	1), 3)
	Short-billed Dowitcher	57.0	34.1	0.090	3)
	Spotted Sandpiper	23.5	25.1	No data	2)
	Whimbrel	87.2	58.1	0.310	3), 3)
	Willet	55.0	55.9	0.200	2), 3)

1) Manual of Neotropical Birds (Blake 1977)

2) Handbook of the birds of the world (del Hoyo et al. 1996)

3) Birds of North America (Poole and Gill 2000)

Table 23. Size/AFDW relationships of the benthic taxa calculated with help of a reference sample. Given are variables and formulas which were used to transform the size data into AFDW data. The benthic samples of the study contained also individuals which were smaller or larger than the individuals of the reference sample. For the smaller individuals the AFDW of the smallest reference individual was taken. For the larger individuals an extra function was calculated with the 10 largest individuals of the reference sample. Since no other approximation for the weight of those large individuals was possible, the function was extrapolated inappropriately to obtain AFDW. If taxa were not represented with enough individuals in the reference sample to calculate an individual formula, they were grouped in the next higher taxon instead.

Size of individuals:	< reference sample		= reference sample					> reference sample					comment
Calculation:	AFDW of the smallest of the reference sample		Fitting of a function in the reference sample ($y=a*x^b+c$)					Fitting of a function in the 10 largest animals of the reference sample ($y=a*x^b+c$) and inappropriate extrapolation					
Taxa	Size [cm]	AFDW [mg]	Size [cm]	a	b	c	R ²	Size [cm]	a	b	c	R ²	
Bivalvia	-	-	0.3-3.4	1.0	4.6	1.7	0.997	> 3.4	0.8	4.7	3.5	0.999	
Tagelus plebeius	< 1,2	2,147	1.2-2.43	7.0	2.5	-8.8	0.986	> 2.43	7.0	2.5	-8.8	0.986	a)
Tellina radiata	< 0.45	0.015	0.45-1.91	3.2	3.4	-0.2	0.991	-	-	-	-	-	
Gastropoda	< 0.77	2.068	0.77-1.4	5.3	4.0	0.3	0.842	> 1.4	5.3	4.0	0.3	0.842	a)
Crustacea	< 0.45	0.044	0.45-2.7	32.0	3.5	-1.9	0.981	> 2.7	41.6	3.2	-23.1	0.988	
Pinnotheridae	< 0.24	0.040	0.24-1.45	9.8	1.2	-1.8	0.72	-	-	-	-	-	
Uca maracoani	-	-	0.23-2.7	52.0	3.0	-0.5	0.994	-	-	-	-	-	
Polychaeta, Sipunculida and Nemertinea	< 1.2	0.001	1.2-19.8	0.4	0.9	-0.5	0.64	> 19.8	19.6	0.2	-31.6	0.669	

a) The data base of the reference sample was not large enough to do a separate function fitting for only the 10 largest animals; the function of the reference sample was used

Table 24. Identified prey by fragments found in the droppings in 2002. Taxa which are not listed could not be identified.

Taxa		Identified by...
Bivalvia		Unidentified shell fragments
	<i>Protothaca sp.</i>	Shell fragments
	<i>Tagelus sp.</i>	Shell fragments
	<i>Tellina sp.</i>	Shell fragments
Gastropoda		Unidentified shell fragments
	<i>Nassarius sp.</i>	Shell fragments
Crustacea		Unidentified cuticula fragments
	Callianassidae	Cuticula fragments
	Copepoda	Complete animals
	Idotheidae	Complete animals
	Decapoda	Cuticula fragments
	Pinnotheridae	Cuticula fragments
	<i>Uca sp.</i>	Cuticula fragments
Polychaeta		Cirrae without any more specializing fragments
	Gonididae	Mandibulae, Aciculae, Cirrae
	Lumbrineridae	Mandibulae, Aciculae, Cirrae
	Nephtyidae	Mandibulae, Aciculae, Cirrae
	Nereide	Mandibulae, Aciculae, Cirrae,
	Pilargiidae	Aciculae, Cirrae
	Spionidae	Aciculae, Cirrae
	Terebellidae	Uncini, Aciculae, Cirrae
Insecta and Arachnida		Cuticula fragments
Pisces		Scale fragments
Plants		Plant fibres

Table 25. Results of Contingency tables between the benthic group composition of 2001 and 2002 obtained at the Ilha de Canelas. Abundance data is given in %, although the test was performed on the orginial abundance data.

Taxa	Abundances		Biomasses	
	2001	2002	2001	2002
Bivalvia	11,44	13,35	34,88	19,40
Crustacea	18,48	32,75	59,07	76,50
Gastropoda	3,45	2,27	4,79	2,50
Nemertinea	5,75	3,78	0,19	0,07
Polychaeta	58,23	47,10	1,08	1,53
Sipunculidae	2,64	0,76	0,00	0,00
		X ² =918,086	X ² =6,192	
		P<0.001	p=0,288	
		v=5	v=5	

Table 26. Size/handling time relationship of the benthos organisms. Given are variables and formulas of the relationship calculated on the basis of data obtained during focal observations in 2002. The formula ($y=a*(x^b)+c$) was only applied when $R>0,60$, if no formular could be applied a mean handling time was used. Formula and mean handling times were only used within the size range given by the focal observations, other prey was not included into calulations of profitability.

Species	Benthos taxon	n	size range [cm]	mean handling time [sec]	a	b	c
Scarlet Ibis	Bivalvia	15	1.5-5.8	2.13			
	Crustacea	21	1.5-5.8	5.62			
	Gastropoda	3	1.5-2.9	2.00			
	"Worm"	10	2.9-8.7	2.10			
Collared Plover	Bivalvia	7	0.1-1	1.43			
	Crustacea	3	0.3-4.4	6.00			
	"Worm"	66	0.4-7.3		0.00	2.96	1.18
Grey Plover	Bivalvia	12	0.3-3.6	1.75			
	Crustacea	15	0.3-3.9	5.27			
	Gastropoda	1	0.6-0.6	1.00			
	"Worm"	28	0.9-9	1.50			
Semipalmated Plover	Bivalvia	2	0.5-0.5	2.00			
	Crustacea	1	1-1	2.00			
	"Worm"	179	0.2-9.8	1.26			
Marbled Godwit	Gastropoda	1	1-1	1.00			
	"Worm"	16	1-8.2	1.59			
Red Knot	Bivalvia	12	1.4-4		0.01	4.04	0.79
	Gastropoda	18	0.4-1.1	1.44			
	"Worm"	1	4.3-4.3	2.00			
Ruddy Turnstone	Bivalvia	17	1.2-5.9	13.24			
	Crustacea	2	0.5-0.7	1.00			
	"Worm"	2	1.9-4.7	1.00			
Sanderling	Bivalvia	3	0.8-1.5	1.00			
	Gastropoda	1	0.3-0.3	1.00			
	"Worm"	3	1.3-3.8	2.00			
Semipalmated Sanpiper	Bivalvia	14	0.4-1	1.29			
	Crustacea	1	0.4-0.4	1.00			
	"Worm"	12	0.2-3.9	1.75			
Short-billed Dowitcher	Bivalvia	18	0.6-6.2	1.78			
	Gastropoda	6	0.6-1.7	1.00			
	"Worm"	12	1.1-6.8		0.01	2.92	1.20
Whimbrel	Bivalvia	20	0.9-5.2	1.90			
	Crustacea	8	1.7-6.1	2.50			
	Gastropoda	3	0.9-0.9	1.00			
	"Worm"	4	3.5-5.2	2.33			
Willet	Bivalvia	6	0.5-4.4	2.17			
	Crustacea	10	1.1-4.9	7.70			
	Gastropoda	3	0.5-1.6	1.33			
	"Worm"	1	1.1-1.1	2.00			

11.2 Appendix II: Environmental conditions and the benthic community

Table 27. Sediment characteristics of the plots in 2001 in increasing order.

Plot	Median [phi Φ units]	Quartile deviation [phi Φ units]	Sorting coefficient	Observations
5	2.77 ± 0.01	0.56 ± 0.00	1.22 ± 0.00	Sandy, with small ponds
4	2.77 ± 0.02	0.56 ± 0.01	1.23 ± 0.00	Sandy, with small ponds
1	2.78 ± 0.01	0.56 ± 0.01	1.23 ± 0.00	Sandy, with small ponds
2	2.78 ± 0.01	0.55 ± 0.00	1.22 ± 0.00	Sandy, with small ponds
3	2.78 ± 0.02	0.56 ± 0.01	1.23 ± 0.00	Sandy, with small ponds
38	2.78 ± 0.02	0.56 ± 0.01	1.23 ± 0.00	Sandy
28	2.79 ± 0.01	0.56 ± 0.01	1.23 ± 0.00	Sandy, margin of a furo
41	2.79 ± 0.01	0.56 ± 0.01	1.23 ± 0.00	Sandy
7	2.79 ± 0.02	0.56 ± 0.01	1.23 ± 0.00	Sandy - soft sand
9	2.79 ± 0.02	0.57 ± 0.01	1.23 ± 0.00	Sandy - soft sand
39	2.79 ± 0.02	0.56 ± 0.02	1.23 ± 0.00	sandy
40	2.79 ± 0.02	0.56 ± 0.01	1.22 ± 0.00	sandy
31	2.80 ± 0.02	0.57 ± 0.01	1.23 ± 0.00	Sandy, margin of a furo
37	2.80 ± 0.02	0.57 ± 0.01	1.23 ± 0.00	Sandy, margin of a creek
42	2.81 ± 0.01	0.57 ± 0.00	1.23 ± 0.00	sandy
11	2.81 ± 0.02	0.57 ± 0.01	1.23 ± 0.01	Sandy - soft sand
45	2.82 ± 0.02	0.58 ± 0.01	1.23 ± 0.00	sandy
27	2.82 ± 0.03	0.58 ± 0.01	1.23 ± 0.00	Sandy - soft sand
10	2.83 ± 0.03	0.58 ± 0.02	1.23 ± 0.00	Sandy - soft sand, border of a creek
6	2.83 ± 0.12	0.58 ± 0.06	1.23 ± 0.02	Sandy - soft sand
8	2.84 ± 0.03	0.59 ± 0.01	1.24 ± 0.00	Sandy - soft sand
32	2.84 ± 0.07	0.59 ± 0.04	1.23 ± 0.01	Sandy - soft sand, border of a creek
30	2.85 ± 0.02	0.60 ± 0.01	1.24 ± 0.00	Sandy - soft sand
35	2.85 ± 0.04	0.51 ± 0.20	1.20 ± 0.08	Sandy - soft sand, border of a creek
43	2.85 ± 0.05	0.59 ± 0.03	1.23 ± 0.01	sandy
14	2.86 ± 0.04	0.60 ± 0.02	1.24 ± 0.00	Sandy - soft sand, border of a creek
44	2.86 ± 0.09	0.60 ± 0.04	1.24 ± 0.01	Sandy
12	2.87 ± 0.05	0.61 ± 0.02	1.24 ± 0.01	Sandy - soft sand
20	2.89 ± 0.05	0.62 ± 0.03	1.24 ± 0.01	Sandy – mud, border of a creek
21	2.91 ± 0.04	0.63 ± 0.01	1.25 ± 0.01	Soft sand – mud, border of a creek
46	2.91 ± 0.16	0.66 ± 0.17	1.25 ± 0.05	Sandy
36	2.93 ± 0.06	0.64 ± 0.03	1.25 ± 0.01	Soft sand – mud, border of a creek
13	2.94 ± 0.06	0.64 ± 0.03	1.25 ± 0.01	Sandy – soft sand
33	2.94 ± 0.06	0.64 ± 0.03	1.25 ± 0.01	Soft sand
23	2.96 ± 0.06	0.65 ± 0.03	1.25 ± 0.01	Soft sand, mussle bank
16	2.97 ± 0.04	0.66 ± 0.02	1.25 ± 0.01	Soft sand
18	2.97 ± 0.05	0.66 ± 0.02	1.25 ± 0.01	Soft sand
15	2.98 ± 0.03	0.67 ± 0.02	1.25 ± 0.00	Soft sand, border of a creek
17	3.00 ± 0.08	0.69 ± 0.09	1.26 ± 0.03	Soft sand - muddy
29	3.02 ± 0.07	0.71 ± 0.09	1.27 ± 0.03	Muddy
19	3.04 ± 0.07	0.71 ± 0.06	1.27 ± 0.02	Soft sand - muddy
22	3.08 ± 0.05	0.73 ± 0.06	1.27 ± 0.02	Muddy, border of a creek
24	3.23 ± 0.08	1.05 ± 0.22	1.36 ± 0.06	Soft mud
25	3.28 ± 0.11	1.10 ± 0.21	1.37 ± 0.06	Soft mud
26	3.35 ± 0.62	0.84 ± 0.23	1.30 ± 0.06	Soft mud
34	3.34 ± 0.31	1.04 ± 0.28	1.35 ± 0.07	Soft mud

Table 28. Results of Spearman Rank Correlations between benthic abundances and median grain sizes of the sediment [Φ], time of emergence [minutes] and salinity [‰]. Only benthic taxa with >10 individuals found were included. For the correlations between Median-benthic abundances and salinity-benthic abundances all data were included, which were obtained at the same sampling date in 2001. Time of emergence was only taken at one date and it was assumed, that it remained unchanged at each plot. Thus the same time period was used every time benthic data was obtained at the plots. N of the Median is 272, n of the time of emergence is 149 and n of Salinity is 275.

Taxa	Median		Time of emergence		Salinity	
	r	p	r	P	r	p
Sipunculida	0.145	0.016*	-0.138	0.094	-0.166	0.006*
Nemertinea	0.102	0.092	0.204	0.013*	-0.087	0.152
Bivalvia	0.190	0.001*	0.090	0.274	0.036	0.549
<i>Anomalocardia brasiliiana</i>	0.157	0.009*	-0.103	0.213	-0.039	0.519
<i>Lucina pectinata</i>	0.243	0.000*	0.005	0.950	0.052	0.387
<i>Tagelus plebeius</i>	0.265	0.000*	0.090	0.273	-0.039	0.524
<i>Tellina radiata</i>	-0.077	0.204	0.013	0.871	0.012	0.842
Gastropoda	0.214	0.000*	-0.121	0.141	-0.004	0.950
<i>Nassarius vibrex</i>	0.186	0.002*	-0.081	0.328	-0.091	0.134
<i>Natica nyarochiensis</i>	0.122	0.045*	-0.038	0.649	0.119	0.048*
Crustacea	-0.234	0.000*	0.087	0.289	0.173	0.004*
Callianassidae	0.009	0.881	0.144	0.080	0.134	0.026*
Copepoda	0.012	0.844	-0.011	0.896	0.024	0.688
Gammaridea	-0.140	0.021*	0.057	0.491	-0.038	0.535
Idotheidae	-0.159	0.009*	0.053	0.520	-0.101	0.096
Mysidae	-0.156	0.010*	-0.018	0.824	-0.032	0.599
Pinnotheridae	-0.291	0.000*	0.024	0.773	0.282	0.000*
<i>Uca maracoani</i>	0.280	0.000*	0.046	0.575	-0.021	0.735
Polychaeta	-0.032	0.594	-0.058	0.483	-0.042	0.484
Capitellidae	0.315	0.000*	-0.016	0.896	0.164	0.006*
Gonididae	0.244	0.000*	0.060	0.465	-0.012	0.839
Lumbrineridae	0.035	0.566	-0.089	0.278	0.029	0.636
Magelonidae	0.043	0.479	0.004	0.959	-0.050	0.407
Nephtyidae	-0.314	0.000*	-0.087	0.291	-0.134	0.027*
Nereide	0.296	0.000*	0.038	0.648	0.058	0.340
Opheliidae	-0.194	0.001*	0.243	0.003*	-0.021	0.733
Orbiniidae	-0.244	0.000*	-0.034	0.680	-0.009	0.877
Pilargiidae	0.186	0.002*	-0.111	0.176	0.040	0.513
PilargiidaeB	0.093	0.125	-0.007	0.932	0.006	0.920
total	-0.016	0.795	-0.034	0.681	0.016	0.796

Table 29. All identified benthic taxa with their abundances and biomasses at the study area in 2001/2002.

Taxa		Indiv. found in habitats				Densities [indiv./m ²]		Biomass [mgAFDW/m ²]	
		n	C	FC	FG	Mean ± Std dev	Range	Mean ± Std dev	Range
Sipunculidae		40	X	X		2.84 ± 10.34	0 – 79.64	0.01 ± 0.11	0 – 1.98
Nemertinea		121	X	X	X	9.00 ± 16.52	0 – 119.46	3.60 ± 17.14	0 – 244.48
Bivalvia	<i>Anomalocardia brasiliiana</i> (Gmelin 1791)	14	X			0.93 ± 6.23	0 – 59.73	154.91 ± 105.47	0 – 11,318.16
	<i>Divaricella quadrisulcata</i> (Orbigny 1842)	1	X			0.07 ± 1.15	0 – 19.91	0.12 ± 2.04	0 – 35.37
	<i>Donax striatus</i> (Linnaeus 1758)	1	X			0.07 ± 1-15	0 – 19.91	0.13 ± 2.34	0 – 40.58
	<i>Lucina pectinata</i> (Gmelin 1791)	41	X			2.71 ± 8.86	0 – 59.73	6.16 ± 23.92	0 – 295.92
	<i>Protothaca pectorina</i> (Lamarck 1818)	11	X		X	0.73 ± 4.68	0 – 59.73	92.98 ± 749.96	0 – 8,019.65
	<i>Tagelus plebeius</i> (Lightfoot 1786)	45	X	X	X	2.98 ± 10.92	0 – 99.55	229.37 ± 1,220.29	0 – 12,697.29
	<i>Tellina lineata</i> (Turton 1819)	5	X	X		0.33 ± 2.55	0 – 19.91	12.04 ± 142.39	0 – 2,236.01
	<i>Tellina radiata</i> (Linnaeus 1758)	131	X	X	X	8.68 ± 17.96	0 – 159.28	15.57 ± 61.79	0 – 563.66
	UK (25)*	3	X			0.20 ± 1.98	0 – 19.91	0.36 ± 3.58	0 – 36.72
	Species total		9	3	3				
Gastropoda	<i>Anachis</i> sp.	2	X			0.13 ± 1.62	0 – 19.91	0.27 ± 3.35	0 – 41.17
	<i>Nassarius vibrex</i> (Say 1822)	47	X			3.11 ± 14.53	0 – 139.37	64.58 ± 321.90	0 – 3,463.16
	<i>Natica nyarochiensis</i> (Gmelin 1791)	12	X		X	0.79 ± 3.90	0 – 19.91	1.65 ± 8.10	0 – 43.05
	Species total		3	0	1				

Taxa		Indiv. found in habitats				Densities [indiv./m ²]		Biomass [mgAFDW/m ²]	
		n	C	FC	FG	Mean ± Std dev	Range	Mean ± Std dev	Range
Crustacea	Brachyura	8	X		X	0.53 ± 3.21	0 – 19.91	0.02 ± 0.14	0 – 0.87
	Callianassidae	38	X	X		2.51 ± 7.56	0 – 59.73	785.79 ± 3,837.30	0 – 25,589.50
	<i>Callinectes sp.</i>	2	X			0.13 ± 1.62	0 – 19.91	0.26 ± 3.18	0 – 45.79
	Copepoda	15	X	X	X	0.99 ± 6.32	0 – 59.73	0.04 ± 0.28	0 – 2.60
	“hermid crab”	2	X			0.13 ± 1.62	0 – 19.91	No data	No data
	Decapoda	9	X			0.60 ± 3.77	0 – 39.82	33.00 ± 296.69	0 – 3,950.58
	<i>Eurytium limosum</i> (Say 1818)	2	X			0.13 ± 2.30	0 – 39.82	0.21 ± 3.66	0 – 63.47
	Gammaridea	344	X	X		22.75 ± 73.36	0 – 438.02	5.96 ± 39.66	0 – 528.03
	Gnathiidae	2	X		X	0.13 ± 1.62	0 – 19.91	0.02 ± 0.07	0 – 0.87
	Hippolythidae	3	X	X		0.20 ± 1.98	0 – 19.91	2.59 ± 30.04	0 – 455.93
	Idotheidae	78	X	X	X	5.16 ± 15.41	0 – 139.37	6.61 ± 45.96	0 – 474.73
	Mysidae	33	X		X	2.18 ± 8.08	0 – 79.64	41.10 ± 194.15	0 – 1,639.93
	Pinnotheridae	306	X	X	X	20.24 ± 42.00	0 – 258.83	23.68 ± 61.38	0 – 692.76
	Stomatopoda	1	X			0.07 ± 1.15	0 – 19.91	2.92 ± 50.62	0 – 878.28
	Tanaidacea	1	X			0.07 <± 1.15	0 – 19.91	(<0 .01)± 0.05	0 – 0.87
	<i>Uca maracoani</i> (Latreille 1802-1803)	23	X		X	1.52 ± 8.70	0 – 99.55	115.85 ± 930.05	0 – 13,194.05
	<i>Uca rapax</i> (Smith 1870)	1			X	0.07 ± 1.15	0 – 19.91	1.58 ± 27.36	0 – 474.73
	<i>Uca sp.</i>	3			X	0.20 ± 2.56	0 – 19.91	0.55 ± 9.45	0 – 163.95
Species total			16	6	9				
Olygochaeta		1	X			0.07 ± 1.15	0 – 19.91	0.08 ± 1.40	0 – 24.35

Taxa		Indiv. found in habitats				Densities [indiv./m ²]		Biomass [mgAFDW/m ²]	
		n	C	FC	FG	Mean ± Std dev	Range	Mean ± Std dev	Range
Polychaeta	Ampharetidae	4	X			0.26 ± 2.28	0 – 19.91	0.01 ± 0.16	0 – 2.22
	Capitellidae	323	X	X	X	21 ± 53.43	0 – 497.75	8.13 ± 30.66	0 – 379.54
	Eulepethidae	3	X			0.20 ± 1.98	0 – 19.91	0.07 ± 0.91	0 – 14.04
	Glyceridae	7	X	X		0.46 ± 4.12	0 – 59.73	0.33 ± 3.04	0 – 44.78
	Goniadidae	63	X	X		4.17 ± 12.48	0 – 79.64	0.47 ± 2.04	0 – 20.10
	Hesionidae	5	X		X	0.33 ± 3.02	0 – 39.82	(<0.01) ± (<0.01)	0 – 0.02
	Lumbrineridae	20	X			1.32 ± 6.16	0 – 59.73	0.70 ± 5.81	0 – 91.72
	Magelonidae	37	X	X	X	2.45 – 9.08	0 – 79.64	0.62 ± 3.21	0 – 31.71
	Nephtyidae	1048	X	X	X	69.32 ± 79.98	0 – 497.75	13.20 ± 17.36	0 – 95.40
	Nereidae	135	X	X	X	8.93 ± 21.48	0 – 219.01	3.18 ± 9.14	0 – 68.73
	Onuphidae	4	X			0.26 ± 2.80	0 – 39.82	0.23 ± 2.67	0 – 37.55
	Opheliidae	28	X	X	X	1.85 ± 8.40	0 – 179.19	0.01 ± 0.18	0 – 3.17
	Orbiniidae	90	X	X		5.95 ± 21.48	0 – 179.19	1.46 ± 6.69	0 – 63.11
	Pectinariidae	1	X			0.07 ± 1.15	0 – 19.91	(<0.01) ± (<0.01)	0 – 0.01
	Phyllodocidae	2	X			0.13 ± 1.62	0 – 19.91	0.03 ± 0.51	0 – 8.80
	Pilargiidae	35	X	X	X	2.32 ± 8.20	0 – 59.73	0.30 ± 1.61	0 – 14.29
	Pilargiidae (B)*	26	X	X		1.72 ± 7.78	0 – 59.73	0.82 ± 4.55	0 – 47.38
	Saccocirridae	1	X			0.07 – 1.15	0 – 19.91	0.02 ± 0.31	0 – 5.41
	Spionidae	7	X			0.46 ± 3.78	0 – 39.82	0.03 ± 0.43	0 – 6.27
	Uk34*	10	X			0.66 ± 5.10	0 – 59.73	0.06 ± 0.58	0 – 6.96
	Species total		20	10	7				
Insecta		1		X		0.07 – 1.15	0 – 19.91	No data	No data
Total			51	22	21				

* no further identified species

Table 30. Annual variance of benthic densities at the Canelas plots in 2001 and 2002. Given are the results of Mann-Whitney U-tests based on individuals/m² per plot (2001 n=25, 2002 n=5).

Taxa	February			March			April			May			June		
	U	Z	p	U	Z	p	U	Z	p	u	z	p	u	Z	p
Sipunculidae	45.0	0.87	0.39	45.0	0.97	0.33	62.50	0	1	48.5	-0.78	0.44	49.5	0.03	0.97
Nemertinea	55.0	-0.29	0.77	46.5	0.89	0.37	59.50	-0.17	0.87	48.0	-0.81	0.42	39.0	-0.70	0.49
<i>Anomalocardia br.</i>	57.5	0.14	0.89	62.5	0	1	55.00	0.42	0.68	62.5	0	1	50.0	0	1
<i>Lucina pectinata</i>	56.0	-0.23	0.82	61.5	0.06	0.96	47.5	-0.83	0.40	59.5	0.17	0.87	37.5	-0.79	0.43
<i>Tagelus plebeius</i>	48.0	-0.69	0.49	57.5	0.28	0.78	57.0	0.31	0.76	52.0	-0.58	0.56	50.0	0	1
<i>Tellina radiata</i>	57.0	-0.17	0.86	47.5	0.83	0.40	49.5	-0.72	0.47	48.5	-0.78	0.44	35.5	-0.92	0.36
<i>Nassarius vibrex</i>	40.0	1.15	0.25	58.5	-0.22	0.82	55.0	0.42	0.68	41.5	-1.17	0.24	37.5	-0.79	0.43
<i>Natica nyarochiensis</i>	50.5	-0.55	0.58	60.0	0.14	0.89	57.5	0.28	0.78	60.0	0.14	0.89	44.0	0.38	0.70
Callianassidae	43.5	-0.95	0.34	50.0	0.70	0.49	41.5	-1.17	0.24	62.5	0	1	34.0	1.01	0.31
Gammaridea	53.0	-0.40	0.69	52.0	-0.58	0.56	57.5	0.28	0.78	60.0	0.14	0.89	50.0	0	1
Idotheidae	55.5	-0.26	0.80	52.5	0.56	0.58	60.0	-0.14	0.89	60.0	0.14	0.89	50.0	0	1
Mysidae	56.0	-0.23	0.82	45.0	-0.97	0.33	50.0	0.70	0.49	61.5	0.56	0.96	39.5	-0.66	0.51
Pinnotheridae	19.0	-2.4	0.02*	12.5	-2.78	0.01*	17.0	-2.53	0.01*	23.0	-2.20	0.03*	26.5	-1.49	0.14
<i>Uca maracoani</i>	60.0	0	1	60.0	0.14	0.89	55.0	0.42	0.68	62.5	0	1	46.0	0.25	0.80
Capitellidae	50.0	-0.58	0.56	61.5	0.06	0.96	27.0	-1.98	0.05*	30.0	-1.81	0.07	30.0	-1.26	0.21
Goniadidae	48.5	-0.66	0.51	52.5	0.56	0.58	50.5	0.67	0.50	37.5	-1.39	0.16	30.0	-1.26	0.21
Lumbrineridae	36.0	-1.39	0.17	62.5	0	1	50.0	-0.70	0.49	37.5	-1.39	0.16	50.0	0	1
Magelonidae	53.5	0.38	0.71	55.0	-0.42	0.68	55.0	0.42	0.68	55.0	0.42	0.68	25.0	-1.59	0.11
Nephtyidae	26.5	1.93	0.05	50.5	0.67	0.50	30.5	-1.8	0.07	62.0	-0.03	0.98	48.0	0.13	0.90
Nereidae	48.5	0.66	0.51	61.5	0.56	0.96	55.5	-0.39	0.70	40.0	-1.25	0.21	42.0	-0.51	0.61
Opheliidae	55.0	0.29	0.77	55.0	0.42	0.68	55.0	0.42	0.68	50.0	0.70	0.49	48.0	0.13	0.90
Orbiniidae	41.0	-1.10	0.27	62.5	0	1	35.0	-1.53	0.13	45.0	-0.97	0.33	50.0	0	1
Pilargiidae	50.5	-0.55	0.58	18.0	-2.48	0.01*	57.5	0.28	0.78	33.0	-1.64	0.10	29.0	-1.33	0.18
Pilargiidae b	52.5	0.43	0.67	60.0	0.14	0.89	45.0	0.97	0.33	60.0	0.14	0.89	50	0	1

Table 31. Mean benthic abundances/m² at each plot in 2001.

Plot			Bivalvia										Gastropoda		
	Sipunculidae	Nemertinea	Anomalocardia brasiliana	Divaricella quadrisulcata	Donax striatus	Lucina pectinata	Protothaca pectorina	Tagelus plebeius	Tellina lineata	Tellina radiata	uk25	Anachis sp	Nassarius vibrex	Natica nyarochiensis	
Ilha de Canelas		10,0								16,6					
		10,0								10,0					
					3,3					23,2					
		3,3								6,6		3,3			
		3,3								13,3					
	3,3	13,3								29,9					
	6,6	10,0								26,5		3,3			
		26,5						3,3		3,3		3,3			
		6,6								3,3				3,3	
	10,0	10,0						3,3		13,3		3,3		3,3	
	6,6	6,6		3,3						16,6		3,3			
	10,0	6,6				3,3				3,3		3,3			
	3,3	6,6				3,3				3,3				3,3	
	10,0	6,6				3,3		3,3		10,0				3,3	
	26,5	23,2				6,6				10,0	3,3		3,3	3,3	
	6,6	19,9	10,0				3,3	19,9					6,6	3,3	
	3,3	6,6	3,3			6,6	3,3	3,3	3,3				3,3		
		3,3	3,3			13,3		3,3	3,3	3,3			6,6		
	16,6	19,9	10,0			10,0		13,3		3,3			3,3	3,3	
	6,6	33,2				13,3		16,6	3,3	6,6	3,3		3,3		
		13,3				19,9		10,0		16,6			3,3		
	6,6	6,6				3,3		10,0		13,3			19,9		
	3,3	6,6	19,9			6,6	16,6	6,6	3,3	13,3			59,7	3,3	
	10,0	16,6				10,0	3,3			6,6				3,3	
		13,3				3,3		10,0		3,3			3,3	3,3	
Furo Grnade		6,6						19,9		3,3					
		3,3								16,6				3,3	
		10,0								3,3					
		6,6					3,3								
		10,0								6,6					
										6,6					
Furo do Chato		6,6								3,3					
		13,3						3,3		13,3					
		10,0								33,2					
	3,3							3,3		13,3					
		6,6							3,3	10,0					
		6,6								13,3					
		6,6													
		10,0								3,3					
		6,6													
		6,6													
		3,3													
										3,3					
	6,6								3,3						

Plot		Crustacea																		
		Brachyura	Callianassidae	Callinectes sp	Copepoda	Decapoda	Einsiedlerkrebs	Eurytium Limosum	Gammaridea	Gnathidae	Hippolytidae	Idotheidae	Mysidae	Pinnotheridae	Stomatopoda	Tanaidacea	Uca maracoani	uca rapax	Uca sp	Oligochaeta
Ilha de Canelas	1		3,3						3,3			6,6	10,0	39,8						
	2		3,3									3,3	10,0	46,5						
	3		6,6						10,0				3,3	43,1						
	4								3,3			3,3	3,3	69,7						
	5		3,3									6,6	10,0	16,6		3,3				
	6		10,0									3,3	3,3	53,1						
	7		6,6						6,6			6,6	3,3	43,1						
	8	3,3	3,3						3,3	3,3		3,3		6,6						
	9		3,3										3,3	66,4						
	10		3,3	3,3		3,3	3,3	6,6					6,6	3,3						
	11		13,3										6,6	59,7						
	12		6,6			6,6						3,3	3,3	23,2						
	13					3,3	3,3					3,3		6,6						
	14		3,3			3,3							3,3	6,6						
	15		3,3			3,3						3,3	3,3	13,3	3,3		3,3			
	16												3,3							
	17													3,3						
	18		10,0		3,3				3,3					6,6						
	19											3,3								
	20		10,0	3,3								3,3		19,9						
	21																			
	22													3,3						
	23																13,3			
	24										3,3	6,6	13,3	3,3			13,3			
	25		6,6														13,3			
Furo Gande	26				10,0					3,3				3,3			23,2		3,3	
	27													19,9						
	28	3,3												3,3						
	29											3,3	3,3				10,0	3,3	6,6	
	30												3,3	3,3						3,3
	31																			
Furo do Chato	32		3,3		3,3							3,3		3,3						
	33		3,3											29,9						
	34																			
	35													13,3						
	36		3,3											6,6						
	37				6,6				3,3			3,3		10,0						
	38				3,3				3,3	3,3	3,3			10,0						
	39								10,0											
	40				6,6				13,3					6,6						
	41								19,9		3,3			23,2						
	42				3,3				132,7			43,1								
	43				3,3				212,4			26,5		6,6						
	44				10,0				192,5			46,5								
	45								272,1			23,2								
	46								235,6			43,1								

Plot	Polychaeta																			Insektenlarve
	Ampharetidae	Capitellidae	Eulepethidae	Glyceridae	Goniadidae	Hesionidae	Lumbrineridae	Magelonidae	Nephtyidae	Nereidae	Onuphidae	Ophelidae	Orbiniidae	Pectinariidae	Phyllodocidae	Pilargidae	PilargidaeB	Saccocirridae	Spionidae	
Ilha de Canelas	1	6,6		6,6		3,3			79,6			6,6	10,0							
	2	3,3						3,3	73,0	6,6		13,3	3,3							
	3	13,3						3,3	66,4	3,3		3,3	6,6		3,3					
	4	3,3			3,3		3,3		83,0			3,3	26,5			3,3				
	5				3,3			6,6	59,7			3,3	6,6					3,3		
	6	3,3			3,3	6,6			106,2	3,3		13,3								
	7	26,5		10,0		3,3		3,3	96,2	23,2		16,6	10,0				3,3			
	8	33,2			3,3			6,6	79,6				6,6			3,3	6,6			
	9	13,3							106,2	6,6		13,3								
	10	26,5			3,3		6,6	6,6	66,4		3,3	3,3					6,6			
	11	13,3							142,7							3,3				
	12	53,1	3,3				3,3		59,7	13,3								3,3		
	13	29,9			16,6			6,6	73,0	16,6				3,3				6,6		
	14	23,2	6,6		16,6		3,3	13,3	102,9	13,3			6,6			10,0	10,0			
	15	26,5			3,3		3,3	13,3	36,5	10,0						3,3	10,0		3,3	
	16	23,2			3,3		3,3	6,6	23,2	6,6										
	17	13,3			3,3		3,3	6,6	19,9	3,3						3,3	6,6			
	18	13,3					10,0	6,6	46,5	3,3				3,3						
	19	23,2			13,3		3,3	3,3	39,8	3,3						6,6	6,6			
	20	3,3	19,9		6,6		6,6	3,3	29,9	16,6							13,3			
	21		23,2		13,3			3,3		10,0	3,3					6,6				
	22		26,5		3,3	23,2				43,1	23,2					6,6				
	23		16,6				3,3			16,6	19,9					3,3	3,3			
	24	3,3	36,5		13,3			3,3	10,0	13,3							6,6			
	25		33,2		26,5				13,3	16,6										
Furo Gande	26	288,7						6,6	10,0	13,3										
	27	6,6				3,3			69,7	6,6		10,0				3,3				
	28	19,9							29,9	3,3										
	29	6,6							10,0	16,6						3,3				
	30	6,6							43,1	29,9										
	31	10,0							13,3	3,3										
Furo do Chaot	32	6,6							185,8											
	33	10,0							185,8	10,0						3,3				
	34	6,6			19,9				26,5	26,5						3,3	3,3		3,3	
	35				3,3				258,8	43,1										
	36	56,4			3,3				83,0	33,2			6,6			3,3				
	37	3,3					3,3		102,9	6,6			16,6							
	38								92,9				33,2							
	39								96,2				26,5							
	40	3,3							59,7				63,0							
	41								73,0				10,0							
	42								36,5											
	43								36,5				3,3							
	44								73,0			6,6	3,3							
	45			3,3					152,6				3,3							
	46								152,6				6,6							

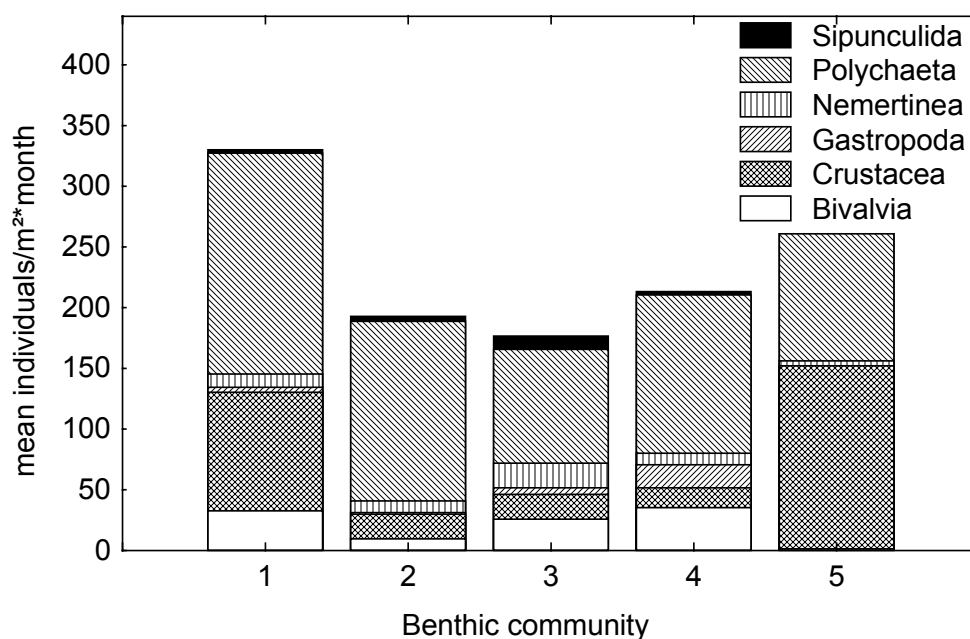


Fig. 40. Taxonomic composition of the benthos at the faunistic zones. Given are mean abundances of benthic groups within the areas of the benthic communities.

Table 32. Results of Mann-Whitney U-tests between median particle sizes in the faunistic zones 1-5. The test is done on the mean median particle sizes of the plots over the study period. Given are significant p values (with a Bonferroni-Correction of $\alpha=0.05/15=0.0039$).

		Faunistic zones				
		1	2	3	4	5
Faunistic zones	1		<0.001	<0.001	0.002	n.s.
	2	<0.001		0.003	n.s.	n.s.
	3	<0.001	0.003		n.s.	0.001
	4	0.002	n.s.	n.s.		n.s.
	5	n.s.	n.s.	0.001	n.s.	

Table 33. Vertical distribution of the benthic taxa. The distribution is given in % of all individuals found (n). Presence of taxa with less than 10 individuals is indicated by “*”.

Taxa		0-5cm	5-10cm	10-20cm	n
Sipunculidae		90	10	0	40
Nemertinea		8	5	3	743
Bivalvia	<i>Anomalocardia brasiliana</i>	93	7	0	14
	<i>Divaricella quadrisulcata</i>	*	0	0	1
	<i>Donax striatus</i>	0	0	*	1
	<i>Lucina pectinata</i>	61	29	10	31
	<i>Protothaca pectorina</i>	*	*	*	9
	<i>Tagelus plebeius</i>	28	26	46	39
	<i>Tellina lineata</i>	0	*	0	5
	<i>Tellina radiata</i>	74	18	9	117
	uk25	0	0	*	2
	total	62	21	16	219
Gastropoda	<i>Anachis sp.</i>	0	*	*	2
	<i>Nassarius vibrex</i>	74	10	15	39
	<i>Natica nyarochiensis</i>	91	0	9	11
	total	75	10	15	52
Crustacea	Brachyura	*	0	0	2
	Callianassidae	28	38	34	32
	<i>Callinectes sp.</i>	*	0	*	2
	Copepoda	27	33	40	15
	Decapoda	67	0	33	6
	“hermid crab”	*	0	0	2
	<i>Eurytium limosum</i>	*	0	0	2
	Gammaridea	91	4	5	339
	Gnathiidae	*	0	0	2
	Hippolytidae	*	0	*	3
	Idotheidae	91	3	7	76
	Mysidae	68	11	21	28
	Pinnotheridae	26	45	30	203
	Stomatopoda	0	0	*	1
	Tanaidacea	0	*	0	1
	<i>Uca maracoani</i>	70	30	0	23
	<i>uca rapax</i>	0	0	*	1
	<i>Uca sp.</i>	*	0	0	3
	total	67	18	15	741
Oligochaeta		0	*	0	1
Polychaeta	Ampharetidae	*	0	*	2
	Capitellidae	46	35	19	280
	Eulepethidae	*	*	*	3
	Glyceridae	29	71	0	7
	Goniadidae	87	9	4	55
	Hesionidae	0	*	*	5
	Lumbrineridae	27	40	33	15
	Magelonidae	59	28	13	32
	Nephtyidae	78	13	9	984
	Nereidae	61	33	7	122
	Onuphidae	*	0	0	2
	Opheliidae	4	21	75	28
	Orbiniidae	33	54	13	76
	Pectinariidae	*	0	0	1
	Phyllodocidae	*	0	0	2
	Pilargiidae	45	20	35	20
	PilargiidaeB	58	38	4	26
	Saccocirridae	*	0	0	1
	Spionidae	*	0	0	1
	total	66	21	12	1662
Insektenlarve		*	0	0	1

Table 34. Consistency of the vertical distribution of the ten most abundant benthic taxa. Given area the results of a Contingency table. Only plots/month with >10 individuals were included since this number was expected to be able to reflect a trend. Therefore, the result might be only applicable to localities with high densities of the observed taxa.

Taxa	Variation over the plots			Variation in time		
	χ^2	v	p	χ^2	v	p
Capitellidae	22.615	9	0.004*	84.686	11	0.000*
Gammaridea	5.786	9	0.671	35.504	11	0.000*
Goniadidae				2.702	3	0.259
Idotheidae	1.984	3	0.371	3.339	4	0.342
Nemertinea				11.650	11	0.309
Nephtyidae	139.518	67	0.000*	39.167	11	0.000*
Nereidae				5.674	11	0.841
Orbiniidae	6.270	3	0.044*	13.997	3	0.001*
Pinnotheridae	23.774	15	0.049*	35.180	7	0.000*
<i>Tellina radiata</i>				20.720	9	0.008*

Table 35. Monthly precipitation and air temperature from January-May/June in 2001 and 2002. The data is obtained from a data logger located at the Furo Grande study site.

Year	Month	Precipitation [mm]	Mean air temperature [°C]
2001	January	17.2	26.1
	February	25.2	25.7
	March	22.5	26.2
	April	18.0	25.7
	May	3.2	27.6
2002	January	17.8	26.6
	February	11.1	26.9
	March	15.9	26.4
	April	15.7	26.3
	May	0.0	26.4
	June	2.5	27.0

11.3 Appendix III: Distribution and structure of the avian community

Table 36 Annual variation of the avian composition of 2001 and 2002. Given are the results of a Contingency table performed on total numbers of individuals counted during the low tide counts at the Canelas plots. Only species with > 5 % of all individuals counted in 2001 were included.

Species	2001	2002
knot	361	18
sbdo	538	13
sppl	122	41
spsa	444	70
turn	156	0
whim	227	18
will	128	6
$X^2=136.156$		
$P<0.001$		
$v=6$		

Table 37. Annual variation of monthly avian species abundances in 2001 and 2002. Given are the results of Mann-Whiney U-tests at the Canelas plots. Only species were included which obtained in 2001 >5 % of all birds counted. The tests were done only for the months of the first three months of the year since avian abundances were not sufficient for statistical testing later in the year. N (2001)=25, n(2002)=5.

Species		January			February			March		
		U	Z	p	U	Z	p	U	Z	p
Plover	Grey Plover	36	0.885	0.376	41	-0.569	0.569	44	0.348	0.728
	Semipalmated Plover	27.5	1.95	0.051	2	-3.367	<0.001	53	0.529	0.597
Sandpiper, Snipes etc.	Red Knot	22.5	2.226	0.026	39	1.308	0.191	32.5	1.669	0.085
	Ruddy Turnstone	45	0.974	0.330	30	1.809	0.071	50	0.696	0.487
	Semipalmated Sandpiper	15	2.643	0.008	24	-2.142	0.032	42.5	1.113	0.266
	Short-billed Dowitcher	12.5	2.782	0.005	42.5	1.113	0.268	37	1.419	0.156
	Whimbrel	17.5	2.504	0.012	35.5	1.503	0.133	42	-1.141	0.254
	Willet	27.5	1.948	0.051	48.5	0.779	0.436	32.5	1.669	0.095

Table 38. Birds found at the different habitats and densities at the sampling sites during January – March and April – June 2001. Given is the range of the mean densities during low tide for each plot and month.

Taxonomy		Indiv. found in habitats				Range of Densities [birds/ha]	
		n	C	FG	FC	January - March	April - June
Hérons, egrets and ibises	Great Egret	3	X			0	0-5
	Little Blue Heron	10	X		X	0-2	0-2
	Snowy Egret	83	X	X	X	0-5	0-9
	Tricolored Heron	17	X			0-1	0-7
	Yellow-crowned Nightheron	3	X	X		0-1	0-1
	Scarlet Ibis	29	X	X	X	0-6	0-4
Plover	Collared Plover	74	X	X	X	0-8	0-5
	Grey Plover	87	X	X	X	0-5	0-3
	Semipalmated Plover	159	X	X	X	0-14	0-7
Sandpiper, Snipes etc.	Greater Yellowlegs	2	X			0-1	0
	Marbled Godwit	10	X			0-3	0
	Red Knot	361	X			0-33	0-8
	Ruddy Turnstone	159	X	X		0-35	0-2
	Sanderling	27	X			0-4	0-2
	Semipalmated Sandpiper	528	X		X	0-40	0-13
	Short-billed Dowitcher	538	X			0-104	0-2
	Spotted Sandpiper	67		X		0-70	0-3
	Whimbrel	254	X	X	X	0-35	0-2
	Willet	130	X	X		0-12	0-2
total		2540				0-127	0-20

Table 39. Results of Spearman Rank Correlations between avian abundances and salinity [‰], median grain sizes of the sediment [Φ], time of emergence [minutes] and densities of burrow openings at the sediment surface [numbers/m²]. Only bird species with >10 individuals found were included. For the correlations all data were included, which were obtained at the same sampling date in 2001. Time of emergence was only taken at one date and it was assumed, that it remained unchanged at each plot. Thus the same time period was used every time avian abundances was obtained at the plots. N of each test is given in brackets.

Species	Salinity (275)		Sediment median (272)		Time of emergence (150)		Burrow openings (268)	
	r	p	r	p	r	P	r	p
Herons, egrets and ibises	0.117	0.052	0.070	0.250	0.002	0.978	0.273	<0.001
Little Blue heron	0.087	0.150	0.171	0.005	-0.051	0.536	0.106	0.082
Scarlet Ibis	0.087	0.150	0.171	0.005	-0.051	0.536	0.106	0.082
Snowy Egret	0.106	0.078	-0.035	0.565	-0.007	0.930	0.212	<0.001
Tricolored Heron	-0.113	0.061	0.003	0.965	-0.237	0.003	0.110	0.071
Plover	-0.055	0.363	0.392	<0.001	0.315	<0.001	0.110	0.071
Collared plover	0.235	<0.001	0.250	<0.001	0.264	0.001	0.038	0.532
Grey plover	-0.174	0.004	0.297	<0.001	0.272	<0.001	0.077	0.207
Semipalmated plover	-0.223	<0.001	0.275	<0.001	0.264	<0.001	0.038	0.532
Sandpiper	-0.134	0.026	0.310	<0.001	0.065	0.429	0.306	<0.001
Marbled Godwit	-0.052	0.393	-0.054	0.379	-0.043	0.599	0.209	<0.001
Red Knot	-0.162	0.007	0.195	0.001	-0.075	0.360	0.232	<0.001
Ruddy Turnstone	-0.090	0.138	0.317	<0.001	-0.068	0.411	0.060	<0.001
Sanderling	-0.130	0.031	-0.146	0.016	0.196	0.016	0.192	0.002
Short-billed Dowitcher	-0.056	0.353	0.217	<0.001	-0.025	0.762	0.256	<0.001
Spotted Sandpiper	-0.143	0.018	0.185	0.002	0.340	<0.001	0.145	0.018
Semipalmated Sandpiper	-0.031	0.613	0.212	<0.001	0.187	0.022	0.271	<0.001
Whimbrel	-0.236	<0.001	0.135	0.026	0.036	0.662	0.249	<0.001
Willet	-0.189	0.002	0.117	0.053	-0.046	0.576	0.306	<0.001
total	-0.068	0.254	0.343	<0.001	0.068	0.407	0.300	<0.001

Table 40. Foraging depths of the bird species observed in 2002. If observations were done at watercovered areas the water depth was subtracted by the bill insert depth. The “relevant depth” of available prey individuals was calculated with the observed searching depth (>5 observations) or, if not possible due to too few observations, by the bill length obtained in the literature (Table 22).

Species	Mean with Std.dev. [mm]	Max [mm]	n	Relevant depth [cm]
Scarlet Ibis	115.3±55.6	174.7	53	0-20
Collared Plover	6.1±5.0	14.5	57	0-5
Grey Plover	15±11.5	35.9	46	0-5
Semipalmated Plover	7.8±3.8	12.2	55	0-5
Red Knot	22.9±11.2	39.7	48	0-5
Marbled Godwit	106.2±11.4	125.7	9	0-20
Sanderling	19.7±9.5	25.5	7	0-5
Short-billed Dowitcher	38.5±20.3	62.7	56	0-10
Semipalmated Sandpiper	12.5±7.3	19.5	61	0-5
Ruddy Turnstone	13.7±9.8	28.3	39	0-5
Whimbrel	41.3±32.9	104.6	54	0-120
Willet	22.3±17.9	60.4	50	0-10

11.4 Appendix IV: The birds in relation to the benthic community

Table 41. Prey items found in the droppings of the birds in 2002. The information is only qualitative. Unknown items were termed “uk”.

Species	Bivalvia	Gastropoda	Crustacea	Polychaeta	Insecta	Fish	Plant	n
Little Blue Heron			Callianassidae uk		uk		uk	1
Snowy Egret					uk			1
Tricolored Heron	Tagelus sp. Tellina sp.		Callianassidae Copepoda uk	Nereidae	uk	uk		3
Scarlet Ibis	Tagelus sp. uk		Callianassidae Copepoda Uca maracoani Idotheidae Zoea larvae uk	uk	uk	uk	uk	11
Collared Plover	Tellina sp. uk	uk	Callianassidae Copepoda Pinnotheridae uk	Nereidae Spionidae Goniadidae uk	uk			9
Grey Plover	Protothaca sp. Tagelus sp. Tellina sp. uk		Callianassidae Copepoda Pinnotheridae uk	Nereidae Spionidae Goniadidae uk	uk			11
Semipalmated Plover	Tellina sp.		Callianassidae Copepoda uk	Nereide Nephtyidae Goniadidae Lumbrineridae	uk			7
Marbled Godwit								0
Red Knot	Protothaca sp. Tagelus sp. Tellina sp. uk	Nassarius sp.	Copepoda Decapoda uk		uk			4
Ruddy Turnstone	Tellina sp.	Nassarius sp.	Callianassidae Copepoda	Nereide uk	uk			2
Sanderling	Tellina sp.		Callianassidae	Nereide Spionidae				1
Short-billed Dowitcher	Tagelus sp. Tellina sp. uk		Callianassidae Copepoda Idotheidae uk	Nereidae uk	uk			6
Semipalmated Sandpiper	Tellina sp.		Callianassidae Copepoda uk	Terebellidae Nereidae Pilargiidae uk	uk			6
Whimbrel								1
Willet	Protothaca sp. Tagelus sp. Tellina sp.		Callianassidae Copepoda uk	Nereidae uk	uk			5

Table 42. Results of Spearman Rank Correlations between abundances of individual avian species and total benthic abundance, –biomass and mean profitability per plot in 2001. N was always 46. Only the harvestable benthic abundances and biomasses for the individual bird species were considered.

Species	month	abundance		biomass		profitability	
		R	p	R	p	R	p
Scib	January	-	-	0.068	0.654	0.089	0.557
	February	-0.022	0.883	0.086	0.568	0.145	0.337
	March	-0.032	0.834	-0.225	0.133	0.024	0.074
	April	0.715	<0.001*	-0.191	0.204	0.048	0.751
	May	-	-	-0.084	0.580	0.246	0.100
	June	-0.052	0.732	0.239	0.110	-0.151	0.315
Grpl	January	0.278	0.062	0.223	0.136	0.284	0.056
	February	-0.108	0.477	0.068	0.655	-0.154	0.307
	March	-0.013	0.931	0.279	0.060	0.126	0.405
	April	0.061	0.685	0.283	0.057	0.152	0.314
	May	0.232	0.120	-0.172	0.253	0.123	0.415
	June	-0.172	0.254	0.115	0.448	-0.192	0.201
copl	January	-0.178	0.235	0.197	0.189	-0.280	0.060
	February	0.338	0.022*	0.092	0.542	0.038	0.801
	March	0.003	0.983	0.240	0.180	-0.122	0.420
	April	-0.039	0.799	0.113	0.456	-0.059	0.695
	May	-0.078	0.606	0.080	0.597	0.007	0.963
	June	0.229	0.126	0.248	0.096	0.070	0.643
Knot	January	0.117	0.440	0.545	<0.001*	0.513	<0.001*
	February	0.026	0.865	0.197	0.190	0.229	0.125
	March	-0.353	0.016*	-0.046	0.762	0.066	0.664
	April	-0.339	0.021*	-0.049	0.747	-0.013	0.930
	May	0.072	0.633	-0.111	0.462	0.162	0.283
	June	-0.047	0.757	-0.104	0.490	-0.104	0.490
sppl	January	0.367	0.012*	0.010	0.950	0.159	0.292
	February	0.056	0.711	0.242	0.105	0.020	0.896
	March	0.326	0.027*	0.183	0.224	0.034	0.821
	April	0.302	0.041	-0.111	0.461	-0.231	0.122
	May	0.083	0.582	0.023	0.880	0.082	0.588
	June	0.253	0.090	-0.096	0.527	0.152	0.315
spsa	January	0.227	0.130	0.202	0.178	0.184	0.221
	February	0.162	0.283	-0.010	0.948	-0.058	0.700
	March	-0.149	0.325	0.078	0.607	0.041	0.785
	April	-0.078	0.605	0.149	0.323	-0.300	0.043*
	May	0.117	0.438	0.291	0.050*	0.119	0.432
	June	0.150	0.320	0.299	0.044*	-0.161	0.286

Species	month	abundance		biomass		profitability	
		R	p	R	p	R	p
turn	January	0.357	0.015*	0.174	0.248	-0.005	0.976
	February	0.274	0.065	-0.043	0.775	0.104	0.493
	March	0.422	0.004*	0.134	0.374	0.075	0.721
	April	0.431	0.003*	0.121	0.421	0.283	0.057
	May	-0.131	0.384	0.261	0.080	0.008	0.958
	June	-	-	-	-	-	-
Sbdo	January	0.084	0.580	0.451	0.002*	0.468	0.001*
	February	0.168	0.265	0.276	0.063	0.316	0.033*
	March	0.139	0.358	0.382	0.009*	0.279	0.060
	April	0.049	0.744	-0.208	0.166	0.107	0.478
	May	0.254	0.089	0.140	0.352	0.219	0.144
	June	0.213	0.156	0.127	0.402	-0.032	0.834
Will	January	0.459	0.001*	0.545	<0.001*	0.434	0.002*
	February	0.414	0.004*	0.516	<0.001*	0.342	0.020*
	March	0.214	0.152	0.176	0.243	0.200	0.182
	April	0.294	0.047*	0.284	0.056	0.266	0.074
	May	-	-	-	-	-	-
	June	-	-	-	-	-	-
whim	January	0.411	0.005*	0.398	0.006*	0.386	0.008*
	February	-0.005	0.975	0.014	0.927	0.241	0.106
	March	-0.032	0.834	0.157	0.297	0.125	0.409
	April	0.199	0.896	0.112	0.458	0.227	0.128
	May	-0.063	0.677	0.050	0.744	0.067	0.656
	June	0.039	0.797	-0.171	0.257	-0.022	0.884

Table 43. Results of Multiple Regressions between avian abundances and abundances, and biomasses of individual benthic taxa per plot. Only the harvestable benthic abundances and biomasses for the individual bird species were considered. Given are the adjusted R^2 of each test. If the adjusted R^2 were not given by the program (*), R^2 were given. All data were log transformed.

Species	month	Abundances		Biomasses	
		Taxa	Groups	Taxa	Groups
grpl	January	0.50	0.08	0.18	0.17*
	February	0.24	0.09	0.06	0.03
	March	0.18	0.05	0.06	-
	April	0.16	0.09	0.05	0.03
	May				
	June				
copl	January	0.45	0.19	0.24	0.09*
	February	0.44	0.39	0.15	0.23
	March				
	April				
	May				
	June	0.22	0.09	0.23	0.04
knot	January	0.21	0.14	<0.01	0.47
	February	0.39	0.24	0.08	0.30
	March	0.37	0.24	0.16	
	April	0.38	0.28	0.41	0.30
	May				
	June				
sdsa	January	0.27	0.08	0.26	0.09*
	February	0.21	0.25	0.02	0.06
	March	0.18	0.07	0.06	0.01
	April				
	May				
	June				
sppl	January	0.20	0.08	0.07	0.19
	February	0.38	0.17	0.03	0.07
	March	0.28	0.28	0.16	0.15
	April	0.43	0.32	0.01	0.48
	May				
	June				

Species	month	Taxa (abund)	Groups (abund)	Taxa (biomass)	Groups (biomass)
spsa	January	0.33	0.04	0.21	0.09*
	February	0.24	0.08	-	0.02
	March	0.16	0.07	0.12	0.03
	April	0.29	0.23	0.10	0.12
	May	0.29	0.29	0.40	0.29
	June	0.19	0.22	0.01	-
turn	January	0.24	0.23	0.04	0.14
	February	0.50	0.39	0.01	0.48
	March	0.48	0.44	0.40	0.35
	April				
	May				
	June				
Sbdo	January	0.53	0.31	0.11	0.17
	February	0.36	0.37	0.25	0.26
	March	0.57	0.47	0.33	0.29
	April				
	May				
	June				
Will	January	0.40	0.21	0.37	0.24
	February	0.49	0.15	0.31	0.06
	March	0.42	0.18	0.01	0.11
	April				
	May				
	June				
whim	January	0.70	0.42	0.16	0.20
	February	0.23	0.03	0.30	<0.01
	March	0.11	0.08	0.08	0.12
	April	0.21	0.18	0.12	0.14
	May				
	June				

Table 44. Avian preferences for faunistic zones. Given are results of Kruskal Wallis Tests and Mann-Whitney U-tests between the mean abundances (tide calibrated) of the bird species at the plots of different faunistic zones in 2001. N differed between the zones: zone 1=11, zone 2=9, zone 3=7, zone 4=5, zone 5=9.

Species	Kruskal Wallis Test		Significant different zones according to Mann-Whitney U-tests with Bonferroni correction ($\alpha=0.05/10=0.005$)
	H	p	P of the Mann Whitney U-test is given in brackets
Little Blue Heron	12.585	0.014	-
Snowy Egret	15.804	0.003	1-5 (<0.001)
Tricolored Heron	7.841	0.098	-
Scarlet Ibis	5.057	0.282	
Collared Plover	6.715	0.152	
Grey Plover	6.880	0.142	
Semipalmated Plover	21.969	0.028	1-4 (0.002), 2-4 (0.003), 4-5 (0.003)
Marbled Godwit	8.878	0.064	
Red Knot	15.499	0.004	3-5 (0.001)
Ruddy Turnstone	24.373	<0.001	1-3 (<0.001), 1-4 (0.002), 2-3 (0.002), 2-4 (0.003)
Sanderling	7.387	0.117	
Spotted Sandpiper	10.859	0.028	-
Semipalmated Sandpiper	9.520	0.049	-
Short-billed Dowitcher	20.266	<0.001	1-3 (0.004), 3-5 (<0.001), 4-5 (0.003)
Whimbrel	15.109	0.005	-
Willet	20.288	<0.001	3-5 (<0.001)

Table 45. Relationship between avian bill sizes and chosen prey sizes. Given are the results of Spearman Rank Correlations. Mean prey sizes were calculated from the data of the focal observations of 2002. Only shorebirds were included. N depended on the included number of species which was 11.

Prey group	R	p
Crustacea	0.714	0.047
Bivalvia	0.900	<0.001
"Worm"	0.566	0.548

Table 46. Results of Canonical Correlations between different avian groupings and benthos groupings. Given is the sum of eigenvalues. The data was untransformed, only the analyses on differentiated according to foraging depths was done on log transformed data. Empty cells indicate that no analysis was done.

Bird groupings	Benthos groupings	Benthos									
		January		February		March		April		June	
		Abund.	Biom.	Abund.	Biom.	Abund.	Biom.	Abund.	Biom.	Abund.	Biom.
Total											
	Taxa	1.18*	1.13*	0.81*	0.76	1.00*	0.42	0.41	0.50	0.21	0.21
	Higher taxon. groups	0.64*	0.33	0.50	0.50	0.33	0.31	0.36	0.38	0.16	0.12
	Groups 1	0.55	0.29	0.44	0.38	0.21	0.24	0.23	0.27	0.20	0.19
	Groups 2	0.34	0.19	0.39	0.31	0.20	0.20	0.20	0.23	0.15	0.12
Only plover	Taxa	0.34									
	Higher taxon. groups	0.14									
Only sandpiper	Taxa	0.62									
Birds reaching:											
0-5 cm depth	Taxa	1.19*		0.69*		0.46		0.38			
0-20 cm depth	Taxa	0.10		0.27		0.30					

*: The first two axes have a sum of eigenvalues of >0.50, thus a diagram would be meaningful and can be drawn

Groups 1: Bivalvia-Crustacea-Gastropoda-"Worms"

Groups 2: Mollusca-Crustacea-"Worms"

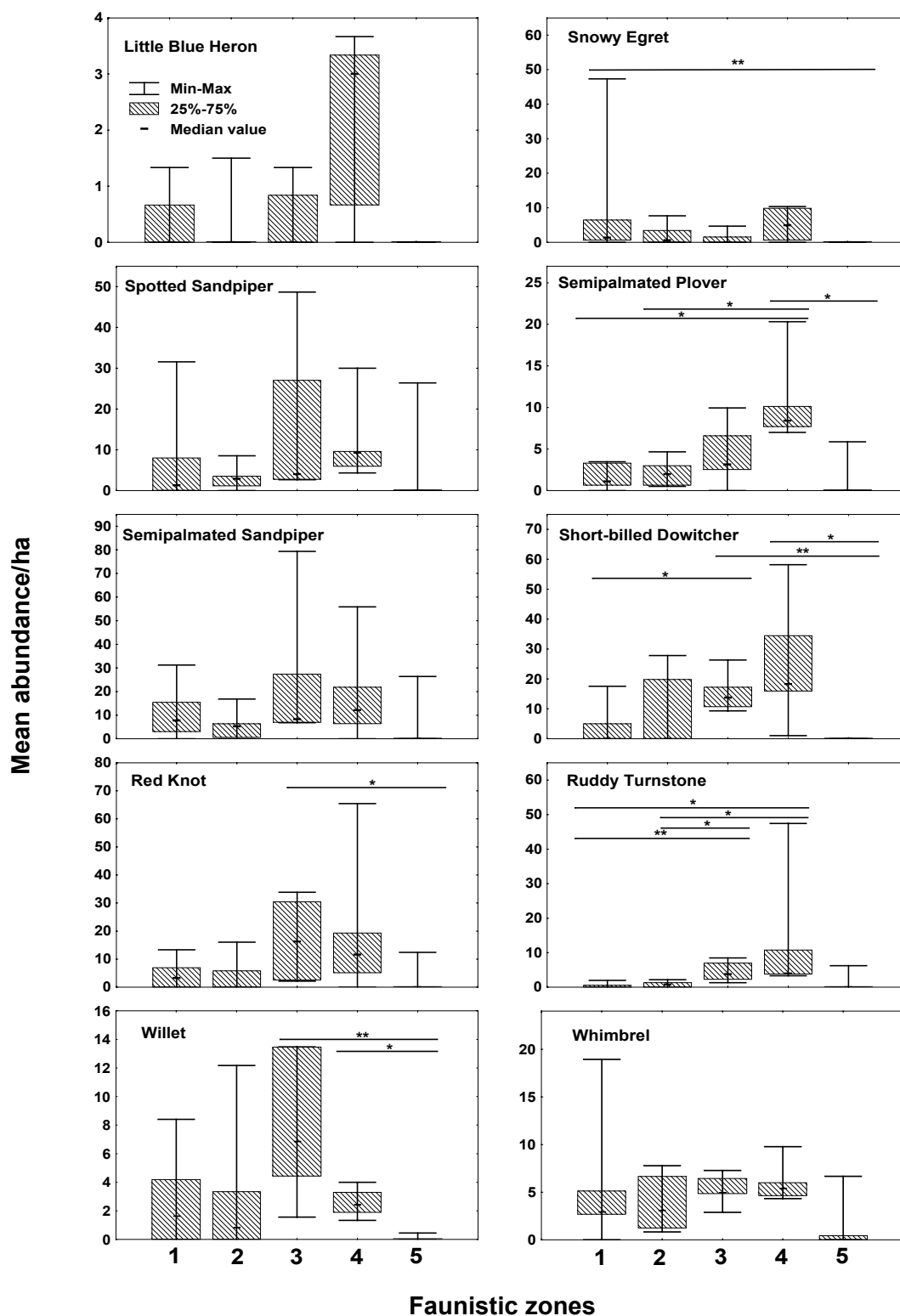


Fig. 41. Mean abundances of bird species which had significant different densities at the faunistic zones. Given are the mean densities at the plots of the faunistic zones obtained in 2001 (tide calibrated).

11.5 Appendix V: Avian consumption and foraging behaviour

Table 47. Benthic taxa with total number of individuals found in each experimental treatment of the exclosures.

Taxa		exclosures	controls	procedural controls
Sipunculidae		3	2	
Nemertinea		6	7	4
Bivalvia	<i>Lucina pectinata</i>		3	
	<i>Protothaca pectorina</i>		3	1
	<i>Tagelus plebeius</i>	3	1	1
	<i>Tellina goldii</i>	1		
	<i>Tellina radiata</i>	24	24	23
	<i>Tellina sp.</i>	5	8	9
	uk32		1	
Gastropoda	<i>Nassarius vibrex</i>	5	5	2
	<i>Natica nyarochiensis</i>		2	1
Crustacea	Brachiura	3	2	1
	Callianassidae	4	10	3
	Copepoda	2		
	Decapoda	1		
	Gammaridea		4	1
	Idotheidae	3	5	3
	Mysidae	1	1	2
	Pinnotheridae	60	52	60
	Tanaidacea			1
Polychaeta	Capitellidae	24	27	31
	Goniadidae	2	4	5
	Lumbrineridae		1	3
	Magelonidae	2	5	6
	Nephtyidae	36	31	44
	Nereide	5	6	4
	Onuphidae	1		
	Opheliidae			2
	Orbiniidae	13	9	8
	Pilargiidae	12	6	11
	Polynoidae	1	1	
	Spionidae	6	3	
	uk34		1	1

Table 48. Size differences of the benthos organisms in the treatments. Given are the results of Kruskal-Wallis tests. Tests were only applied when n was larger than 5 per treatment.

Taxa	Month	Kruskal-Wallis test	
		H	p
Tellina radiata	January	1.092	0.579
	February	0.112	0.946
Pinnotheridae	January	0.616	0.735
	February	3.017	0.221
	March	0.628	0.731
	April	3.727	0.155
	May	0.319	0.853
	May	0.905	0.636

Table 49. Prey intake rate differences between birds foraging solitary and floc- associated birds. Given are the results of Mann-Whitney U-test. Little Blue Herons, Marbled Godwits and Sanderlings had too few individuals in one of the categories to be tested.

Species	Number of prey			Prey biomass			Difference
	U	Z	p	U	Z	p	
Little Blue Heron	-	-	-	-	-	-	
Snowy Egret	68.0	-0.938	0.348	24.0	0.340	0.734	
Tricolored Heron	27.0	-2.518	0.012*	7.0	-1.323	0.186	More prey gregarious
Scarlet Ibis	195.0	0.807	0.420	206.0	-0.538	0.591	
Collared Plover	190.5	-0.557	0.578	194.0	-0.477	0.633	
Grey Plover	103.0	0.658	0.510	113.5	-0.304	0.761	
Semipalmated Plover	69.0	1.976	0.048*	130.0	0.229	0.819	More prey solitary
Marbled Godwit	-	-	-	-	-	-	
Red Knot	117.5	-0.094	0.925	119.0	-0.038	0.970	
Ruddy Turnstone	29.0	1.072	0.284	32.5	-0.784	0.433	
Sanderling	-	-	-	-	-	-	
Short-billed Dowitcher	232.5	-0.799	0.425	214.5	1.182	0.237	
Semipalmated Sandpiper	121.5	1.722	0.085	149.0	0.920	0.358	
Whimbrel	92.5	-0.881	0.378	109.0	0.235	0.814	
Willet	102.5	0.516	0.606	166.5	0.595	0.552	