SANDY BEACH MORPHODYNAMICS AND MACROBENTHIC COMMUNITIES IN TEMPERATE, SUBTROPICAL AND TROPICAL REGIONS - A MACROECOLOGICAL APPROACH

Alexandre Goulart Soares

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Promoter: Dr. D. Schoeman
Co-promoter: Prof. A. McLachlan

To the better future Taiana and Camila

and

To Mother Nature for being greater than the sum of the parts

Life is a Beach

Drifting away from sea and land
Where walls of water turn rocks into sands
Nature experiments patiently and wise
Polishing forms to adapt and survive
To changing conditions where only few strive

And life thrives to such perfection
Facilitating a multitude of interactions
Which link and chain all its components
Producing certainty in an uncertain environment

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Summary

A comprehensive study involving 52 microtidal beaches spanning from reflective to dissipative states and located in tropical, subtropical and temperate regions in the Atlantic, Pacific and Indian oceans was carried out to unravel the relative roles of latitude and beach morphodynamics in determining beach macrobenthic species richness, abundance, biomass and mean individual body sizes. Since beach slope is one of the most important factors controlling beach fauna, a model based on beach geometry was applied to the sub-aerial beach deposit to understand the role of physical factors in predicting equilibrium beach slopes. Additionally, it was tested if the occurrence of beach types is related to latitude, and how physical factors change with morphodynamics and latitude.

The beach morphometric model makes three assumptions: 1) that the cross-section of a beach deposit is equivalent to a right-angled triangle, 2) that the physical hydrodynamic factors (wave height and spring tide amplitude) and the beach deposit characteristics (sand grain size, beach slope and width) are interchangeable with their geometric counterparts producing an equation to explain beach geometry, and 3) that the predicted beach slope is in equilibrium with the hydrodynamic and sedimentological forces. The equation for predicting beach slope was derived and then tested against field data collected over 52 beaches. The predicted slopes were not significantly different from the observed slopes of the studied natural beaches. However some estimated slopes were different than observed ones. Possible sources of deviation between calculated and observed slopes may be the systematic sampling errors associated with field data. Alternatively, observed slopes could be the result of past hydrodynamic conditions, explaining the differences with the slopes calculated by the beach morphometric model, which assumes a state of equilibrium between beach slope and hydrodynamic conditions. A higher correlation of beach faunal structure with observed slopes rather than with present hydrodynamic conditions could then be indicative of faunal responses to previous hydrodynamic conditions in the same way was the observed slopes. The beach morphometric model could therefore be also useful in predicting faunal responses to changing hydrodynamic conditions. Since the model does not consider wave period, it is concluded that further tests should be done using laboratory and time-series field data and incorporating the role of wave period and beach permeability to ascertain its predictive value.

Tropical regions had significantly more beaches in a reflective state than temperate and subtropical regions. Some tropical beaches were fronted by coral reefs, which not only provided coarse carbonate particles, but also additionally dissipated the low wave energy present in these climatic areas. Only one dissipative beach with high energy was found in the tropics, in southeast Madagascar. Temperate and subtropical regions, on the other hand, were dominated by dissipative beaches with medium to fine sands. Open oceanic reflective beaches were non-existent in the subtropics and rare in temperate regions, only occurring in estuaries, enclosed bays or on islands facing the continent. Intermediate beaches were more common in the subtropics but also occurred frequently in the other two regions, having higher energy in temperate regions. Reflective beaches had significantly steeper slopes, coarser sands, smaller waves and shorter swash lengths when compared to dissipative beaches. Additionally, reflective beaches were narrower, had deeper water tables and in consequence shorter saturation zones. Wave periods and surfzone widths were on average larger on dissipative than on reflective beaches. The frequency of occurrence of beach types is therefore related to the climatic signature of each latitude. Mid latitudes would be predicted to have more dissipative beaches with large and long waves because of their proximity to the storm generating belt around 50-60° S - these beaches will have a predominantly finer sands because of the input by rivers in rainy areas. Lower latitudes will have more reflective beaches due to a modal low energy wave climate and also because of the presence of inshore and offshore biotic structures such as coral reefs that dissipate even more the energy from the waves.

Tropical and subtropical regions had larger marine species pools than temperate regions. After controlling for biogeographical differences in total species pool, dissipative beaches were on average significantly richer than intermediate and reflective beaches. Crustaceans were also more diverse on dissipative beaches, this difference being not significant for either molluscs or polychaetes. Significant relationships were found between total beach species richness (with or without terrestrial species), crustacean and mollusc species richness with beach morphodynamics as represented by the Dean's index. Indices incorporating the role of tide, such as BSI, were less important in predicting species richness on the microtidal beaches studied here. Several other physical factors were also significantly correlated with species richness, the most important being the Beach Deposit Index, i.e. BDI, a composite index of beach slope and grain size. The highest correlation was between BDI and relative species richness, i.e. local beach species richness / regional species richness. Total regional marine species richness was higher in Madagascar and North Brazil (tropical beaches) than in Southeast Brazil (subtropical), or the West Coast of South Africa and South-Central Chile (temperate beaches). Not only was the pool of species capable of colonizing beaches richer in tropical and subtropical regions, but also local diversity of each morphodynamic beach type was higher among tropical beaches than their temperate counterparts. Although the results of this study agree with the predictions of the swash exclusion hypotheses, several reflective and intermediate beaches had higher species richness than predicted before and this seems to be linked to the presence of finer sediments and a less turbulent flow for larvae to settle. It is concluded that beach species richness is not necessarily controlled by one major morphodynamic parameter; this control is complex and probably involves multiple interacting biotic (biological interactions) and abiotic (e.g. grain size, wave height, beach slope and width, water table) factors. Species richness seems to be controlled on two different scales: on an evolutionary one where tropical and subtropical regions have higher regional and local diversity due to higher speciation rates; and on an ecological scale, where fine grained sand beaches have their carrying capacity enhanced by higher larval settlement rates and survival of recruits towards adulthood.

On average dissipative beaches had higher total densities and macrofaunal abundances than reflective ones. Crustaceans, terrestrial species and cirolanid isopods such as *Excirolana* spp. were also more abundant on dissipative beaches. The difference was not significant for molluscs and polychaetes. Significant relationships were found between total abundance, crustacean species richness and beach morphodynamics as represented by the Dean's index. Again, BSI was less important than individual physical factors in determining faunal abundance on the studied microtidal beaches. Several other physical factors were also significantly correlated with abundance, the most important being the Beach Deposit Index (BDI). The highest correlation was between BDI and total macrofaunal abundance. Factors related to surf zone processes, and possibly productivity, were highly correlated with total community, crustaceans, *Excirolana* spp. and terrestrial species abundances. The abundances of polychaetes and molluscs were better correlated with factors related to the beach deposit (BDI, slope, grain size and water table depth). Significant differences were observed between latitudinal regions for the average beach and also for each beach type. In general temperate beaches harboured larger community densities and abundances, and also crustacean, *Excirolana* spp. and terrestrial abundances. Mollusc and polychaete abundances were larger on subtropical and tropical beaches. The control of abundance on a sandy beach is complex and involves multifactorial processes at evolutionary and ecological scales. At evolutionary scales animals seem to attain higher abundances in the region where they first evolved, e.g. amphipods and isopods in temperate regions. At ecological scales they attain higher abundances where productivity is higher (total macrofaunal, crustaceans, *Excirolana* spp., terrestrial spp.) or where the settlement environment is more benign (molluscs and polychaetes).

Dissipative beaches supported larger average and total community biomass than reflective beaches. Crustaceans, terrestrial species and cirolanid isopods such as *Excirolana* spp. also had larger biomass on dissipative beaches. The difference was not significant for molluscs and polychaetes. Significant relationships were found between the biomass of community and taxonomic groups with beach morphodynamics as represented by the Dean's morphodynamic index. On the microtidal beaches studied here, BSI was less important than other morphodynamic indices and single physical factors in determining faunal biomass and mean individual body size. Surf zone characteristics such as wave height, period and surf zone width had the highest correlations with community, crustacean, *Excirolana* spp. and terrestrial biomass. Polychaete biomass was better correlated with characteristics of the beach deposit, such as grain size, beach slope and water table. Mollusc biomass was correlated with saturation distance. Biomass of the community and taxonomic groups was significantly larger on temperate beaches. Only polychaete and mollusc biomass did not vary between latitudes. Mean individual body sizes of crustaceans, polychaetes, molluscs and *Excirolana* spp. were significantly larger at temperate beaches, on all beach types. Both morphodynamics, through surf zone processes, and latitude, through differences in productivity, seem to control biomass of beach macrofauna. Body sizes of crustaceans and polychaetes seem to be related to latitudinal differences in productivity and molluscs with the degree of reflectiveness of the beach.

Samevatting

‘n Uitgebreide studie van 52 strande, van reflektief tot disspatief en geleë in tropiese, subtropiese en gematigde gebiede is uitgevoer aan die kuste van die Atlantiese, Stille en Indiese oseane om die relatiewe rol van breedtegraad en strandmorfodinamika op makrobenthos species diversiteit en hoeveelheid, biomassa en gemiddelde liggaamsgrootte te bepaal. Daar strandhelling een van die belangrikste descriptors is wat strandfauna beïnvloed, is ’n geometriese model. gebruik op die subareale strandgedeelte om die rol van fisiese faktore te bepaal in die voorspelling van die ekwillibrium strandhelling.

’n Geometriese benadering, gebasseer op reghoekige driehoeksmeting is gebruik op die subareale strandgedeelte om die ekwillibrium strandhelling te voorspel. Deur die deursnee van die strand as ’n reghoekige driehoek voor te stel en die fisiese hydrodinamiese descriptors (golfhoogte, springgety amplitude) en die sand eienskappe (sandkorrelgrootte, strandhelling en -breedte) te vervang in die regtehoeksformule, kan strand geometrie voorspel word. Hierdie formule is op die data van bogenoemde strande getoets. Die resultate het nie betekenisvol verskil van die waargenome strandhellings nie. Die verskil van sommige voorspelde strandhellings in vergelyking met die werklik heid kan te wyte wees aan sistematiese foute in monsterneming. Verder kan waargenome strandhellings die resultaat wees van vorige hydrodinamiese toestand, wat die verskil kan verklaar met die strandhellings bereken met die geometriese formule (met die aanname van ’n staat van ekwillibrium tussen strandhelling en hydrodinamiese toestande). ’n Groter korrelasie van strandfauna struktuur met waargenome hellings as met huidige hydrodinamiese toestande kan ook die gevolg wees van die strandfauna se reaksie op vorige hydrodinamiese toestande. Die geometriese model kan dus moontlik ook die reaksie van strandfauna op veranderende hydrodinamiese toestande voorspel. Daar hierdie model nie golfperiode in ag neem, moet verdere toetse gedoen word op die rol van golfperiode en stranddreinering in die laboratorium en met tyd-reeks velddata, om die voorspellende waarde te bepaal.

Meer strande in tropiese gebiede was in ’n reflektiewe toestand dan díe in subtropiese en gematigde gebiede. Voor sommige tropiese strande was daar koraalriwwe, wat nie alleen growwe koolstofdeeltjies voorsien het, maar ook die alreeds lae golf energie in hierdie klimaat verder geabsorbeer het. Daar was net een dissipatiewe strand met hoë energie in die

trope, in suidoos Madagascar. Gematigde en subtropiese gebiede, inteendeel, was oorheers deur dissipatiewe strande met medium tot fyn sand. Oop oseaan reflektiewe strande was afwesig in die subtrope en skaars in gematigde gebiede, en dan slegs in riviermondings, ingeslote baaitjies en op eilande gerig na die vasteland. Intermediêre strande was meer algemeen in die subtrope, maar ook redelik vollop in die ander twee gebiede, en met hoër golfenergie in gematigde gebiede. Reflektiewe strande het steiler hellings, met growwer sand, kleiner golwe en korter ‘swash’ lengtes dan dissipatiewe strande. Verder was hulle ook nouer, met dieper grondwatertafels en gevolglik kleiner waterversadigde zones. Golf periodes en branderzone wydtes was hier gemiddeld ook kleiner dan by dissipatiewe strande. Die voorkoms van verskillende strandtipes is dus afhanklik van die klimatiese aard van elke breedtegraad. Die middel breedtegrade het meer dissipatiewe strande met hoë en lang golwe weens die nabyheid van die stormagtige gordel rond 50 –60^{o}S. Hierdie strande het hoofsaaklik fyn sand a.g.v. die toevoer vanuit riviere in reënagtige gebiede. Laer breedtegrade het meer reflektiewe strande weens die modale lae golfenergie en die teenwoordigheid van biotiese strukture soos koraalriwwe wat die golfenergie verder dissipeer.

Tropiese en sub-tropiese gebiede vertoon ‘n groter mariene speciespoel (verskeidenheid) dan gematigde gebiede. Na korreksies vir breedtegraadverskille in die totale speciespoel, was dissipatiewe strande gemiddeld speciesryker dan intermediêre en reflektiewe strande. Die species diversiteit van crustacea was hoër op dissipatiewe strande terwyl daar geen betekenisvolle verskil was by polychaete en molluske. Daar is betekenisvolle verwantskappe gevind tussen totale species diversiteit (met of sonder terrestriële species), crustacea en mollusk species diversiteit met strand morfodinamika in terme van Deans se indeks. Indekse soos BSI, wat die rol van getye in ag neem, was minder belangrik in die bepaling van species diversiteit op die mikrogety strande in hierdie studie. Verskeie ander fisiese faktore was ook betekenisvol gekorreleer met species diversiteit – waarvan die belangrikste die BDI (strand morfometriese indeks), ’n saamgestelde indeks van strandhelling en sandkorrelgrootte. Die hoogste korrelasie was tussen BDI en relatiewe species diversiteit (= lokale species diversiteit / regionale species diversiteit). Die totale regionale mariene species diversiteit was hoër in Madagascar en Noord Brasilië (tropies) dan in Suidoos Brasilië (subtropies), die Weskus van Suid-Afrika en Suid-centraal Chili (gematigd). Alhoewel die resultate van hierdie studie ooreenstem met die voorspellings van die ‘swash-exclusion ‘ hipotese, had verskillende intermediêre en reflektiewe strand ’n groter species diversiteit dan voorheen voorspel. Dit is moontlik te verklaar deur die fyner sediment en ‘n minder turbulente watervloei waardeur larwes hulself makliker kan vestig. Die gevolgtrekking is dat strandspecies diversiteit nie alleen beheer word deur een oorwegende morfodinamiese parameter. Die beheer is kompleks en behels verskillende interaktiewe biotiese (biologiese interaksies) en abiotiese faktore (sandkorrelgrootte, golfhoogte, die helling en breedte van die strand, watertafeldiepte). Species diversiteit word blykbaar op twee verskillende skale beheer: op ’n evolusionêre skaal, waar tropiese en subtropiese gebiede ‘n hoër lokale en regionale species diversiteit het weens ’n hoër tempo van speciesvorming, en op ’n ekologiese skaal waar fyn sandstrande ’n hoër draagkrag vertoon met beter vestiging en oorlewing van larwes tot volwassenheid.

Die totale digtheid en aantal van die makrofauna was gemiddeld hoër op dissipatiewe as op reflektiewe strande. Crustacea, terrestriële species en cirolanid isopode soos *Excirolana* spp. was ook meer talryk op dissipatiewe strande. Die verskil was nie betekenisvol vir molluske en polychaete.

Daar was betekenisvolle verwantskappe tussen totale aantal/specie, crustacea species diversiteit en strandmorfodinamika soos voorgestel deur Dean se indeks. Weereens was BSI minder belangrik dan individuele fisiese faktore om die aantal/species op die bestudeerde mikrogetystrande te bepaal. Verskillende ander fisiese faktore was ook betekenisvol gekorreleer met aantal/specie, waarvan die belangrikste BDI was. Die hoogste korrelasie was tussen BDI en totale aantal/hoeveelheid van die makrofauna. Faktore verbonde aan prosesse in die branderzone en moontlik ook produktiwiteit was hoogs gekorreleerd met die aantal/hoeveelheid van die crustacea, *Excirolana* en terrestriële species. Die talrykheid van polychaete en molluske was meer gekoppel aan faktore van die sediment (BDI, strandhelling, sandkorrelgrootte, watertafeldiepte). Daar was ook verskille tussen strandtipes op verskillende breedtegrade. In die algemeen huisves gematigde strande digter en talryker crustacea, *Excirolana* en terrestriële gemeenskappe. Molluske en polychaete was meer talryk op subtropies en tropiese strande. Die faktore wat talrykheid op sandstrande beïnvloed is kompleks en behels multifaktoriale prosesse op evolusionêre en ekologiese vlakke. Op evolusionêre vlak is fauna meer talryk in gebiede waar hulle oorspronklik ontstaan het, bv. amfipode en isopode in gematigde gebiede. Op ekologiese vlak is hulle meer talryk waar die

produktiwiteit groter is.(totale makrofauna, crustacea, *Excirolana* spp., terrestriële spp.) of waar die vestigingsomgewing vir larwe meer gunstig is (molluske en polychaete).

Die gemiddelde en totale biomassa van die fauna gemeenskap was groter op dissipatiewe as op reflektiewe strande. Dieselfde geld vir die biomassa van crustacea, terrestriële species en cirolanid isopode soos *Excirolana* spp., met geen noemenswaardige verskil vir molluske en polychaete. Daar was 'n betekenisvolle verwantskap tussen biomassa en strandmorfodinamika soos voorgestel deur Dean se indeks. Weereens was BSI minder belangrik dan individuele fisiese faktore om die biomassa en gemiddelde individuele liggaamsgrootte van die fauna op die bestudeerde mikrogetystrande te bepaal. Eienskappe van die branderzone, soos golfhoogte en -periode en branderzonewydte vertoon die hoogste korrelasies met die biomassa van die fauna gemeenskap, crustacea, *Excirolana* en terrestriële species. Die biomassa van polychaete was beter gekorreleer met eienskappe van die sediment soos sandkorrelgrootte, strandhelling en watertafel. Mollusk biomassa was afhanklik van afstand vanaf die waterversadigde zone. Die biomassa van die fauna gemeenskap en taxagroepe was hoër op gematigde strande. Alleen polychaete en molluske het nie verskil met breedtegraad. Die gemiddelde liggaamsgewig van crustacea, polychaete, molluske en *Excirolana* spp. was betekenisvol groter op gematigde strande van alle strandtipes. Beide morfodinamika, deur middel van branderzone prosesse, en breedtegraad, d.m.v. verskille in produktiwiteit, blyk die biomassa van strandmakrofauna te beïnvloed. Liggaamsgrootte van crustacea en polychaete is blykbaar verbonde aan breedtegraadverskille in produktiwiteit en dié van molluske aan die graad van reflektiwiteit van die strand.

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1. General introduction

Sandy beaches are one of the most dynamic coastal environments. The interaction of breaking waves, tides and sediment determines the morphology and slope of the beach, as well the circulation patterns of the surf zone (Wright and Short, 1984; Masselink and Short, 1993). This interaction has been called beach morphodynamics (Carter, 1988).

Depending on wave energy and sediment particle size, microtidal beaches can be in a "dissipative", "intermediate" or "reflective" state (Wright and Short, 1984). Dissipative beaches have high wave energy and fine sands. Waves start to break far from the shore in a series of spilling breakers that "dissipate" their energy along the broad surf zones. This generates slow swashes with long periods on the gently sloping beach face. Intermediate beaches can vary from high to low wave energy, coarse to fine sand and steep to moderate beach slopes with or without beach cusps; plunging breakers are typical and surf zones usually present rip currents, bars and troughs. Reflective beaches are on the extreme of low wave energy. Surf zones are narrow or non-existent and waves surge or break straight on the shore generating fast swashes with short periods. During the breaking process, part of the wave energy is "reflected" back to the sea by the very steep beach face (Fig. 1).

Beach states can be estimated by the "dimensionless fall velocity", or Dean's index (Wright and Short, 1984):

$$\Omega = Hb \,/\, Ws \,.\, T \qquad (1.1)$$

where Hb is breaker height in cm, Ws is average fall velocity of the subaerial beach sediment in cm/s and T is wave period in seconds. Reflective beaches generally have $\Omega < 1$, intermediate beaches $1 < \Omega < 6$ and dissipative ones $\Omega > 6$. Despite beach states being dynamic in space and time, they have a "modal state", e.g. a single most recurrent morphodynamic state in time (Wright and Short, 1984). Modal states are generally determined by the wave climate, sediment availability and roughness of the inner shelf (Wright and Short, 1984).

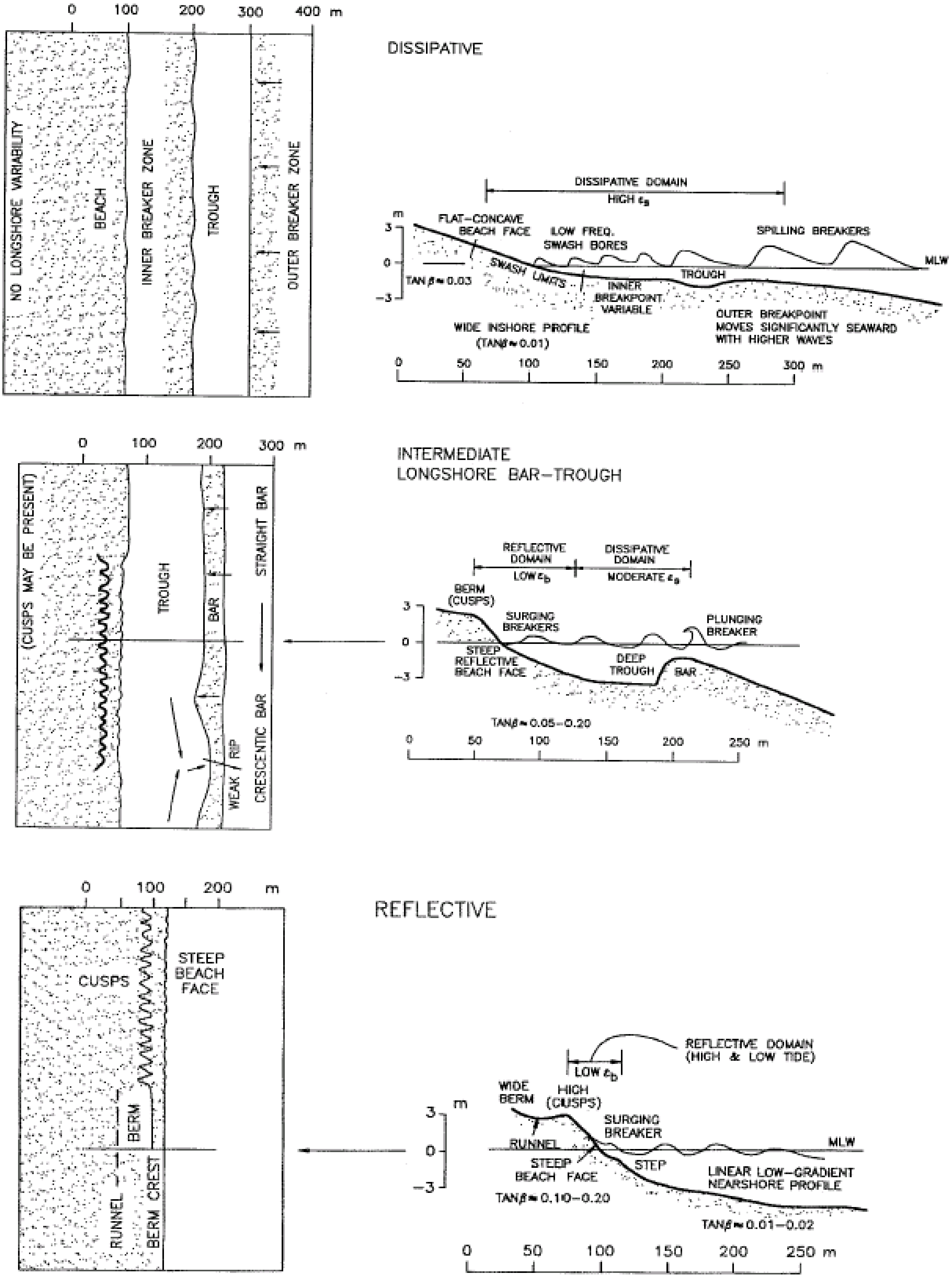

Figure 1: Plan and profile views of the three main beach morphodynamic types and main morphological features (adapted from Wright and Short (1984) description of Australian beaches).

Although descriptive (Hardisty, 1990), the morphodynamic model of Wright and Short (1984) has integrated several disparate variables into a logical framework of forcing and response variables, that are constantly interacting with each other and shifting their roles.

This integrative property of beach morphodynamics provided sandy beach ecologists for the first time with a powerful and relatively easy way to describe and understand the beach physical environment and its dominant forms and processes. Subsequently, some authors started to incorporate qualitative statements on beach morphodynamics in their description of the environment (Dexter,1983; 1984; 1996; Jaramillo and Gonzales, 1991; Defeo et al., 1992; Giménez and Yannicelli, 1997) or in relation to responses of intertidal benthic populations (McLachlan and Hesp, 1984; Santos, 1991; James, 1999) and surf zone communities (Fleischack and Freitas, 1993; Barros et al., 2001; 2002).

Descriptive linear models were then developed (McLachlan, 1990) showing that the intertidal communities over broad geographical areas respond to a series of physical factors. A predictable increase of species richness, abundance and total biomass was found from reflective to dissipative modal beach states. Although other physical factors such as sand particle size, beach slope and wave height were significantly correlated with the above biological variables, it was suggested that beach morphodynamics (calculated by Dean's index) was the most important controlling parameter through swash processes. Flat, dissipative beaches would be conducive of a diverse and abundant community as a result of longer and more benign swashes that provide animals with more time to feed and move. Conversely, steep reflective beaches would have less species adapted to the harsher conditions of the fast and short swashes that provide less time to feed and burrow.

Subsequent models incorporated more beaches as well as the effect of tide range (McLachlan et al., 1993). The previous hypothesis was upgraded to the "swash exclusion hypotheses". This hypothesis states that dissipative beaches would accommodate all beach species known to occur in one geographical region, a gradual loss of species occurring through intermediate towards fully reflective states, where only species living outside of the swash would remain (McArdle and McLachlan, 1991; 1992; McLachlan et al., 1993; McLachlan et al., 1995, McLachlan, 2001).

Although the importance of morphodynamics controlling the physical and biological beach environment seems to be overriding for both intertidal (Brown and McLachlan, 1990; Santos, 1991; McLachlan, 1990; Jaramillo and McLachlan, 1993; McLachlan et al., 1996a; Hacking, 1998; McLachlan et al., 1998; Brown, 2001; McLachlan, 2001) and surf zone communities (Borzone et al., 1996), this control does not seem to hold at all ecological scales studied, especially for studies of temporal variability in population and community dynamics (Souza and Gianuca, 1995; Jaramillo et al., 1996; 2001; Gómez and Defeo, 1999; Cardoso and Veloso, 2003). It has been argued in some of these cases, that density-dependent processes, such as stock-recruitment relations (Defeo, 1996), adult-juvenile competition (Soares et al., 1996) and intra-guild competition (Cardoso and Veloso, 2003) may be as important as morphodynamics in structuring beach communities and populations. Recent temporal studies comparing population dynamics of the same species on beaches with different morphodynamics have demonstrated that both biological and morphodynamic factors can affect sandy beach populations (Gómez and Defeo, 1999; Defeo et al., 2002, Defeo and Cardoso, 2002). The control of beach communities and populations would seem to be multifactorial and the relative importance of each factor appears dependent on the scale analysed (Bruce and Soares, 1996; Soares et al., 1996; Brazeiro, 1999; 2001; Schoeman and Richardson, 2002).

Another dispute concerning structuring forces on natural communities deals with the predictable increase in species diversity from poles to tropics found in several aquatic and terrestrial communities (Fisher, 1960; Pianka, 1966; Rohde, 1992; 1999; Rosenzweig, 1995; Gaston and Blackburn, 2000). Various hypotheses were developed to explain this trend, namely: the time hypothesis, the climatic stability hypothesis, the spatial heterogeneity hypothesis, the competition hypothesis, the predation hypothesis, the productivity hypothesis (Pianka, 1966), the time-stability hypothesis (Sanders, 1968), the species-area relationship (Rosenzweig, 1995) and the "effective evolutionary time" hypothesis (Rohde, 1992; 1999; Allen et al., 2002). All of them suppose that their underlying factor, e.g. time, spatial heterogeneity, competition, etc, reaches, with diversity, its higher expression in the tropics, suggesting a cause-effect relationship.

Challenging the assumptions of the previous hypotheses that all communities are maintained at an equilibrium state, Connell (1978) suggested that higher diversity in tropical coral reefs and rain forest communities might be maintained in a nonequilibrium state by intermediate levels of disturbance, i.e. "Intermediate Disturbance Hypothesis". Subsequent developments by Huston (1979) and Menge and Sutherland (1987) have adopted a more realistic approach considering the interplay of various physical and biological factors in regulating community structure under varying combinations of recruitment density, population growth and mortality, competition, predation and disturbance conditions.

A general increase in diversity from polar to tropical regions has been verified for some benthic communities (Sanders, 1968; Kohn, 1971; Spight, 1977, Atrill et al., 1999; Macpherson, 2002) but not for others (Warwick and Ruswahyuni, 1987; Kendall and Aschan, 1993, Gray, 2002). Thorson (1957) had long suggested that only the diversity of epifaunal species increases towards the tropics for continental shelf communities. More recent reviews on tropical soft-bottom communities (Alongi, 1989; 1990) have suggested that there is no general trend of species diversity towards the tropics because of the more severe environmental stress found on these regions (Moore, 1971; Alongi, 1989).

As a result of the unbalanced concentration of studies on temperate communities as opposed to tropical ones, the latitudinal gradient in species diversity has not been extensively tested for sandy beach communities. Despite the absence of tropical beaches in their data set, McLachlan et al. (1993) concluded that morphodynamics is the most important controlling factor overriding any possible geographical differences in the regulation of beach community structures. So far there are three formal tests of the hypothesis relating to latitudinal trends. In the first, Dexter (1992) detected no significant differences in species diversity between temperate and tropical communities. Dexter (1992) used published data from 284 beaches collected by different authors using different sampling methods. Following this, at least two non-exclusive alternative hypotheses can be raised: 1) Two different habitats were compared in the different regions, e.g. reflective tropical beaches with dissipative temperate beaches. The differences in species diversity reflects inter-habitat rather than inter-region differences. This can especially be true if the occurrence of beach morphodynamic types is related to latitude, i.e. if tropical regions have more reflective and temperate regions more dissipative beaches (Davies, 1980; McLachlan et al., 1996a); 2) The differences in species diversity reflects different sampling designs and the widely varying errors associated with them rather than real ecological differences.

The other two tests were both done on the east coast of Australia (McLachlan et al., 1996a; Hacking, 1997), and although they observed an increase in species richness from temperate to tropical beaches, both authors failed to control for tidal differences, the tropics being macrotidal and the temperate areas being microtidal. These studies have therefore compared inter-habitat rather than latitudinal differences in species diversity.

In a recent review, McLachlan (2001) stated that the factors controlling the large scale patterns of species richness on sandy beaches can be better understood based on three paradigms and two hypotheses: 1) the autoecological hypothesis (Paradigm One) which states that each individual species respond independently to the physical environment with little influence by biological factors; 2) species richness and abundance are coupled to beach state (Paradigm Two) and therefore under the influence of beach morphodynamics (Paradigm Three); 3) the morphodynamic control of species richness on a beach is exerted through the action of the swash climate and the coarseness of the beach sediment (Hypothesis One); and 4) that tropical and/or long beaches will support more diverse communities than temperate and pocket beaches (Hypothesis Two). There is no unequivocal test of Paradigm One, only correlative studies supporting Paradigms Two and Three (se above cited literature) and some experimental studies supporting partially Hypothesis One (e.g. Nel, 1995). Brown, (2001) in another sandy beach ecology review suggested that biomass and body sizes might increase towards high wave energy beaches. Neither of these reviews attempted to predict how patterns of abundance and biomass might vary between tropical and temperate regions and what might be the relative importance of latitude and morphodynamics in determining such paterns.

This thesis attempts to examine how beach physical characteristics and community structure vary along morphodynamic gradients and between different latitudinal regions. In doing so, it tests the following exploratory hypotheses:

1- the occurrence of beach morphodynamic types is related to latitude;

2- physical forces such as wave energy, grain size, beach slope, etc. regulate the structure (species richness, abundance, biomass and body size) of the macrofauna over morphodynamic gradients and in different latitudinal regions;

3- species richness increases and abundance, biomass and mean individual body sizes decrease from temperate to tropical regions;

This thesis will be divided into 8 chapters, 3 general ones (introduction, material and methods and conclusions) and 5 article chapters as follows:

Chapter 3: Beach slope has been shown to be an integrated measure of morphodynamics that is highly correlated with community structure predictors (see Brown and McLachlan, 1990). This chapter therefore attempts to discuss the relative roles of the several forcing physical factors in determining beach slopes. In doing so, I attempt to develop a predictive equation for beach equilibrium slopes that can later be also used for predicting faunal responses;

Chapter 4: Its objective is to describe the physical characteristics of beaches spanning from reflective to dissipative states and to test if the occurrence of beach types is related to latitude;

Chapter 5: In this chapter I examine the relations between physical factors and species richness along morphodynamic gradients and between different latitudinal regions. I test specifically if dissipative beaches are richer than reflective, if tropical beaches are more diverse and also if morphodynamics (as expressed by morphodynamic indices such as Dean's or Beach State Index) is the most important physical factor predicting species richness on sandy beaches at a geographical macroscale;

Chapter 6: This chapter aims to test whether beach faunal abundance varies along morphodynamic gradients and also if it varies between tropical, subtropical and temperate regions, controlling for the effects of tide and morphodynamics;

Chapter 7: The last chapter examines how biomass and mean individual body sizes vary over beaches with different morphodynamic states and attempts to identify which physical factors control community biomass. It also tests if temperate regions are richer in biomass than their tropical counterparts (see Bate et al., 1990; Bustamante et al., 1995; and Ricciardi and Bourget, 1999).

2. General Material and Methods

2.1. Study area

Five geographical areas representing three different latitudinal climatic regions in the southern hemisphere were chosen to test the three hypotheses of this study (Table 1 and Fig. 2):

- Tropics: Two different areas were sampled: Peninsula Masoala and Fort Dauphin in Madagascar; Caravelas and adjacent beaches in Bahia State, northeast Brazil;
- Subtropical: Paraná and the north of Santa Catarina coast, southeast Brazil;
- Temperate: Two different areas were sampled: west coast of South Africa; central-south coast of Chile.

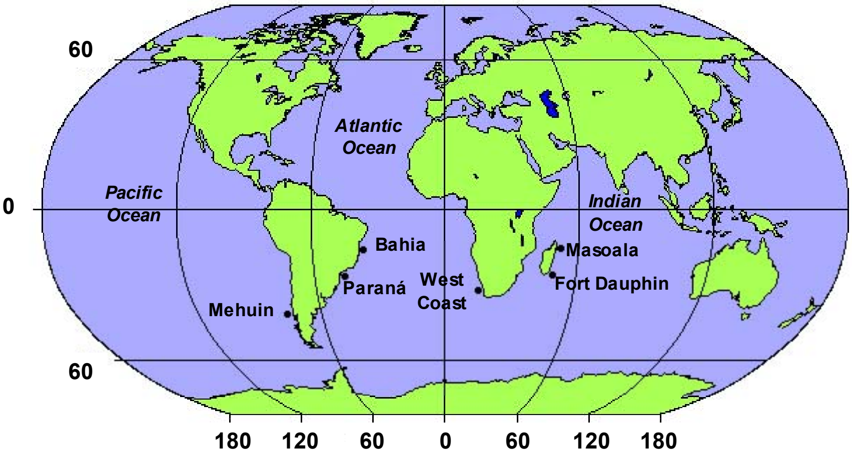

Figure 2: Areas studied in the Southern Hemisphere.

The latitudinal climatic regions were defined according to the water temperature in the surf zone and oceanic region, rather than only by latitudinal coordinates. This was done in order to adjust for differences in temperature on beaches at the same latitude but in different oceans due to unequal displacement of thermal gradients on the east and west coasts in the southern hemisphere (Levinton, 1995) and or decreasing coastal temperatures due to upwelling processes (Shannon, 1985; Soares et al., 1997). Average annual ocean surface temperatures were calculated for each biogeographic region using isotherm maps for February and August (from Sverdrup et al., 1942). Also, average regional surfzone water temperatures were estimated from data collected in situ during this study in each beach. Regional average water temperatures (annual ocean surface and in situ surf zone) was then calculated to classify the regions studied into latitudinal climatic groups. Biogeographical regions with regional average temperatures, i.e. ocean and surf zone, above 25 ° C were classified as tropical, between 15° and 25° C as subtropical and between 10° and 15 ° C as temperate (see also Alongi, 1990 and Dexter, 1992).

2.1.1. Tropics

2.1.1.1. East Madagascar

The description of this area is based on the following sources: world fact book (http://www.odci.gov/cia/publications/factbook/index.html), Anthro TECH (http://www.anthrotech.com/madagascar), Encyclopaedia Britannica 2002 online (http://www.britannica.com), Davies (1980), Battistinni (1985) and Schumann (1997).

Madagascar is the fourth largest island in the world and is located in the Indian Ocean 300 km east of the African continent. Its coast is 4828 km long extending from 12° to 25° S. (Fig. 2). The climate is tropical along the coast, temperate inland and arid in the southwest. There are only two seasons: hot and rainy from November to April and cooler and dry from May to October. Monsoons and cyclones hit the island during the hot season. On average, 7 cyclones hit the Southwest Indian Ocean and islands per year. On the eastern coast studied here, maximum rainfall ranges from 4100 mm at Maroantsetra in the north (Fig. 3) to 1520 mm at Fort Dauphin in the South (Fig. 4) with and annual average of 3000 mm.

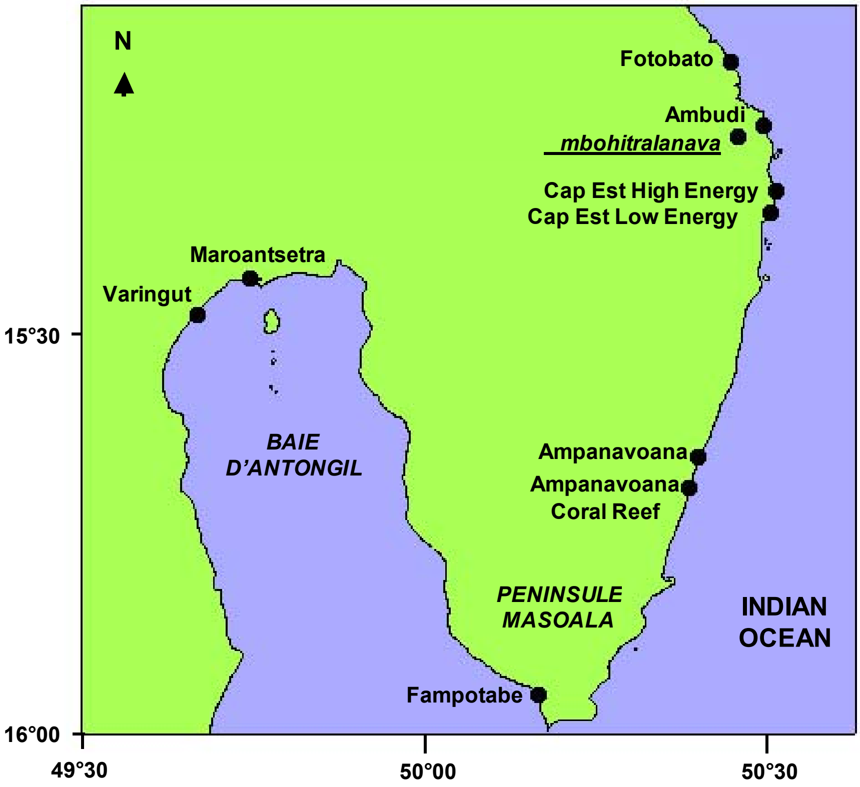

Figure 3: Beaches studied on the northeast cost of Madagascar, Peninsula Masoala (city names are underlined)

Madagascar has a highland plateau fringed by a lowland coastal strip, narrower in the east (50 km) than the west (100–200 km) coast. The east coast has a very narrow continental shelf rapidly reaching depths over 5000 m. It can be classified as an east coast swell environment with trade and monsoon influences. Waves generated by tropical cyclones can give extremely high-energy inputs but for short durations and at infrequent and irregular times. Otherwise on average wave energy levels are generally low to moderate in the northeast increasing slightly to the southeast. Fringing or barrier coral reefs occur only on the west coast, on the northern tip of the island and on the northeast coasts around Masoala Peninsula. A cold upwelling inshore cell with high chlorophyll-a concentrations has been recorded at 25° S on the continental margin in front of Fort Dauphin (Lutjeharms and Machu, 2000).

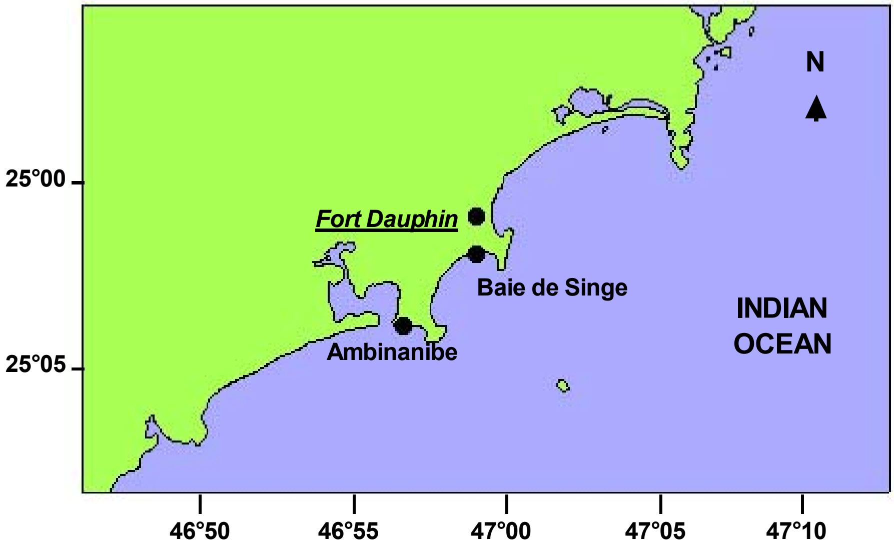

Figure 4: Beaches studied on the southeast cost of Madagascar, Fort Dauphin (city names are underlined).

The area studied had a mean high spring tide of 2.1 m, being classified as microtidal. Surf zone temperatures averaged 27° C and salinities 26 ‰ (Appendix 1). The annual ocean surface temperature was 24.9° C and the regional average was 25.9° C classifying the area as mesohaline tropical. In the southeast, the beaches studied ranged from high energy dissipative (Baie de Singe) to intermediate (Ambinanibe) morphodynamics (Fig. 4 and Appendix 1). In the northeast, Varingut, Maroanstetra and Fotobato were intermediate, Ampanavoana CR, Ambudi, Cap Est Low Energy, and Fampotabe were reflective and Cap Est High Energy and Ampanavoana were in a high energy reflective state (Fig. 3 and Appendix 1). Only three beaches were fronted by coral reef, i.e. Ampanavoana Coral Reef, Cap Est Low Energy and Ambudi.

2.1.1.2. Northeast Brazil - Bahia

The Brazilian coast is 9200 km long extending from latitudes 4° and 32° S (Fig. 2) along the Atlantic Ocean. The warm waters of the southern flowing Brazilian current bath the entire coast. The southern coast of Bahia studied here is within the rainy area of the tropical Atlantic

Forest, i.e. > 2000 mm annually, receiving the discharge of many rivers. It has a wide continental shelf forming the Abrolhos Bank. The Abrolhos bank is an archipelago of islands housing the most extensive coral reef chain in the southern Atlantic. The Bahia coast can be classified as eastern swell coast with low energy waves generated by southeast trade winds and southerly swell arriving from the South Atlantic (Cruz et al., 1985, Davies, 1980).

The area studied is microtidal having a spring tide maximum range of 2.1 m spring tide. Surf zone temperatures averaged 25° C and salinities 33 ‰ (Appendix 1). The annual ocean surface temperature was 25° C and the regional average was 25° C classifying the area as euhaline tropical. No dissipative beach was found in the area studied (Fig. 5). Beaches states ranged from reflective, i.e. Tororão, Iemanjá, Ponta da Baleia, Cumuruxatiba, Porto Marina Hotel, Pontal do Sul, to intermediate, i.e. Zeloris, Hawaizinho, Praia do Farol and Lugar Comum (Fig. 5 and Appendix 1). Cumuruxatiba was the only beach partially fronted by a coral reef.

2.1.2. Subtropics

The subtropical area investigated is the Paraná coast and the São Francisco Island on the north coast of Santa Catarina in the southeast Brazil (Figs. 1 and 6). The climate of the coast is classified as wet semi-tropical lacking a dry season. Annual rainfall is about 2000 mm annually. The area is a microtidal, i.e. 2 m maximum spring tide, eastern swell coast with average deep water wave heights of 0.75 cm and periods varying from 6.5 to 16 s. Water temperatures vary from 18° in July to 29° C in January (Davies, 1980; Souza and Gianuca, 1995). The coast receives great input of nutrients and material from the three estuaries present in the region (Fig. 6).

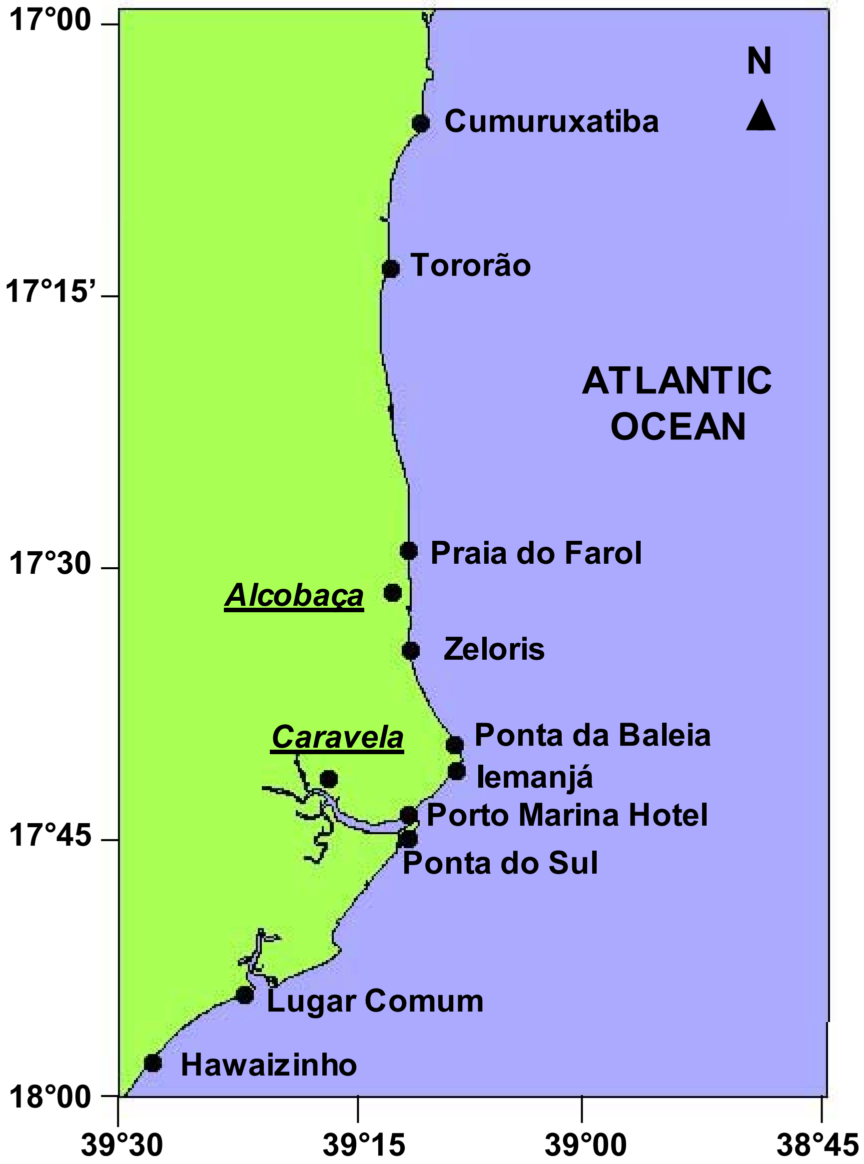

Figure 5: Beaches studied on the northeast cost of Brazil, Bahia (city names are underlined)

No reflective beach was found on oceanic beaches of the region; they were present only within estuarine domains. Surf zone temperatures averaged 22° C and salinities 33 ‰ (Appendix 1). The annual ocean surface temperature was 21° C and the regional average was 21.5° C classifying the area as euhaline subtropical. Beaches studied ranged from high energy intermediate, i.e. Grande São Francisco, to intermediate, i.e. Riviera, Brejatuba, Santiene, Ubatuba, Peças and Grande Ilha do Mel, to dissipative, i.e. Prainha, Praia Deserta, Atami (Fig. 6 and Appendix 1).

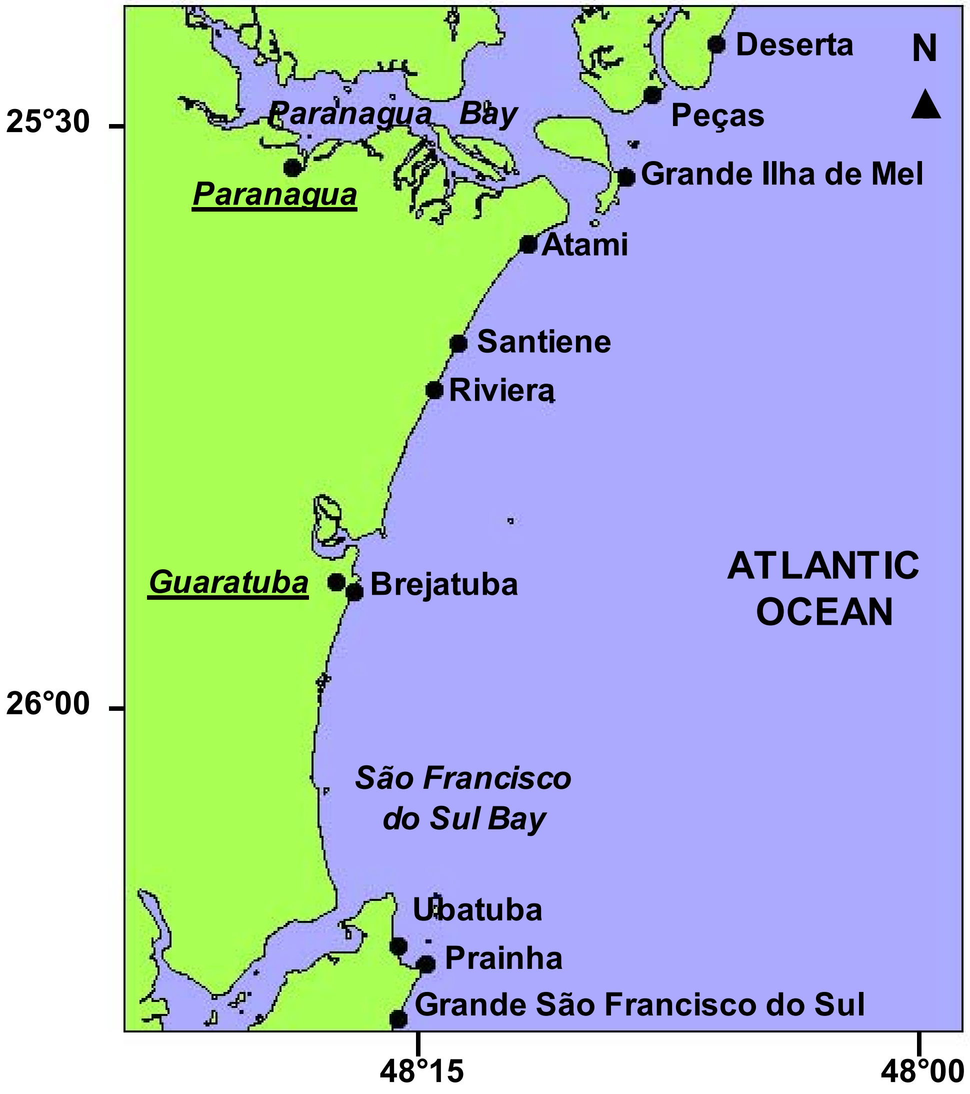

Figure 6: Beaches studied on the southeast cost of Brazil, Paraná (city names are underlined)

2.1.3. Temperate

2.1.3.1. West coast of South Africa

This coast lies within the Benguela coastal upwelling system. The features of this coast has been described in detail elsewhere and will be only briefly summarized here. For further details see (Soares et al., 1997). The Benguela current is a northern flowing branch from circum-Antarctic West Wind Drift, reaching speeds of 55 to 70 cm/s. The Benguela system is classified as a western swell coast with deep water waves coming mostly from the south with heights varying from <1 to >9 m (average ca. 4 m) and periods varying from 5 to 14 s with of average 9 s.

Upwelling in the southern Benguela is highly seasonal and intermittent. It reaches maximum periods of 1 week in summer/spring during strong southeasterly winds. By contrast, westerly winds, which are more frequent in winter, promote downwelling. In the Britannia-Stompneus Bay area, cold and nutrient-enriched waters surface from a depth between 100 and 300 m at a maximum rate of 20 m per day (Soares et al., 1997).

There are several species of kelp in this area reaching vast standing stocks of 774000 tons of fresh weight between Cape Point and Orange River at the border with Namibia (Soares et al., 1997).

The climate between Orange and Olifants River, where Groenrivier, and Spoegrivier are situated, is semi-arid with annual rainfall of less than 100 mm per year. From Olifants river to Cape Agulhas the climate is winter rainy with annual rainfall of 1000 mm (Davies, 1980).

The area studied has a maximum tidal range of 2.1 m being classified as microtidal. Surf zone temperatures averaged 14° C and salinities 33 ‰ (Appendix 1). The annual ocean surface temperature was 15° C and the regional average was 14.5° C classifying the area as euhaline temperate. The beaches studied ranged from low energy reflective, i.e. Stompneus Bay, Velddrif and Slipper Bay, low energy intermediate, i.e. Dwarskesboos, high-energy intermediate, i.e. Groenrivier, Spoegrivier, Brittania Bay and Bloubergstrand, to high-energy dissipative beaches, i.e. Strandfontein and Silwerstroomstrand (Fig. 7 and Appendix 1).

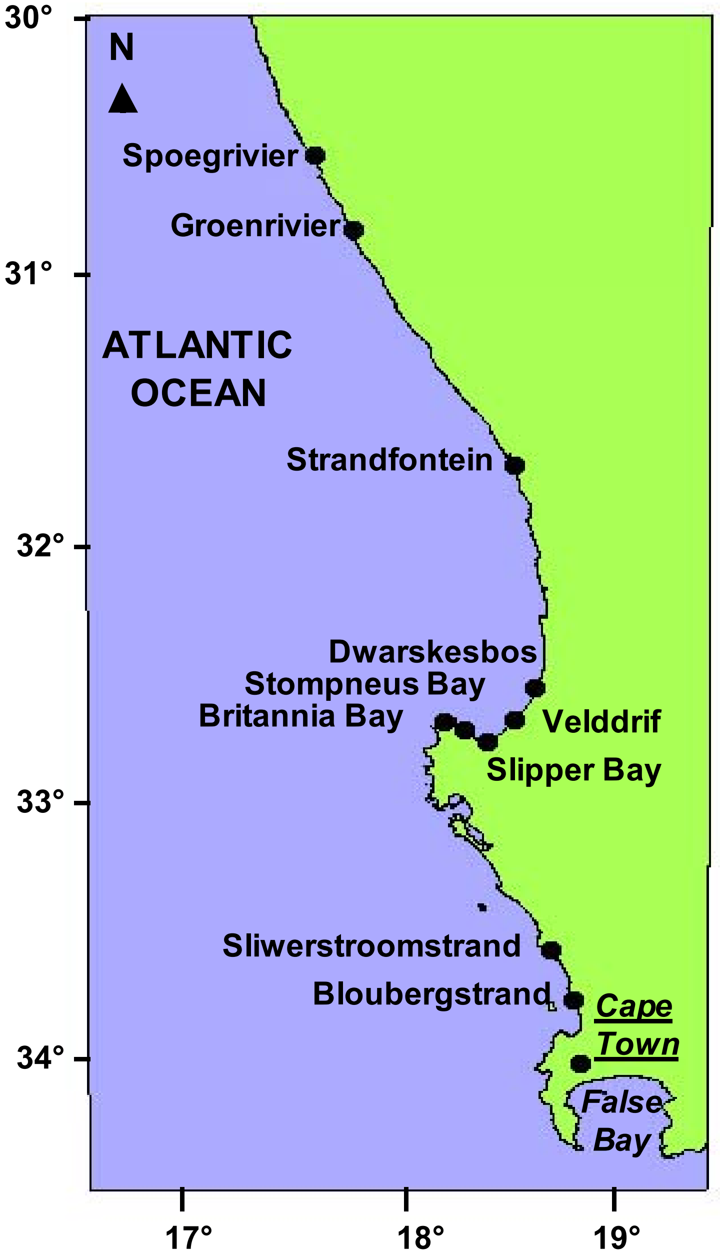

Figure 7: Beaches studied on the west cost of South Africa (city names are underlined)

2.1.3.2. South-Central Chile

Two major currents flow along the Chilean coast. The Circum-Antarctic West Drift around 80-90° S originates two currents: the south flowing Cape Horn Current and the cold (12-15° C) north flowing Humboldt Current. The Humboldt Current flows north up to 4° S deflecting westwards on the north coast of Peru (Santelices, 1989). Sea surface temperature varies only 8° C from north to south-central Chile (Jaramillo, 1987). Upwelling occurs from 18° to 30° S being absent in the area studied here. The intrusion of warm waters into the cold waters Humboldt system, called El Niño, affects mainly the north and central coasts. Several species of kelp occur along the coast with beds varying from 100 to 300 m wide and biomass varying from 1.3 to 10.3 kg/m^2 (Santelices, 1989).

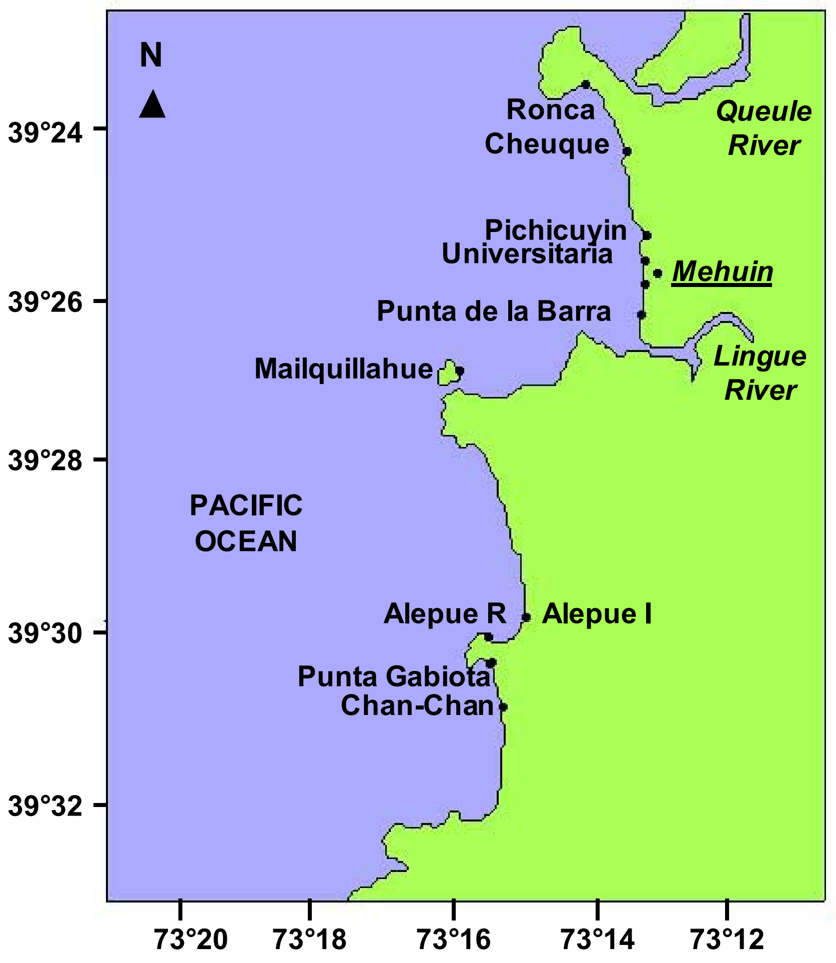

Figure 8: Beaches studied on the south central cost of Chile (city names are underlined)

The area here studied is microtidal having a maximum amplitude of 1.5 m. Surf zone temperatures averaged 13° C and salinities 35 ‰ (Appendix 1). The annual ocean surface temperature was 13.5° C and the regional average was 13.3° C classifying the area as temperate euhaline. Beaches studied ranged from reflective, i.e. Mailquillahaue and Alepue R, high energy intermediate, Punta Gabiota, Chan-Chan, Alepue I, Punta de la Barra, to high energy dissipative, Ronca, Pichicuyin, Universitaria, Mehuin and Cheuque (Fig. 8 and Appendix 1).

2.2. Sampling methods

In order to test the hypotheses that dissipative beaches have higher species richness, abundance and biomass than reflective beaches, representative beaches of each beach type were randomly sampled in each geographical region. The number of beaches per beach type per region was variable and depended on their occurrence in each region. The distance travelled and thereby the latitudinal range investigated in each region was, not only a function of the frequency of occurrence of representative beach types, but also a function of operational and infrastructural constraints.

Therefore, ten to eleven beaches were sampled once each during spring low tide at each geographical area. On each beach a transect was established perpendicular to the shoreline from above the drift line to the lowest spring tide level. Depending on the width of the intertidal (Fig. 9), the transect was divided into 12-15 equally spaced tidal levels (stations): the first above the drift line, the second on the drift line and the last in the lowest spring tide level. At each station, triplicate 0.1 m^2 sand samples were taken one meter apart to a depth of 25 cm into the sediment. The sand was sieved through 1 mm mesh and the fauna retained was first identified to the highest possible resolution, counted and then weighted after drying in an oven for 72 hours at 60^o C. The total area sampled per beach ranged from 3.3 - 4.5 m^2, being above the minimum of 3.0 – 4.0 m^2 suggested by Jaramillo et al. (1995) to be suitable for community studies of microtidal beaches.

The topography of each transect was surveyed with a theodolite and ranging staff. During low tide the top and bottom positions of the swash and the width of the saturation zone were recorded. At each station a hole was dug and the water table depth was measured during low tide. Also, at each station a sediment sample was taken to 10cm for grain size analysis. The grain size analysis was done using mechanical sieving (Buchanan and Kain, 1971) or the settling tube (Emery, 1938), depending on the region (Table 1) and the statistical parameters were calculated using the formulations by Folk and Ward (1957) or by Seward-Thompson and Hails (1973) respectively. Wave heights and periods of the outer surf zone were recorded for each beach. Eight wave heights were measured visually using the measuring staff positioned at low tide as the intersection of the crest of the breaking wave with the horizon (Bascom, 1964). The time period of eleven breaking waves was recorded with a stopwatch three times to calculate the average wave period. Surf zone water salinity and temperature were taken with a hand-held refractometer and a mercury thermometer respectively to characterize the oceanographic conditions of each beach and region.

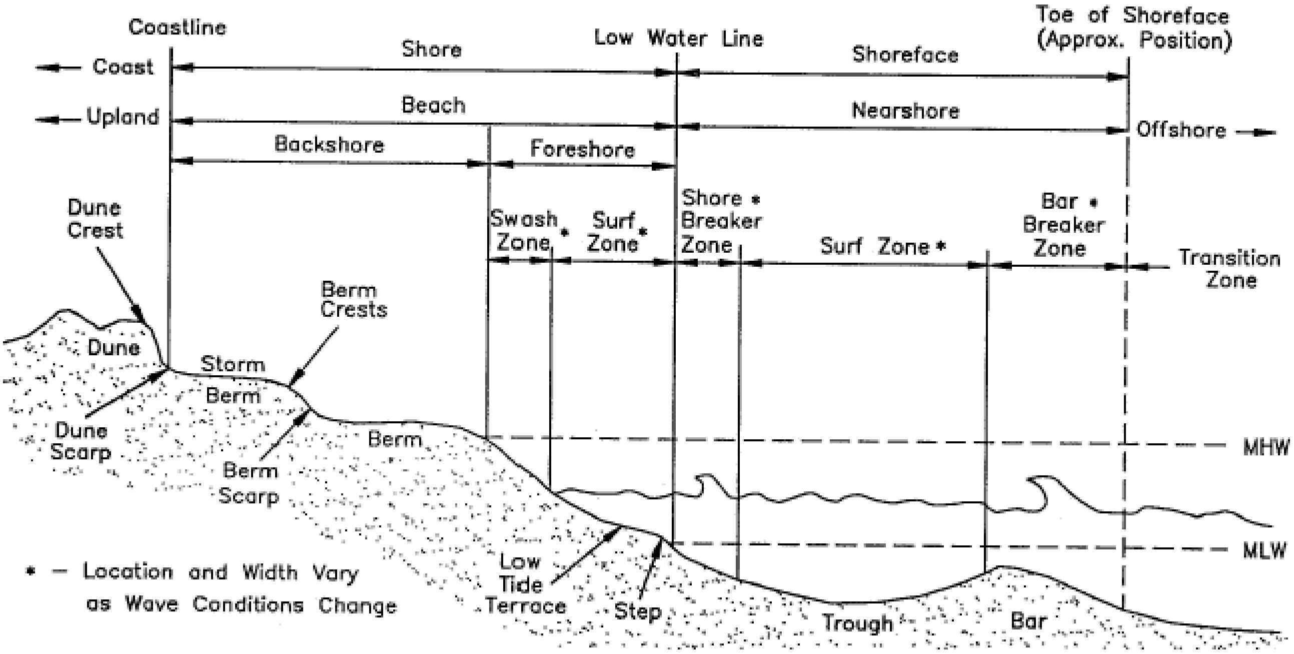

Figure 9. Beach profile showing morphological features and zones. The sampling stations were spread along the intertidal part of the beach or foreshore (adapted from Morang and Parson, 2002)

The index used to calculate morphodynamics was the Dean's parameter as described in Chapter 1, Equation 1.1. The beach state index (BSI), which takes into consideration the influence of the tides (McLachlan et al., 1993), was additionally computed for comparative purposes, even though all studied beaches were in microtidal areas. This index is as follows:

$$BSI = \log \{(\Omega \,.\, TR / E) + 1\} \qquad (2.1)$$

Where Ω is Dean's, TR is the maximum spring tide range in m and $E = 0.8$ is a theoretical equilibrium tide for the earth covered in water (McLachlan et al., 1993).

Table 1. Details of sampling and analyses for the 5 regions sampled.

Locality	Country	Region	No of beaches	Period	Total area sampled (m^2)	Sand analysis
Peninsula Masoala and Fort Dauphin	Madagascar (Northeast and Southeast)	Tropics	11	October - November 1993 and March 1996	47.2	settling tube
Bahia	Brazil (Northeast)	Tropics	10	June 1994	43.8	mechanical sieving
Paraná and Santa Catarina	Brazil (Southeast)	Subtropics	10	May - June 1994	44.1	mechanical sieving
Mehuin	Chile (South-central)	Temperate	11	March 1995	49.5	settling tube
West Coast	South Africa	Temperate	10	May 1992 June 1993	42.3	settling tube

3. A theoretical equation for the prediction of beach slopes: understanding the role of oceanographic factors in shaping sandy beaches

3.1. Introduction

Perhaps the most important question in coastal sciences nowadays is how to predict the adjustments of the coastline to sea-level rise and to other sources of localised erosion such as coastal development. Since beaches are among the coastal environments most utilised by humankind, much research effort has concentrated on understanding the dynamics of these environments. Today we know that sandy beaches adjust their morphology in response to several hydrodynamic factors such as tides (Masselink & Short, 1993) and waves (Wright, 1995; Seymor, 1989), barometric pressures (Fox and Davis, 1978) and catastrophic events such as Tsunamis (Carter, 1988). The study of interactions between sediment characteristics and hydrodynamic forces determining beach morphology has recently gained momentum (reviewed in Carter (1988), but see Seymor (1989) for a field experiment).

Despite those efforts a topic that remains elusive is the prediction of beach slopes from variables such as wave height, grain size, tidal amplitude, wave period, and swash oscillations (Seymor, 1988; Masselink, 1993). Several attempts have been made to develop an empirical equation based on the relationships between observed slopes and isolated physical variables (grain size, Bascom, 1951) or a suite of factors (Sunamura, 1984; Seymour, 1989; Kriebel et al., 1991; Masselink, 1993; Soares, 1994). Unfortunately those equations lack predictive power since their empirical nature does not necessarily imply cause-effect relationships.

There have also been few attempts to develop a theoretical equation to quantitatively predict beach slopes and shapes. The simplest equations were developed considering that the concave form of the nearshore profile, found universally, could be described by a power function in the form of:

$$H(x) = A\,x^{m} \qquad (3.1)$$

Where H is water depth at a distance x offshore (seawards the surf zone), A is scale factor related to sediment characteristics and m is a shape factor found to be 2/3 (Dean, 1983; Dean and Maurmeyer, 1983). Several modifications were proposed to the power equation, with varying levels of success. These equations, however, were developed to predict the nearshore profile and slope (Dubois, 2001). Their application to the sub-aerial part of the beach is limited due to the more complex profile morphology (Araya-Vergara, 1986; Turner, 1995), hydrodynamics and sediment transport of the surf and swash zone (Carter, 1988).

A more complex model using several variables was developed by Hardisty (1990) where the user manipulates the model interactively until fitting the best profile. Another complex model was devised by Masselink (1993) for predicting the profile of macrotidal beaches. Although the model seems to perform well for macrotidal beaches, it has not been tested in microtidal conditions. Recently, Madsen and Plant (1991) developed a model based on wave steepness that could explain only 33% the intertidal slope variance.

Beach slope seems to be directly determined by the dynamics of waves, tides and sand and therefore can be considered as an integrated measure of morphodynamics (Carter, 1988). Beach slope is additionally one of the most important single physical factors controlling both intertidal (Chapter 5; Brazeiro, 1999; Brazeiro, 2001), and subtidal (Borzone et al., 1996) beach fauna. Therefore, understanding the forces controlling slope can lead to the prediction of equilibrium beach slopes and beach faunal responses during changing hydrodynamic conditions.

The objectives of this study are, 1) to calculate and discuss the relative roles of the several forcing physical factors in determining beach slopes and 2) to develop a theoretical equation to quantitatively predict beach slope testing the degree of accuracy of the equation against field data.

3.2. Materials and Methods

3.2.1. Field Data

In this chapter the following measured physical attributes of the 52 beaches were used: beach slope (tan *B*), intertidal beach width (m), maximum horizontal wave run-up (m), wave height (m) and period (s), grain size (mm) and Dean's, computed according to equation 1.1. For details on the data see Appendix 1 and on measurements and study sites please refer to Chapter 2 (General Material and Methods).

3.2.2. Model Development

The cross-section of the sub-aerial beach deposit between the tidal marks can be defined as in Fig. 10: 1) beach elevation – the vertical height of the intertidal beach between the high tide maximum wave run-up and the lowest tide backwash; 2) beach width – defined as the distance between the position of the last high tide swash line and the lowest tide backwash and 3) the maximum horizontal wave run-up - defined by the position of the last high tide swash line.

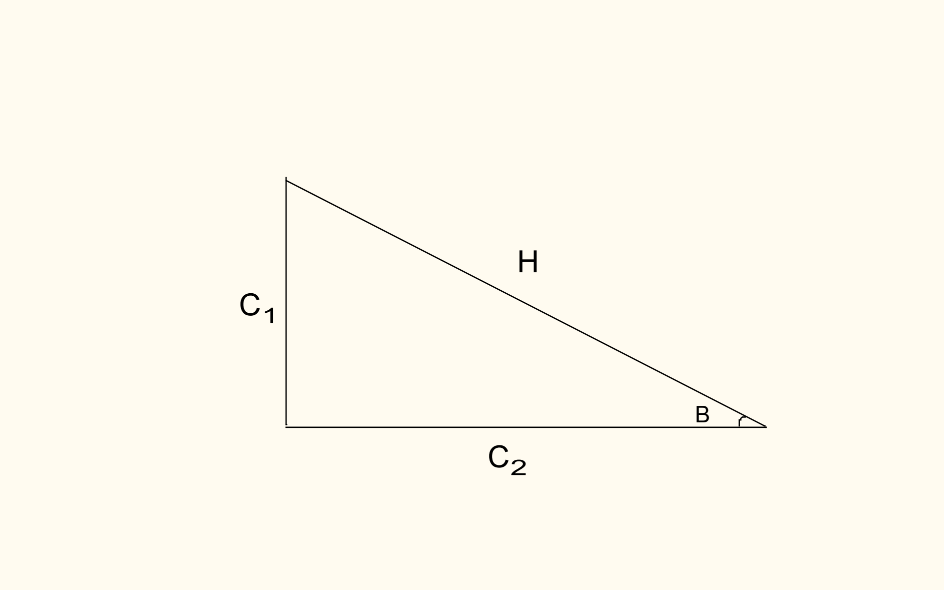

Figure 10. Cross-section beach geometry as represented by the right-angled triangle. B-beach angle, C_1 -subaerial elevation, C_2 – intertidal beach width and H - maximum horizontal wave run-up.

Pythagoras proposed his famous theorem to describe the geometric relationship between the parts of a right-angled triangle (Fig.10):

$$H^2 = C_1^2 + C_2^2 \qquad (3.2)$$

Where C_1 is the vertical side of the triangle, C_2 the horizontal side of the triangle and H the sloping side of the triangle or hypotenuse.

Considering that the cross-section of a smooth sub-aerial beach deposit between the tidal marks in equilibrium with the physical controlling forces can approach a rectangular triangle form, the following relationships could be devised:

H = maximum horizontal wave run up, C_1 = beach elevation, C_2 = beach width (BW), and tan B = beach slope (Fig. 10).

Considering that the beach elevation of a uniformly impermeable, smooth slope will be set by the high tide spring (HTS) and the wave height (H_b), then,

$$C_1 = HTS + H_b \qquad (3.3)$$

From the trigonometric relations of the right-angled triangle its is known that,

$$\tan B = C_1 / C_2 \qquad (3.4)$$

Substituting the terms by the hydrodynamic equivalents results in:

$$\mathrm{Tan}\ B = (HTS + H_b) / BW \qquad (3.5)$$

Squaring both sides of the equation,

$$(\mathrm{Tan}\ B)^2 = ((HTS + H_b) / BW)^2 \qquad (3.6)$$

However the beach deposit is not impermeable and its permeability varies according to grain size (Carter, 1988; Turner, 1993). Therefore the infiltration of the wave column, i.e. $HTS + H_b$, traversing the intertidal zone must be considered. The results of some trial estimations indicate that beach slope squared has the best fit with the root-root of grain size (Mz) in mm ($r = 0.68$, $P < 0.01$). Using the root-root of the average mean beach grain size as a surrogate for the deposit permeability and incorporating this in the equation results:

$$(\mathrm{Tan}\ B)^2 = (HTS + H_b)^2 * ((Mz)^{0.5})^{0.5} / BW^2 \qquad (3.7)$$

To render the slope dimensionless, a constant is introduced in the numerator of the grain size term, i.e. $a = 1.03125$ mm. This constant represents the median grain size of the sand particle size classification. Thus,

$$(\mathrm{Tan}\, B)^2 = (HTS + H_b)^2 * ((Mz / a)^{0.5})^{0.5} / BW^2 \qquad (3.8)$$

Taking the root of both sides the final equation is:

$$\mathrm{Tan}\, B = \{(HTS + H_b)^2 * ((Mz / a)^{0.5})^{0.5} / BW^2\}^{0.5} \qquad (3.9)$$

This beach morphometric model will be used to calculate the equilibrium beach slope based on: HTS - high tide spring amplitude in m, H_b - average breaker height in m, BW - beach width in m, Mz - average intertidal grain size in mm and $a = 1.03125$ mm.

3.2.3. Statistical procedures

Data from the 52 beaches were used to compute observed slopes and calculate predicted slopes with the beach morphometric model. In addition to the beach morphometric model, three other empirical equations (Sunamura, 1984; Kriebel et al., 1991; Masselink, 1993) were used to estimate beach slopes for comparison with the values estimated by the morphometric equation. The paired-sample T - test was used to test if there were significant differences between calculated and observed slopes for all equations (Zar, 1984). Additionally, the degree of goodness of fit between calculated and observed values was computed using the Pearson Product Moment correlation (Zar, 1984). This correlation index was also used to assess the relationships between slope and the other physical factors.

3.3. Results

The slopes calculated by the beach morphometric model were not significantly different from the observed slopes (Table 2). Additionally, the slopes predicted by this equation had the highest correlation with the observed slopes, i.e. 0.77. More than 59 % of the variation of the observed slopes can be explained by the beach morphometric model, while the other equations tested explain only 28 % of the variation.

Table 2. Correlations between physical factors and slope for 52 beaches and paired-sample T-tests between observed and predicted slopes.

Parameter/ tan *B* equation	Correlation (r) observed tan *B*	Paired-sample T-test (Obs x calc tan *B*)	Source
Wave period (T)	- 0.40	-	present study
Wave height (H_b)	- 0.47	-	present study
Dean's (H_b / W_s . T)	- 0.63	-	present study
Grain size (Mz)	0.62	-	present study
Beach width (BW)	- 0.77	-	present study
(0.116 Dean's $^{0.5}$)	0.53	-3.76*	Masselink (1993)
(0.15 Dean's $^{0.5}$)	0.53	-6.32*	Kriebel et al. (1991)
(H_b / $g^{0.5}$ $Mz^{0.5}$ $T^{0.5}$)	0.45	1.74^{ns}	Sunamura (1984)
$\{(HTS + H_b)^2 ((Mz/a)^{0.5})^{0.5} / BW^2\}^{0.5}$	0.77	1.37^{ns}	present study

where W_s - mean intertidal sediment settling velocity (cm/s); g - 9.8 m/s^2 * $P < 0.05$; ^{ns} $P > 0.05$

The empirical equations suggested by Masselink (1993) and Kriebel et al. (1991) provided estimates of slopes that were significantly different from and had a low correlation with the observed slopes (Table 2). Sunamura's equation predicted slopes that were not significantly different from observed slopes, but these predictions could explain only 20% of the variability in data (Table 2 and Fig. 11)

The beach morphometric model had a better performance predicting slopes of beaches with fine sands in the 5 regions analysed. Many of these beaches were in a dissipative state. Conversely, regions such as Bahia and Madagascar had spurious predictions (Fig. 11) since they were mainly comprised of reflective beaches with moderately sorted coarse sands. There was also a large departure between predicted and observed slopes for the coarse sand reflective beaches of the west coast of South Africa.

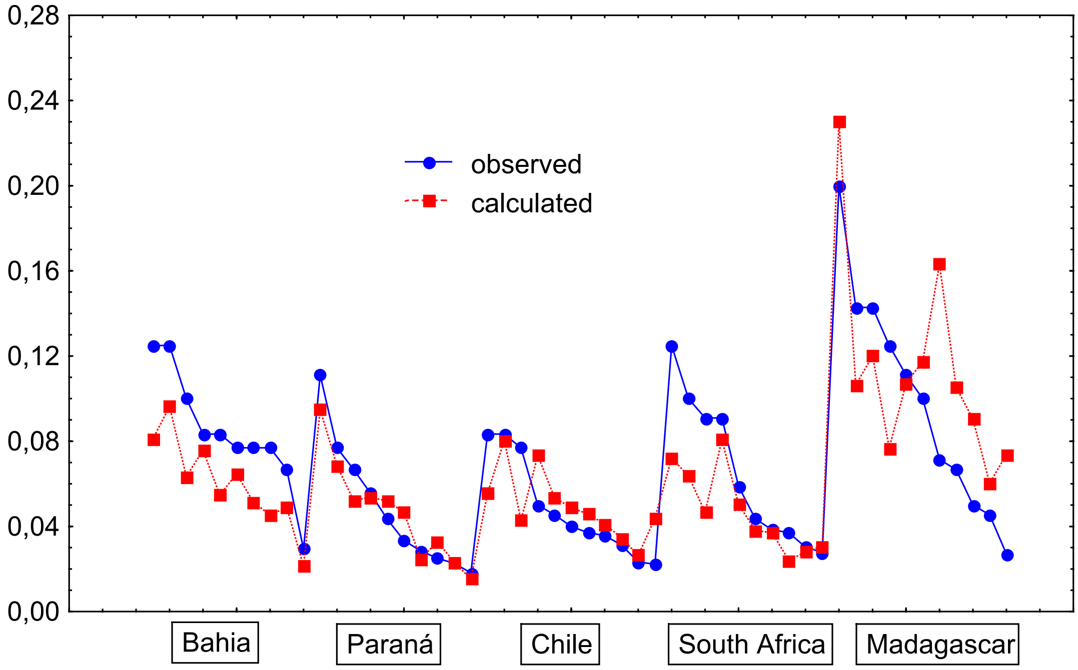

Figure 11. Observed and calculated slopes using the beach morphometric model.

From all the variables analysed the tidal amplitude was more or less constant since all the study beaches fell in the category of microtidal environments, i.e. tide < 2.0 m. For this reason the tide had no significant correlation with slope. By contrast, slope was significantly correlated with all other physical factors (Table 2). Thus, beach slopes increased with decreasing beach width, wave height and period and increasing grain size. Also, slopes increased with decreasing Dean's, i.e. towards more reflective beach states.

3.4. Discussion

The beach morphometric model suggested in this paper yielded more accurate predictions for beach slopes than any of the other empirical equations (Sunamura, 1984; Kriebel et al., 1991 and Masselink, 1993). Empirical relations generally suffer from a lack of predictive power because they can only predict values included in the range of the original correlation. Also, their results are highly dependent on the quality of the data set used. In general, inclusion of new data is likely to alter the constants of the equation and, in consequence, the results. Additionally, there are no agreed criteria to define when to stop data inclusion for the refinement of the equation (or model). Further data inclusion may improve or deteriorate the predictive power of an empirical model, thus, in the end, data choice can be subjective. These highly undesirable qualities are the main drawbacks preventing empirical equations from building coherent theories.

The morphometric equation is based on a well-established mathematical theorem. Therefore its structure is totally independent of data sets, relying only on the variables chosen to describe it. The model assumes that the morphometry, i.e. elevation, width, slope, of the sub-aerial beach deposit interacts and is in equilibrium with the physical forces, i.e. wave height and tide, and the characteristics of the deposit, i.e. grain size. In this context, the model can be classified as morphodynamic (sensu Wright, 1995).

The degree of accuracy of the beach morphometric model is remarkable despite the few physical variables included in the model. Only wave height, tide amplitude, beach width and grain size seem to reasonably predict beach slope. Both laboratory and field experiments have showed that large waves are generally destructive, i.e. they flatten the profile, whereas small waves are constructive (King, 1972; Carter, 1988). This agrees well with the results of the present study. It is easy to understand this relationship, since according to Bruun’s rule, the higher the water level, the greater the erosion required to keep the equilibrium beach profile (Dean & Maurmeyer, 1983). Moreover, following the same principle, it is expected that high tidal amplitudes will generate a flatter beach profile, whereas smaller amplitudes may produce a steeper profile, everything else being constant. Indeed this is a common pattern on natural beaches (Masselink, 1993; Masselink and Short, 1993). Although the beaches analysed did not vary much in tidal amplitude, it is clear from the beach morphometric model that ignoring this variable leads to inaccurate estimates of beach slope, since the water column travelling over the beach is a function of both tide and wave height. Grain size affects the porosity and permeability of the beach deposit, determining the volume of the backwash - the higher this volume, the greater the erosion (King, 1972). Thus, the higher infiltration on more permeable coarser deposits decreases the volume of backwash producing steeper profiles (Hanslow and Nielsen, 1993). Conversely, beaches with less permeable, finer sands will have a larger volume of backwash carrying sediments and therefore flattening the profile. This can explain the flatter slopes on medium to high-energy dissipative beaches. On low energy beaches the tide acts as a long wave flattening the slope during the ebb flow (Masselink & Short, 1993; Jackson et al., 2002). This is in agreement with the present results.

Beach width is highly correlated with morphodynamic indices such as Dean's ($r = 0.66$, $P < 0.01$), denoting a response to forcing factors. However, the wider the beach, the further from shore the waves will feel the bottom and break, flattening the slope and making the profile more dissipative. This is a classic example of feedback interaction between response and forcing variables showing the morphodynamic nature of natural beaches.

The morphometric equation performed very well even though it did not consider the effect of wave period. Many other models of beach profile do not include wave period, but still have a reasonable predictive value (for a review see Dean & Maurmeyer, 1993 and Dubois, 2001). The role of wave period is not very clear and contradictory interpretations have been suggested in the literature. For example, Wright & Short (1984) stated that reflective beaches with steep slopes are favoured by long swell waves of low amplitude, and vice-versa for flat dissipative beaches. This is probably influenced by the notion that during beach cycles, an eroding, flat profile is formed by steep waves, i.e. with large amplitudes and short periods, whereas an accreting, steep profile is formed by small waves, i.e. with small amplitudes and long periods (Madsen and Plant, 2001). This is generally the result found for laboratory experiments controlling wave steepness, i.e. the ratio between wave height and length, using monochromatic waves (King, 1972). However, a geographical analysis of beach types (Chapter 4) showed that the tropics harbour more reflective beaches than temperate regions and that these steep, reflective beaches have wave periods significantly shorter than the flat, dissipative temperate ones. Oceanic temperate beaches occur in latitudes closer to the storm-belt, around 60°, which generates the high swells that impinge on most of the open coasts (Davies, 1980). On natural beaches wave height is probably the most important factor determining whether erosion will occur or not. King (1972) observed, for natural and laboratory beaches, that flatter profiles are associated with longer wave periods. In fact this inverse relationship was also observed in the present study for the 52 beaches analysed. Since longer wave periods acting on plain sea bed produce a lower critical shear stress needed for setting a grain in motion (Voulgaris et al., 1995), they will transport a higher load of sediment than short waves (King, 1972), thereby facilitating erosion. Large and long swells can therefore carry a greater load of sediments offshore, flattening the profile. It is possible, however, that wave period may increase in importance as wave height decreases to a certain threshold low value (such as found in laboratory experiments) from which a longer small wave may build a steeper profile. On natural beaches wave period alone can explain only between 16 % (Table 2) and 26 % of the intertidal slope variance (Madsen and Plant, 2001). More studies are needed to disentangle the specific roles of wave height and period in determining beach profiles.

All beach slopes and physical factors were measured only once in this study. Therefore, correlations between forcing and response factors were solely dependent on the conditions during the measurements. Considering the possibility that the observed beach slope and morphology were produced by antecedent hydrodynamic conditions (Wright et al., 1985), the departures of estimates from observed slopes could be indicative of disequilibrium between observed slopes and the present hydrodynamic conditions. The calculated beach slopes would therefore represent the equilibrium slopes with the present hydrodynamic conditions.

Since beach slope is one of the most important physical factors controlling beach fauna (Chapter 5; 6; 7; Borzone et al., 1996; Brazeiro, 1999; 2001), it would be useful to be able to predict its changes due to changing hydrodynamic conditions. Considering the possibility that the observed slopes were the result of antecedent hydrodynamic conditions (Wright et al., 1985), a higher correlation of beach species richness with observed slopes rather than with present hydrodynamic conditions (Chapters 5; see also Jaramillo et al., 1996; 2001 and Dugan and Hubbard, 1996), could then be indicative of coupled faunal-slope responses to previous hydrodynamic conditions. The beach morphometric model could then be useful in predicting coupled slope-faunal responses to changing wave and tide regimes.

In conclusion, a simple theoretical model based on beach geometry determined by few variables such as wave height, tidal amplitude, grain size and intertidal beach width seems to predict sub-aerial beach slopes fairly well when compared with more empirical models. This model can be of special importance in aiding coastal engineering projects, such as beach nourishment or modifications of the coast for development purposes. It can also be useful in predicting beach slope changes based on forecasted hydrodynamic climatic changes. It should be noticed that no effort was made to calculate beach slopes in relation to modal morphodynamic conditions. The equation presented here is only a first attempt to develop an equilibrium slope model for the sub-aerial beach. Future studies should therefore focus on improving its predictive capacity by inserting the role of wave period and replacing grain size by permeability indexes. Additionally, the model should also be tested more extensively using data from laboratory and natural beaches to ascertain its predictive value.

4. A geographical comparison of beach morphodynamics in the southern hemisphere

4.1. Introduction

Sandy beaches are the most common and dynamic coastal environments comprising 40 % percent of the world's coastline (Bird, 2000). Although heavily utilised by humans for recreational purposes (De Ruyck et al., 1995; 1997a; 1997b), only recently has a reasonable understanding of the complex feedback interactions between beach morphology and hydrodynamic forces been developed. The so-called morphodynamic approach was initiated with the studies of Sonu (1973) and Davis and Fox (1972) and was further developed by Australian geomorphologists into a beach morphodynamic model (reviewed by Wright, 1995 and Short, 1996). Wright and Short (1984) developed a model that classified microtidal beaches into three main morphodynamic types, i.e. reflective, intermediate and dissipative, with wave energy increasing and sand grain size decreasing from reflective to dissipative beaches. This model was recently refined to include the influence of tides (Masselink and Short, 1993), multiple nearshore bars (Short and Aargard, 1993) and headlands (Short, 1996) to describe the morphodynamics of all beaches.

Although these models attempt a universal classification of beach morphodynamics, they were developed on the basis of observations of temporal variability of local beaches (Wright et al., 1985) or spatial comparisons of beaches in the same geographical region (Wright and Short, 1984; Masselink and Short, 1993). The only attempt to classify beach types over wider geographical scales was by McLachlan et al. (1993), who compared meso- and micro tidal beaches from six geographical areas. However, as in the previous studies, most of the beaches analysed were in temperate regions. Although the literature suggests that reflective beaches probably dominate in tropical areas (Davis, 1980) whereas dissipative states may prevail in temperate regions (Short, 1996), there have been no attempts so far to classify and quantify the occurrence of beach types within the same tide range in different latitudes.

The several hydrodynamic and morphologic features proposed by Wright and Short (1984) to characterise the different beach types have been verified by other studies (see review in Carter, 1988, and Chapter Three). Thus the roles of two of the variables used in Dean's equation, i.e. grain size and wave height, are well established in determining beach types.

However, there is some disagreement concerning the role of wave period; some authors suggest that steep reflective beaches are "favoured" by longer periods (Short, 1996) while others suggest the contrary (King, 1972; Chapter One). Also, although it is well know that the water table level controls beach erosion and deposition (Waddell, 1976; Turner, 1995) and differs amongst beach types (McLachlan and Turner, 1994), no comprehensive morphodynamic or geographical comparison of this parameter has been done.

The objectives of this chapter are twofold: i) to test the hypothesis that the frequency of occurrence of beach types is related to latitude; and ii) to compare morphological and hydrodynamic characteristics amongst reflective, intermediate and dissipative beaches.

4.2. Material and Methods

4.2.1. Field data

Fifty-two beaches in five geographical areas in four coasts and three oceans representing three different climatic regions were studied. On each area 10 to 11 beaches differing in wave energy and morphology were sampled once. More details on study sites please refer to Chapter 2.

In this chapter the following measured physical attributes of the beach were used: beach slope (tan B); intertidal beach width; saturation zone and swash distance (m); surf zone width (m); wave height (m) and period (s); grain size (mm); water table depth (cm); surf zone temperature (°C) and salinity (‰). For details on the data see Appendix 1 and their measurements please refer to Chapter 2 (General Material and Methods).

4.2.2. Beach type

The dimensionless fall velocity index Ω, also known as Dean's parameter, was used to calculate the morphodynamic state of each beach (Wright and Short, 1984) according to the equation 1.1.

Short (1996) defined beach types as dissipative when $\Omega > 6$, as intermediate when $1 < \Omega < 6$ and as reflective when $\Omega < 1$. These thresholds are not rigid and reflective morphologies can exist with Ω up to 2, whereas dissipative profiles can occur with values Ω of as low as 5, depending on visual characteristics of the surf zone, such as width, presence of bars and troughs and rip-currents (Table 1 in Short, 1996). Thus, both surf zone characteristics and Dean's values were used to correctly classify beach types.

4.2.3. Statistical treatment

Means of the following physical characteristics were calculated according to beach type and latitudinal region: wave height and period; swash length; saturation zone width; surf zone width; beach width; mean intertidal grain size; slope (tan B); mean water table level; surf zone temperature; salinity and Dean's.

In order to test the hypothesis that reflective beaches are more common in tropical regions whereas dissipative beaches predominate in temperate regions the five biogeographical areas sampled were grouped into tropical (Madagascar and Bahia), subtropical (Paraná) and temperate regions (south-central Chile and west coast of South Africa). The Kolmogorov-Smirnov test was used to test if there are differences in the frequency of occurrence of beach types between regions. To characterise the physical differences between the different beach types, beaches were grouped as reflective, intermediate and dissipative according to Wright and Short (1984) classification, and the means of the physical factors were calculated. Differences between regions and beach types in the mean values of all physical attributes analysed were tested separately using two one-way MANOVAs (Multivariate Analysis of Variance). A two-way MANOVA was not possible because reflective beaches were absent in the sub-tropical region, making the design incomplete to test for factor interactions (Hair et al., 1992). The Newman-Keuls *a posteriori* test of multiple means range was used to identify which group of regions and beach types differed significantly for each physical attribute. The logarithmic transformation (x +1) was applied to the data to satisfy the MANOVA assumption of homogeneity of variances, tested by the Cochran C test (Zar, 1984). In cases where this assumption was not met after data transformation, the non-parametric equivalent of ANOVA, Kruskal-Wallis H test, was applied to double-check the results of the univariate

ANOVAs. Non-parametric tests are distribution free and are therefore not affected by heterocedasticity of variances (Zar, 1984).

4.3. Results

4.3.1. Beach type comparison

The MANOVA of the 52 beaches divided in reflective, intermediate and dissipative states yielded a Wilk's lambda very close to zero, showing a perfect discrimination between beach types based on the 12 physical variables tested. As a consequence, the Raos's R transformation of the Wilk's lambda was highly significant. All physical characteristics tested, with the exception of salinity and temperature, were significantly different amongst beach types (MANOVA, univariate Fs and Newman's-Keuls test, Table 3). Only grain size, beach slope and surf zone width variances continued to be heterogeneous after data transformation (Table 3), but the Kruskal-Wallis test confirmed the results of the univariate ANOVAs, with both variables differing significantly among beach types, i.e. grain size (Kruskal-Wallis H = 22, DF = 2, 52; P < 0.0001), surf zone width (Kruskal-Wallis H = 31, DF = 2, 52; P < 0.0001) and slope (Kruskal-Wallis H = 28, DF = 2, 52; P < 0.0001).

For the 52 beaches tested, the average value of Dean's for reflective beaches was 0.73, for intermediate beaches was 2.55 and for dissipative beaches was 6.72 (Fig. 12). As expected, average wave height was significantly larger, sand grain size smaller, and slope flatter on dissipative beaches in comparison to intermediate and reflective beaches (Table 3 and Fig. 12). Average swash length was four times longer on dissipative than on reflective beaches. The difference of swash length was, however, not significant between dissipative and intermediate beaches (Newman-Keuls test, Table 3). Surf zone, beach and saturation zone widths were on average 13, 2.5 and 3.5 times wider in dissipative than in reflective beaches, respectively (Fig. 12). Again, the difference for saturation zone was not significant between intermediate and dissipative beaches (Newman-Keuls test, Table 3). Average salinities and temperatures varied respectively from 30 ‰ and 22°C in reflective, 32 ‰ and 20.7°C in intermediate to 34.8 ‰ and 17.3°C in dissipative beaches, with no significant differences among beach types (Univariate Fs Table 3).

Table 3. Summary of the MANOVA to test if physical characteristics differ significantly among beach types.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test				
0.052	10.76	24	76	0.0	Independent variable - beach type				
Dependent variable	Mean square effect	Mean square error	F (2, 49)	P-level	Reflective (R)		Intermediate (I)		Dissipative (D)
Dean's (D)	1.52	0.01	145	0	D	<	D	<	D
wave height (H_b)	2.45	0.077	32	0	H_b	<	H_b	<	H_b
wave period (T)	0.15	0.026	6	0.006	T	<	T	=	T
sand size (Mz)*	0.022	0.001	16	0	Mz	>	Mz	>	Mz
surf zone width (SZW)	7.89	0.24	33	0	SZW	<	SZW	<	SZW
swash length (SL)	1.89	0.075	25	0	SL	<	SL	=	SL
saturation width (STW)	1.35	0.104	13	0	STW	<	STW	=	STW
water table (WT)	0.4	0.065	6	0.004	WT	=	WT	>	WT
beach width (BW)	0.82	0.031	26	0	BW	<	BW	<	BW
slope (Tan B)*	0.003	0.0001	28	0	tg B	>	tg B	>	tg B
temperature (TC)*	0.046	0.045	3	0.07	-	-	-	-	-
salinity (SL)*	0.15	0.17	0.86	0.42	-	-	-	-	-

* heterogeneous variance; N-K test sign of among group differences < or > ($P < 0.05$) and = ($P > 0.05$); - not tested

The average level of the water table depth was significantly deeper on reflective and intermediate than on dissipative beaches (Table 3 and Fig. 12), depths varying from 54.8 in the former to 25.2 cm in the latter. Wave periods were on average shorter in reflective beaches in comparison to intermediate and dissipative beaches (Table 3, Fig.12).

4.3.2. Latitudinal comparison

The tropics had significantly more reflective beaches, i.e. 57 %, than subtropical (Kolmogorov-Smirnov test $D = -0.80$, $DF = 31$, $P < 0.05$) or temperate regions (Kolmogorov-Smirnov test $D = -0.57$, DF 42, $P < 0.05$). Only one dissipative beach was found in the tropics, in Madagascar. Reflective oceanic beaches were, on the other hand, absent in the sub-tropics and rare in the temperate region. In these two regions, intermediate beaches prevailed

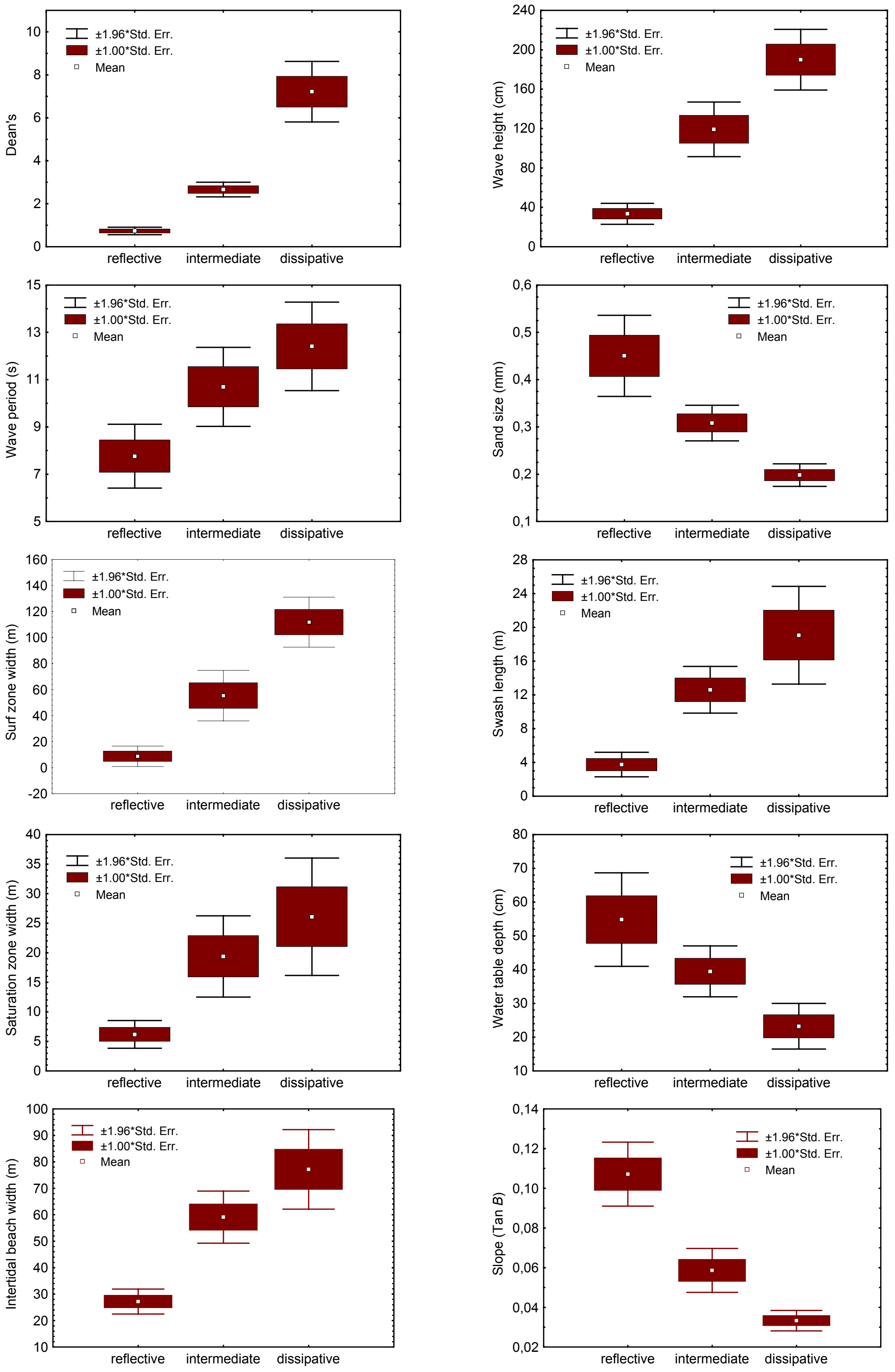

Figure 12. Means of the physical factors for each beach type.

accounting, respectively, for 70 and 43 % of the beach types, whereas dissipative beaches were the second most common accounting for 30 and 33 % of the total per region.

Considering the physical factors analysed through MANOVA, the comparison among regions yielded a very low Wilk's lambda, denoting high group discrimination, and it was highly significant according to Rao's R value (Table 4). All physical factors, except saturation zone width and salinity, were significantly different among tropical, sub-tropical and temperate regions (Univariate Fs, Table 4). Only swash length variance continued heterogeneous after data transformation (Table 4), but the Kruskal-Wallis test confirmed the results of the univariate ANOVAs, with swash lengths differing significantly among latitudinal regions, i.e. (Kruskal-Wallis H = 10, DF = 2, 52; P < 0.005).

Table 4. Summary of the MANOVA to test if beach types and their physical attributes differ significantly among tropical, subtropical and temperate regions.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test				
0.014	23.79	24	76	0.0	Independent variable - region				
Dependent variable	Mean square effect	Mean square error	F (2, 49)	P-level	Tropics		Subtropics		Temperate
Dean's (D)	0.53	0.51	11	0	D	<	D	=	D
Wave height (H_b)	1.03	0.136	8	0.001	H_b	<	H_b	=	H_b
Wave period (T)	0.26	0.021	12	0	T	=	T	<	T
Sand size (Mz)	0.008	0.002	4	0.02	Mz	>	Mz	=	Mz[1]
Surf zone width (SZW)	2.2	0.473	4.65	0.014	SZW	=	SZW	=	SZW[2]
Swash length (SL)*	0.9	0.116	8	0.01	SL	<	SL	=	SL
Saturation width (STW)	0.32	0.146	2	0.12	STW	-	STW	-	STW
Water table (WT)	0.23	0.072	3	0.047	WT	>	WT	=	WT[1]
Beach width (BW)	0.58	0.042	14	0	BW	<	BW	=	BW
Slope (Tan B)	0.001	0.0002	8	0.001	Tan B	>	Tan B	=	Tan B
Temperature (TC)*	1.41	0.089	551	0	TC	>	TC	>	TC
Salinity (SL)*	0.36	0.165	2	0.12	SL	-	SL	-	SL

* Heterogeneous variance; N-K test sign of among group differences < or > (P < 0.05) and = (P > 0.05); - not tested; [1] Temperate = Tropics (P > 0.05); [2] Temperate > Tropics (P < 0.05)

On average Dean's parameter values were significantly lower in the tropics, corroborating the hypothesis that reflective beaches prevail in low latitudes. In general, the tropics differed significantly from the sub-tropics and temperate regions in six of the 10 physical features analysed; tropical beaches had smaller wave heights, swash lengths, narrower beach and surf zone widths and steeper slopes (Table 4 and Fig. 13). Sand grain size was larger and water table level deeper in the tropics than in the subtropics, the difference being not significant between tropical and temperate regions (Newman-Keuls test, Table 4). Wave periods were on average significantly shorter and surf zone water temperatures higher in the tropics (25.95° C) than in the subtropical (21.80° C) or the temperate region (13.37° C, Table 4 and Fig. 13). No significant differences were found between the sub-tropics and temperate regions in the following aspects: Dean's; wave height; sand grain size; swash length; water table depth; beach and surf zone widths; and beach slope (Newman-Keuls test, Table 4). Average salinities and saturation zone widths varied respectively from 29.2 % and 13. 5 m in tropical, 33 % and 19.61 m on subtropical to 34.3 % and 12.26 on temperate beaches, with no significant differences among regions (Univariate Fs, Table 4).

4.4. Discussion

Investigation of 52 beaches from five different biogeographic provinces on three oceans and four coasts confirmed the hypothesis that the occurrence of certain beach types is related to latitude; reflective beaches were far more frequently encountered in tropical than in temperate regions. The converse was true for dissipative beaches, which were more common in subtropical and temperate regions. Because beach types can be characterised by certain hydrodynamic and morphological signatures (Short, 1996), these features also differed predictably amongst regions in the present study. For instance, the occurrence of larger waves with longer periods in temperate regions, and the converse in tropical regions, can be explained by climatic differences amongst latitudes. Temperate coasts are closer to the storm generating belt, which moves seasonally around 50-60° S (Davies, 1980), and will therefore be on average impacted by much larger and longer waves, i.e. high energy swell, than tropical

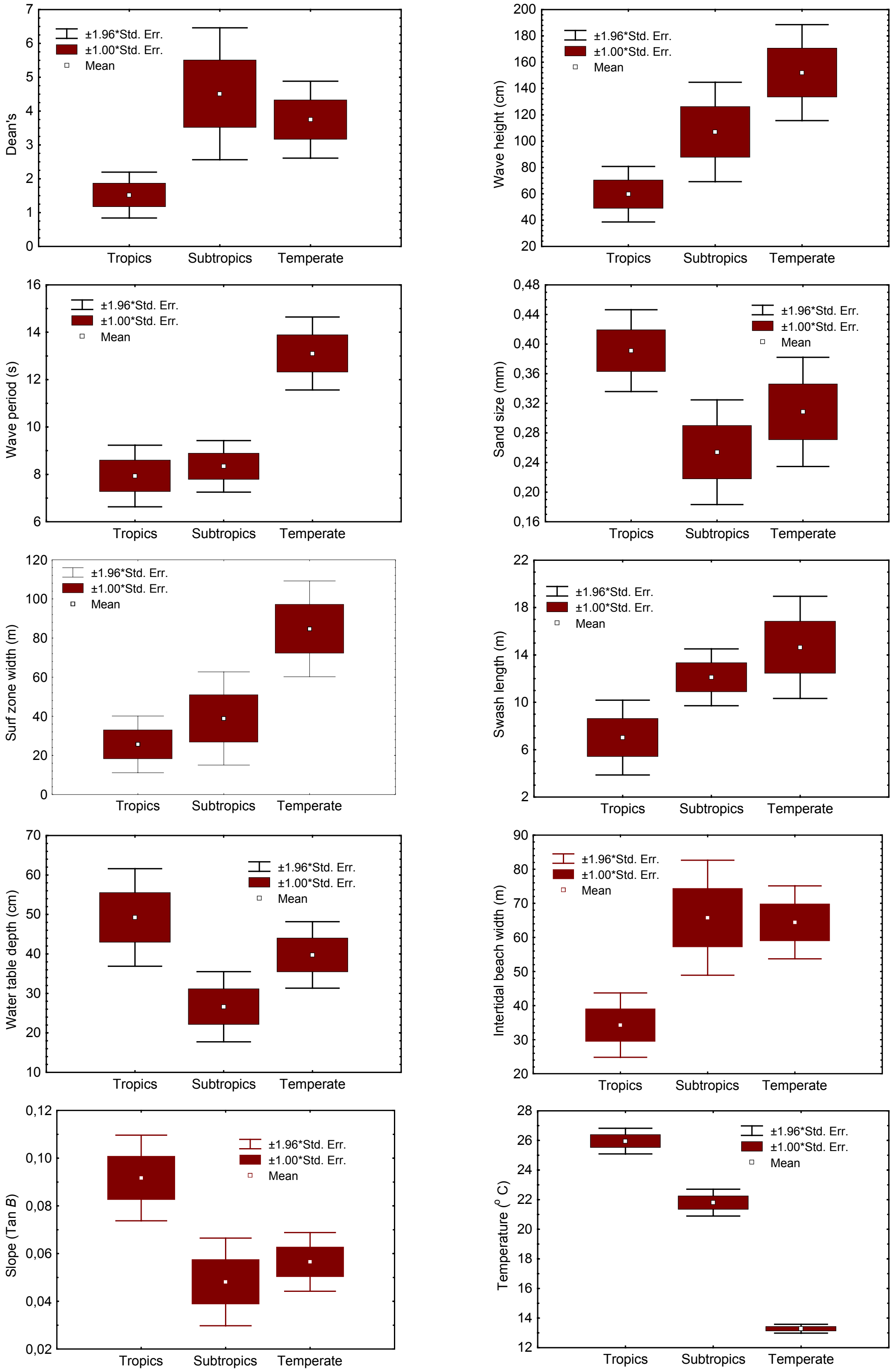

Figure 13. Means of the physical factors in each region.

coasts. Although some tropical regions, such as Madagascar, can be impacted by high energy events, such as ephemeral cyclones, these are highly infrequent and seasonal in their occurrence, following different pathways each time they pass and having a smaller local geomorphic influence in the long term (Davies, 1980). Thus, on average, tropical regions in the southern hemisphere are influenced by low energy easterly winds, which generate waves with lower heights, shorter periods and lower energy (Davies, 1980).

The existence of fringing and barrier reefs in those tropical regions studied here, have an additional influence in decreasing the wave energy reaching some beaches. Most probably the lower wave energy plus the input of carbonate sands by coral reefs (Hayes, 1967), contribute to increase the average grain size found on tropical beaches. Thus, higher occurrence of reflective beaches on the studied tropical regions is explained by the lower wave energy and coarser grain size available on these beaches. Dissipative beaches may develop in places with abundant fine sands brought by large rivers such as the coast of Sergipe near the river São Francisco on the northeast Brazil (Cruz et al., 1985). The large input of sediments on these coasts additionally inhibits the development of coral reefs widely spread along the northeast coast of Brazil. Also western tropical coasts may develop higher energy beaches than eastern tropical coasts, since the former are west coast swell environments (Davies, 1980). Not only are the wave heights higher on those coasts but also the water temperatures lower due to the north flowing branch of the circum-Antarctic west drift current in the southern hemisphere. The tropical west coasts of Chile and Peru in South America, Senegal in Africa and India in Asia are areas of upwelling cold waters, which inhibit the development of coral reefs, resulting in a wider distribution of coral reefs on eastern coasts (Davies, 1980).

Dissipative beaches prevailed in subtropical and temperate regions studied here not only because of high wave energy but also because of high availability of medium to fine sands. In fact, sand is most abundant in mid-latitude coasts of moderate rainfall (Hayes, 1967). Riverine input of fine sands to the coast seems to be significant in temperate regions on both sides of South America (Vergara, 1985; Calliari et al., 1996) as well on subtropical beaches in Brazil (Borzone et al., 1996). Due to its semi-arid climate, the northern part of the west coast of South Africa has sands mostly of marine origin (Shannon, 1985) with less contribution from river discharges.

The interaction between rainfall and wave climate may also be a factor in determining beach types in different latitudes. Bryant (1985) observed that beaches are easily eroded during high rainfall events due to a rise in water table level and fluidisation of the sand, developing large volumes of backwash carrying the suspended sediment into the surf zone. In the temperate regions studied here both rainfall and wave energy are higher in winter (Araya-Vergara, 1985; Shannon, 1985). Thus the association of shallower water tables with larger destructive waves will erode the profile making the beaches more dissipative. Conversely, the deeper water tables and lower wave heights of tropical beaches are conducive to build steep profiles of the prevalent reflective beaches. Also, the higher average wave energy of temperate and subtropical regions can, in the long term, break down sediment size into finer sands, explaining further the prevalence of dissipative beaches in these regions. The absence of oceanic reflective beaches in subtropical areas can be explained by the low occurrence of coarser sand such as coral, pebble or gravel (Hayes, 1967). In these areas reflective beaches seem to occur only associated with estuaries and estuarine-lagunar complexes with limited wave fetch (Barros et al., 2001,Jackson et al., 2002). The higher occurrence of gravel (Hayes, 1967) and pebble (Davies, 1980) can explain the existence of coarse clastic reflective beaches in mid to high temperate and polar latitudes (Carter and Orford, 1993).

The analysis of physical characteristics among the three main beach types confirmed most of the descriptions given by previous studies (Wright and Short, 1984; McArdle and McLachlan, 1992; Hanslow and Nielsen, 1993; McLachlan and Turner, 1994); Reflective beaches had, on average, lower wave heights, narrower surf zones, coarser sands, steeper slopes, and shorter swash lengths than dissipative beaches. Although not extensively analysed in previous studies, beach width, water table depth and saturation zone width differed significantly amongst beach types; reflective beaches were narrower and had deeper water tables and narrower saturation zones. These factors are probably interdependent - narrower beaches, because of the high infiltration of the swashes through the coarse sand (Hanslow and Nielsen, 1993), will have steeper slopes and deeper water tables, producing narrower swash (McArdle and McLachlan, 1992) and saturation zones in comparison to dissipative beaches.

Intermediate beaches were less distinguishable in their physical characteristics in comparison to reflective and dissipative beaches. As implied in the name, intermediate beaches have transitional physical characteristics between reflective and dissipative states, and they are the most spatially and temporally variable beach type (Wright and Short, 1984). In the present study, intermediate beaches were not significantly different from dissipative beaches in wave period, swash length and saturation zone width; they, additionally, did not differ significantly in water table depths when compared to reflective beaches.

Unexpectedly, average wave periods were significantly longer on dissipative and intermediate beaches than on their reflective counterparts. This may be due to the large occurrence in this study of reflective beaches on fetch-limited environments producing low energy waves, i.e. fronted by coral reefs, in embayments, or on islands facing the continent. Wright and Short (1984) model predicts reflective beaches to have long wave periods because Dean's parameter assumes an inverse relationship with wave period (see equation 1.1). Thus, since reflective beaches are conventionally defined by low Dean's values, they should be "favoured" (sensu Short, 1996) by increasing wave period and grain size and decreasing wave height. Although smaller wave heights and coarser sands are generally the common pattern found on those beaches (Wright and Short, 1984; Carter, 1988; Pino and Jaramillo, 1992; McLachlan et al., 1993; this study), reflective beaches can have wave periods varying from as short as 6.5 (McLachlan, 1990) to 10 s (Wright and Short, 1984) As a result, this beach type yields the lowest period recorded across the morphodynamic spectrum (Wright and Short, 1984; McLachlan, 1990; McLachlan et al., 1993; this study).

Longer wave periods generally found in laboratory and field studies in association with flat profiles (King, 1972; Davies, 1980; Chapter One) further contradict the accepted notion (Wright and Short, 1984) that longer periods are associated with building steep profiles such as those found on reflective beaches. Since on natural beaches the response time required to build a beach profile is much longer than to erode it (Carter, 1988), longer wave periods may build steeper profiles only when wave height achieves minimum threshold values for a long period of time (see Chapter One). Sine these calm periods are much less frequent on higher latitudes (Davies, 1980), the high-energy swells on temperate beaches will build flat dissipative profiles. Therefore, on a geographical scale, the distribution of beach types will be more related to the wave height than to the wave period climate - flat dissipative beaches will occur more frequently in temperate areas having high energy swells, whereas steep, reflective beaches will occur more frequently in tropical areas with low energy and short period waves.

In conclusion, the occurrence of beach types is related to latitude - reflective beaches prevailing in tropical regions with low wave energy and periods, and where coral reefs occur, whereas dissipative beaches occur more frequently in subtropical and temperate regions with higher wave energy and periods and an abundance of medium to finer sands. Differences in climate along the latitudinal gradient have a strong influence in determining the occurrence of beach types, with level of wave energy, temperature (controlling coral reef occurrence) and rainfall probably being the most important factors. Also the geographic position of the beaches seems to play an additional role in determining the wave regime and presence of coral reefs, with warmer tropical east coasts having lower wave energy than their west coast counterparts.

Beach types have different average hydrodynamic and morphologic characteristics, all being important in describing the dynamics of the beach environment. The most significant difference with previous beach descriptions is that a shorter wave period is associated here with steeper profiles, coarser sands, deeper water tables, and the shorter saturation and swash zones of reflective beaches. The converse is true for dissipative beaches. Reflective beaches are therefore predicted to occur more frequently in low wave energy environments with short wave periods, such as those inside coral reefs, in embayments, on the continental side of islands and in estuaries.

5. Latitudinal and morphodynamic variation of macrofaunal biodiversity on sandy beaches

5.1. Introduction

The prominent pattern of increasing species diversity from high to low latitudes has been intensively debated with the creation of a new branch of ecology called macroecology (Gaston and Blackburn, 2000). Several hypotheses have been erected to identify and explain its controlling factors, but no general agreement seems to have been reached yet, with each published hypothesis reflecting the author's personal preference (see reviews in Pianka, 1966; Rohde, 1992, 1999 and Rosenzweig, 1995).

Although the latitudinal gradient in species diversity has been well established for terrestrial environments (Rosenzweig, 1995), there are conflicting patterns in the marine environment (Clarke, 1992; Vincent and Clarke, 1995; Ormond et al. 1997). Some taxonomic groups with calcareous bodies, such as molluscs, seem to be more diverse in the tropics (Clarke and Crame, 1997; Roy at al., 1998), whereas others, such as isopods, amphipods and brown algae, are more diverse in temperate regions (Abele, 1982). The same may be said of marine habitats, plankton communities (Levinton, 1995; Macpherson 2002) and benthic decapods and cephalopods (Macpherson 2002), which all increase in richness towards the tropics. By contrast, some soft-bottom benthic communities have not exhibited such trends (Warwick and Ruswahyuni, 1987; Alongi, 1989; Kendall and Aschan, 1993; Gray, 2002). Some authors suggested that the lack of a pattern for intertidal soft-bottom communities could be explained by more severe environmental stress in tropical than temperate areas (Moore, 1972; Alongi, 1989; Dexter, 1992).

Macrofaunal communities in highly dynamic sandy beaches are thought to be controlled purely by physical factors (McLachlan, 1990). A general trend of increasing species diversity from low energy reflective to high-energy dissipative beaches was found when assembling the data from several biogeographical regions into a single linear regression. According to the authors (McLachlan et al., 1993), this suggested that morphodynamics is the most important factor overriding any latitudinal influences. Dexter (1992), analysing data from the literature on 284 beaches, concluded that there were more species per beach on cold temperate than on tropical beaches. McLachlan et al. (1996) suggested that Dexter (1992) most probably mixed beaches of different morphodynamic types, and this could account for her results. McLachlan et al. (1996) and Hacking (1997), nevertheless, compared beaches of different types between regions in Australia, finding that mesotidal tropical beaches were richer than their microtidal temperate counterparts. Since two or more habitats have been compared in these studies, there is no reliable test to verify if real differences in within-habitat species diversity do exist among different latitudes.

Macrofaunal species richness is also high on mesotidal tropical areas such as on the coasts of Thailand (Dexter, 1996) and Oman (McLachlan et al., 1998), but nothing is known for microtidal tropical regions. Additionally, the effect of the total species pool of each biogeographic region, i.e. region species richness (Ricklefs, 1987), on the local sandy beach species richness is not yet known.

The objectives of this chapter are to test the following hypotheses:

1- species diversity and abundance increase from reflective to dissipative microtidal beaches on a geographical macroscale;

2- tropical regions have richer species pool available to colonize sandy beaches than temperate regions;

3- tropical beaches harbour more diverse macrofaunal communities than temperate beaches of the same morphodynamic type

Additionally it will be tested whether physical forces associated to beach morphodynamics, such as wave height, period, grain size, etc, and oceanographic variables, such as temperature and salinity can explain the variability in total marine species and taxa (crustaceans, polychaetes and molluscs) richness on a geographical macroscale scale. A new environmental index able to explain a greater percentage of variance in species richness will be introduced and tested with data from this study and also from the literature.

5.2. Material and methods

5.2.1. Field data

(See Chapter 2)

5.2.2. New Environmental Index

Many biological (Wilson, 1990) and physical factors (Hall, 1994) have been suggested as influential in shaping soft-bottom communities. Sediment size is among the most important physical factors, since it is an indicator of the hydrodynamic and sedimentary characteristics of the deposits in which benthic organisms dwell (Snelgrove and Butmann, 1994). On sandy beaches, a great variance in species richness can be explained by morphodynamic indices such as Dean's or the Beach State Index, both integrating the influence of several physical factors into one value (McLachlan, 2001). However several studies have found equivalent or even better correlations of species diversity with the morphological characteristics of the beach profile, such as slope and sand grain size (Defeo et al., 1992; Jaramillo et al., 1996, 2001; Brazeiro, 1999, 2001). Slope and grain size are directly influenced by the hydrodynamics of the surf and swash (McArdle and McLachlan, 1992, see Chapters 3 and 4). Slope and grain size, in turn, modify the action of the waves (Wright and Short, 1984) producing a gradient of decreasing slope and grain size from low energy reflective to high energy dissipative beaches. However, the existence of low energy beaches with flat slopes or with a high tide reflective and low tide dissipative slope is not well described by the present morphodynamic indices (Jackson et al., 2002). Therefore, when dealing also with low energy intermediate beaches, the integration of slope and grain size into one index may increase the percentage of species richness explained variance in comparison to other morphodynamic indices.

I herewith propose the dimensionless Beach Deposit Index:

$$\mathrm{BDI} = (\,1/\tan B\,)\,.\,(\,a/\mathrm{Mz}\,) \qquad (5.1)$$

Where $\tan B$ is the average intertidal beach slope, $a = 1.03125$ mm is the median grain size of the sand particle size classification scale (see Chapter 3) and Mz is the average intertidal sand size in mm.

To account for beaches with a visible break in slope having a high tide reflective profile, generally with coarse sand, and low tide dissipative profile with fine sands, the index was calculated for each part of the profile separately and then averaged.

The relationship between this index and species richness will be calculated with the Pearson Product Moment correlation for the data of the 52 beaches collected for this study and also using data of 47 beaches from the recent beach literature, where the necessary variables were provided (McLachlan, 1990; McLachlan et al., 1993; McLachlan et al., 1998).

5.2.3. Statistical treatment

Means of the following biological characteristics per beach were calculated according to beach type and latitudinal region: marine species richness (species with a marine origin); relative marine species diversity (beach species richness / region species richness); terrestrial species richness (insects, arachnids and myriapods); polychaete species richness; crustacean species richness; mollusc species richness and “other” species richness (i.e. nemerteans, echinoderms, sipunculids, oligochaetes, etc). For the purpose of this study, regional species richness is the total number of marine species found on all beaches sampled in a biogeographic region.

In order to test the hypothesis that tropical beaches are on average richer than temperate ones the five biogeographic areas sampled were grouped into tropical (Madagascar and Bahia), subtropical (Paraná) and temperate regions (south-central Chile and West Coast of South Africa). To test the hypothesis that dissipative beaches are richer than their reflective counterparts, beaches were grouped as reflective, intermediate and dissipative according to Wright and Short (1984) classification. Differences between regions and beach types in the mean species richness values for each group were tested separately using two one-way MANOVAs (Multivariate Analysis of Variance). A two-way MANOVA was not possible because reflective beaches were absent in the subtropical region, making the design incomplete to test for factor interactions (Hair et al., 1992). Also to test if values of species richness of beaches from the same morphodynamic type differ between latitudes, three one-way MANOVAs were done for each beach type, i.e. reflective, intermediate and dissipative. The Newman-Keuls *a posteriori* test of multiple means range was used to identify which regions and beach types differed significantly for each species richness measure. The logarithmic (x +1) transformation was applied to the data to satisfy the MANOVA assumption of homogeneity of variances, tested by the Cochran C test (Zar, 1984). Two tailed T-tests were additionally used when only two groups were significantly different.

The Pearson Product Moment correlation index was also calculated to assess the relationships between the several measures of species richness and the physical factors (Dean's; BSI; BDI; 1/slope; intertidal beach width; grain size; wave height; wave period; surf zone width; water temperature; water salinity; swash length; saturation zone width; water table depth). Dean's is calculated according to equation 1.1. (Chapter 1) and the Beach State Index, according to equation 2.1 (Chapter 2).

5.3. Results

5.3.1. Regional species richness (species pool)

The 11 Madagascan tropical beaches had in total 64 species, 17 % (11) being terrestrial species and 83 % (53) being marine species. Of the latter, 47 % (25) are crustaceans, 26 % (14) polychaetes, 15 % (8) molluscs and 12 % (6) others.

The 10 North Brazilian tropical beaches had in total 55 species, 24 % (13) being terrestrial species and 76 % (42) being marine species. Of the latter, 52 % (22) are crustaceans, 31 % (13) polychaetes, 12 % (5) molluscs and 5 % (2) others.

The 10 Southeast Brazilian subtropical beaches had in total 49 species, 24 % (12) being terrestrial species and 76 % (37) being marine species. Of the latter, 52 % (20) are crustaceans, 31 % (9) polychaetes, 12 % (6) molluscs and 5 % (2) others.

The 11 South-Central Chilean temperate beaches had in total 47 species, 40 % (19) being terrestrial species and 60 % (28) being marine species. Of the latter, 61 % (17) are crustaceans, 29 % (8) polychaetes, 3 % (1) molluscs and 7 % (2) others.

The 10 West Coast South African temperate beaches had in total 63 species, 41 % (26) being terrestrial species and 59 % (37) being marine species. From these, 57 % (21) are crustaceans, 30 % (11) are polychaetes, 11 % (4) are molluscs and 3 %, (1) others.

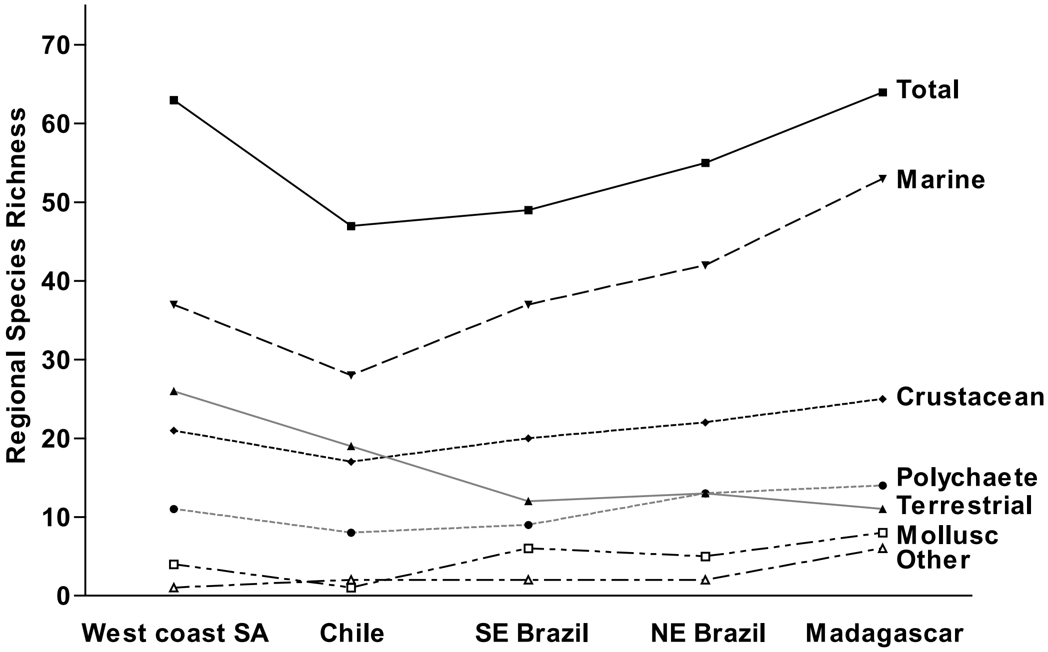

Figure 14: Regional species pool on 52 beaches. West coast SA (n =10), Chile (n = 11), SE Brazil (n = 10), NE Brazil (n = 10), Madagascar (n = 11)

Although Madagascar and the West Coast of South Africa had similar total number of species, it is clear that tropical regions (Madagascar and North Brazil) had a larger pool of marine species than the subtropical Southeast Brazil, and the temperate Chile and the West Coast of South Africa (Fig. 14). Polychaetes, molluscs, crustaceans and the group comprising the less common taxa, i.e. "others", increased towards the tropics. Terrestrial species were the only group increasing towards temperate regions (Fig. 14). There were some differences between regions classified in the same latitudinal group, with Chile having lower pool of species than the West Coast of South Africa and Madagascar having higher species pool than its Atlantic counterpart (Fig. 14).

5.3.2. Beach type comparison

Grouping the 52 beaches of all latitudes into reflective, intermediate, and dissipative types rendered significant differences in species richness amongst beach types. The Wilk's lambda value was relatively high due to the lack of difference in four variables amongst beach types, i.e. polychaete, mollusc, terrestrial and "other" species richness. Nevertheless the remaining three variables, i.e. marine, crustacean and relative species richness, showed significant differences amongst beach types and the Raos's R transformation of the Wilk's lambda was significant ($P < 0.003$, Table 5).

Table 5. Summary of the MANOVA to test if species richness differ significantly among beach types when disregarding latitude.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test			
0.48	2.65	14	86	0.003	Independent variable - beach type			
Dependent variable	Mean square effect	Mean square error	F (2, 49)	P-level	Reflective	Intermediate (I)	Dissipative (D)	Interpretation
Marine species richness*	0.08	0.02	3.30	0.04	1.07	1.15	1.22	R<D
Relative species richness	0.14	0.01	9.62	0	0.27	0.36	0.47	R<I<D
Crustacean species richness	26.47	6.74	3.93	0.03	7.29	8.62	10.09	R<D
Polychaete species richness	0.62	3.76	0.16	0.85 ^{NS}	3.11	3.25	3.54	-
Mollusc species richness	2.78	1.12	2.50	0.09 ^{NS}	1.00	1.42	1.91	
Terrestrial species richness	0.93	8.03	0.11	0.89 ^{NS}	3.47	3.13	3.54	-
"other" species richness	0.10	0.76	0.14	0.87 ^{NS}	0.65	0.75	0.82	-

* Log transformed; < ($P < 0.05$); NS ($P > 0.05$); - not tested

The differences in marine species richness were significant (Table 5), but there was high variability within each beach type caused by biogeographical differences in the total pool of species (Fig. 15). After correcting for latitudinal differences, i.e. calculating the relative marine species richness (beach species richness/ region species richness), the dissipative beaches showed significantly higher relative species richness than intermediate and reflective beaches. Thus, dissipative beaches harbour on average 47 %, intermediate 36 % and reflective 27 % of the species available in the species pool of each biogeographical region (Table 5, Fig. 15).

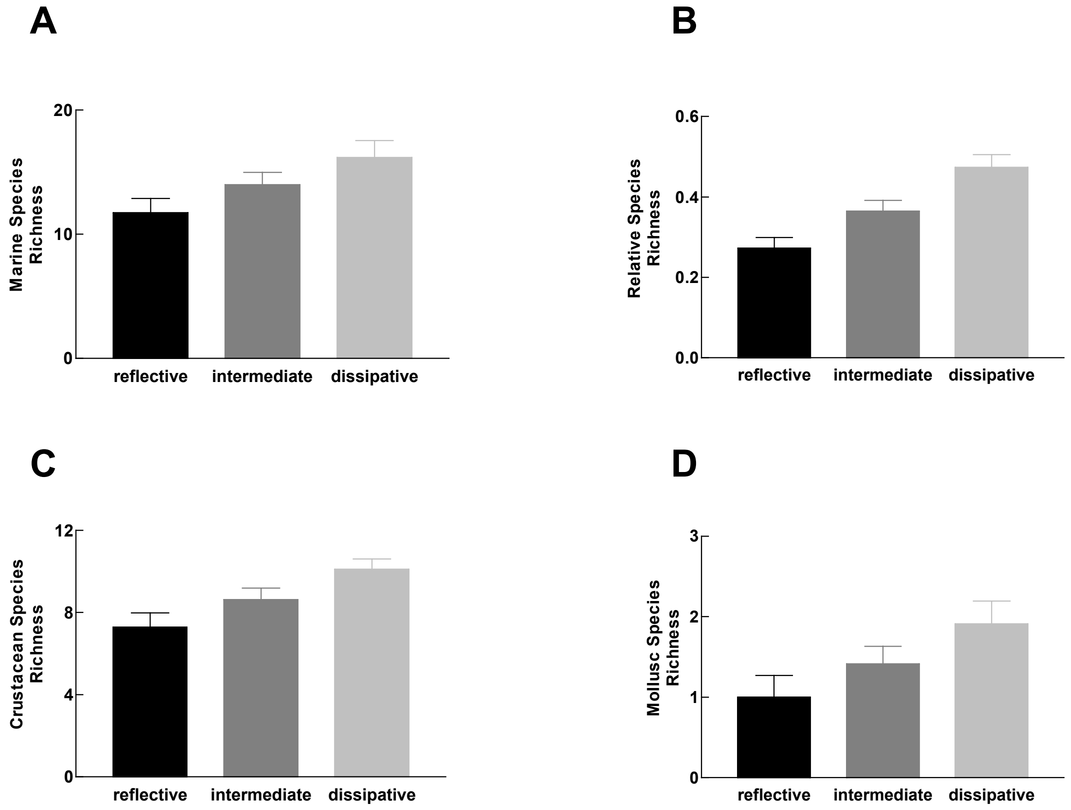

Figure 15: Average species richness in each beach type on 52 beaches. Reflective (n = 17), Intermediate (n = 24), Dissipative (n = 11)

Even when disregarding latitudinal differences between beach types, dissipative beaches had higher crustacean (Table 5, Fig. 15) and mollusc (t = 2,22, $P < 0.03$, DF = 26, Fig. 15) species richness than reflective beaches, while polychaetes, terrestrial and “other” species did not vary significantly among beach types (Table 5).

5.3.3. Latitudinal comparison

5.3.3.1. General trends

Grouping the 52 beaches of all morphodynamic types into temperate, subtropical and tropical beaches yielded significant differences in species richness among latitudes. The Wilk’s lambda value was relatively high due to the lack of difference in two variables among latitudes. Nevertheless the remaining four variables showed significant differences and as a result, Raos’s R transformation of the Wilk’s lambda was highly significant (Table 6).

Table 6. Summary of the MANOVA to test if species richness differs significantly among temperate, subtropical and tropical areas disregarding beach morphodynamic types.

Wilk's lambda	Rao's R	DF 1	DF2	P-level	Newman-Keuls test
0.58	2.26	12	88	0.015	Independent variable - latitude

Dependent variable	Mean square effect	Mean square error	F (2, 49)	P-level	Temperate (Temp)	Subtropical (Sub)	Tropical (Trop)	Interpretation
Marine species richness	99.09	21.81	4.54	0.015	11.48	16.50	14.57[1]	Temp<Sub
Crustacean species richness	8.86	7.45	1.19	0.31^{NS}	7.90	9.50	8.62	-
Polychaete species richness	11.12	3.34	3.32	0.044	2.52	4.20	3.57	Sub>Temp
Mollusc species richness	6.60	0.96	6.88	0.002	0.81	2.10	1.62	Temp<Sub=Trop
Terrestrial species richness	43.01	6.31	6.81	0.002	4.86	1.80	2.52	Temp>Sub=Trop
"other" species richness	1.45	0.72	2.00	0.14^{NS}	0.47	0.70	1.00	-

* heterocedastic; < ($P < 0.05$); NS ($P > 0.05$); - not tested; [1]Trop>Temp (marine species richness) (T=2.26; p<0.03; DF=40

Even when pooling all beach types per region, subtropical beaches had higher total marine, polychaete and mollusc species richness when compared with temperate beaches (Table 6, Fig. 16). Tropical and subtropical beaches did not differ in richness for any tested group. Temperate and tropical beaches did not differ significantly in polychaete species richness. Molluscs attained higher species richness in tropical and subtropical beaches (Table 6, Fig.16). The results of the Newman Keuls multiple comparisons were almost significant when comparing marine species richness between tropical beaches and temperate beaches ($P < 0.07$). A closer inspection on Fig. 16 shows not only that values on tropical beaches are higher than temperate beaches, but also that the variance of both tropical and temperate beaches is much lower than subtropical beaches. The result of the multiple comparisons could have therefore been biased by the higher variance of the subtropical beaches. Thus, a T-test confirmed that tropical beaches are significantly richer than temperate ones ($t = 2,26$, $P < 0.03$, DF = 40, Fig. 16).

Average crustacean species richness per beach did not show any significant difference along the latitudes following the same trend showed by the regional crustacean richness (Fig. 14).

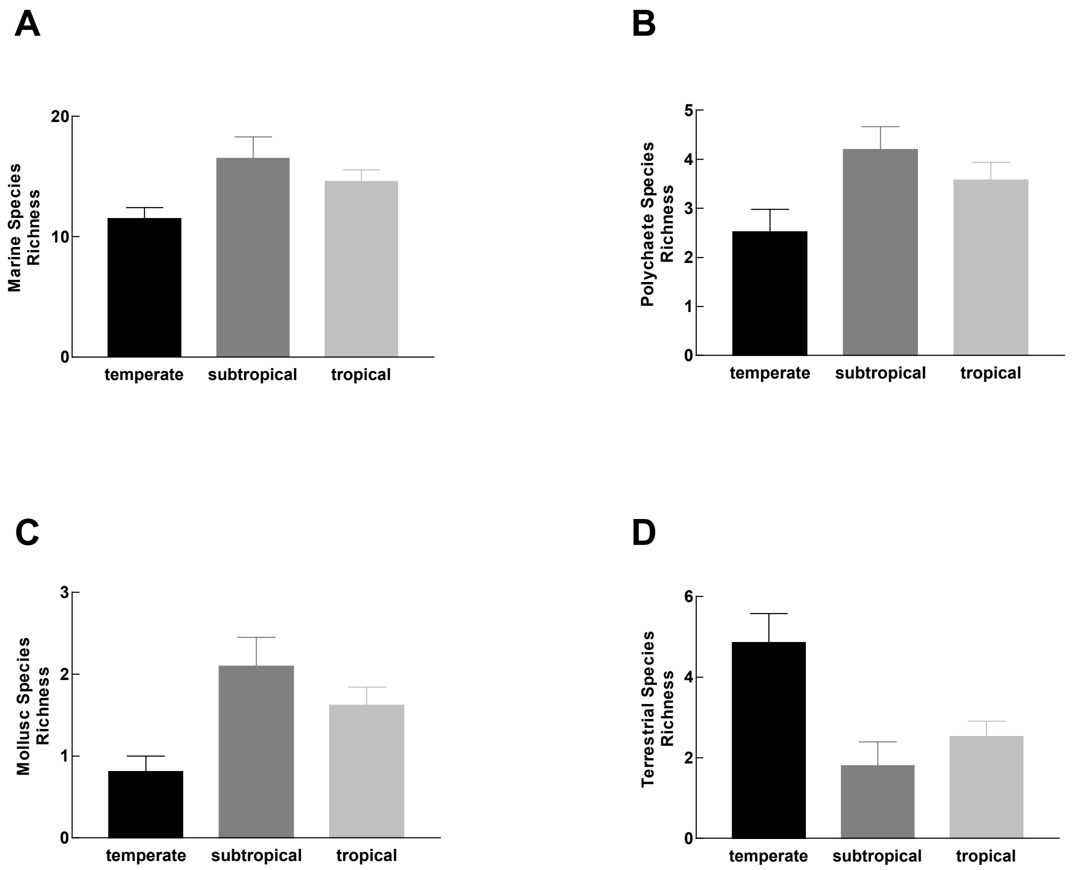

Figure 16: Average species richness per region for 52 beaches. Temperate (n = 21), Subtropical (n = 10), Tropical (n = 21)

5.3.3.2. Reflective beaches

No reflective beach was sampled in the subtropics, thus the latitudinal comparison is restricted to temperate and tropical regions. A MANOVA comparing all measures of species richness on reflective beaches among latitudes was not significant due to the lack of differences in most variables, i.e. polychaete, terrestrial, crustacean and others species richness (Wilk's lambda = 0,52, Rao's R = 1, 20, P = 0.40). Crustacean species richness was apparently higher on the tropical reflective beaches, (P < 0.07, Fig 15).

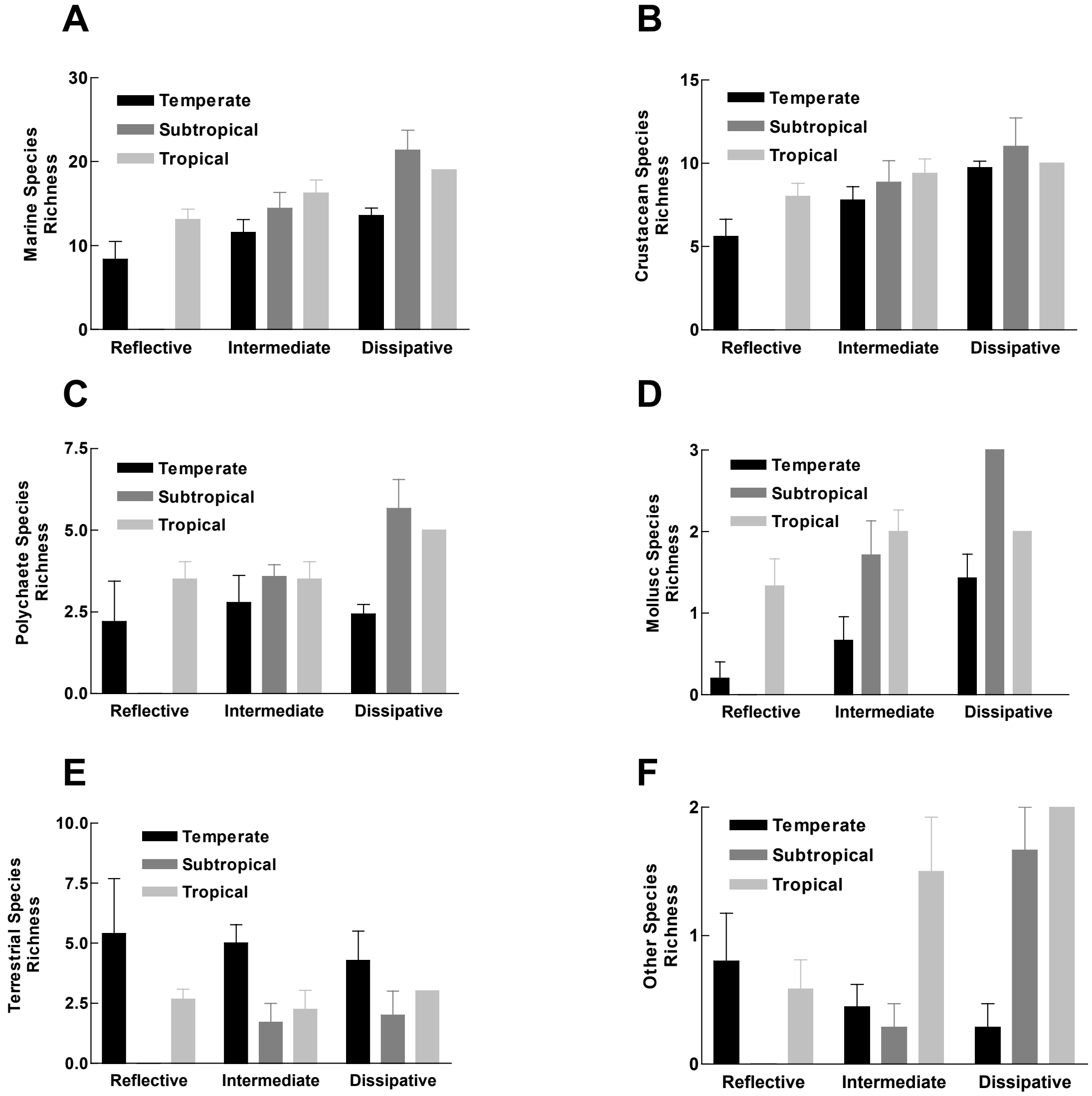

Figure 17: Average species richness per beach type in each latitudinal region.

A MANOVA model including only the variables that differed significantly between the groups, i.e. the log transformed data for marine and mollusc species richness, yielded significant results ($P < 0.03$, Table 7). Thus marine and mollusc species richness were significantly higher on tropical than temperate reflective beaches (Table 7, Fig 17).

Table 7. MANOVA comparison of species richness on reflective beaches among latitudes

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test		
0.61	4.39	2	14	0.03			
Dependent variable	Mean square effect	Mean square error	F (DF 1, 15)	P-level	Temperate		Tropical
Log (Marine species richness +1)	0.14	0.023	5.95	0.03	0.93	<	1.13
Log (Mollusc species richness +1)	0.25	0.035	6.97	0.02	0.06	<	0.32

5.3.3.3. Intermediate beaches

Intermediate beaches were the most abundant beach type occurring in all latitudes (see Chapter 4). The MANOVA of species richness on intermediate beaches between latitudes yielded a significant model ($P < 0.02$, Table 8). Wilk's lambda value was relatively high and three out of six variables did not show differences between latitudes.

Table 8. MANOVA comparison of species richness on intermediate beaches among latitudes.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test			
0.27	2.48	12	32	0.02	Independent variable - latitude			
Dependent variable	Mean square effect	Mean square error	F (2, 49)	P-level	Temperate (Temp)	Subtropical (Sub)	Tropical (Trop)	Interpretation
Marine species richness	47.76	21.69	2.20	0.14^{NS}	11.56	14.43	16.25[1]	-
Crustacean species richness	5.67	7.82	0.72	0.5^{NS}	7.78	8.86	9.36	-
Polychaete species richness	1.62	3.49	0.46	0.64^{NS}	2.77	3.57	3.50	-
Mollusc species richness	4,20	0.83	5.06	0.016	0.67	1.71	2.00	Temp<Sub=Trop
Terrestrial species richness	25.85	5.00	5.17	0.015	5.00	1.71	2.25	Temp>Sub=Trop
"other" species richness	3.42	0.65	5.27	0.013	0.44	0.29	1.50	Temp=Sub<Trop

* heterocedastic; < ($P < 0.05$); NS ($P > 0.05$); - not tested; [1]Trop>Temp (marine species richness) ($T=2.147$; $p<0.048$; $DF=15$)

Tropical and subtropical intermediate beaches had higher mollusc species richness (Table 8, Fig. 15). "Other" species richness was also higher in the tropics in comparison to subtropical and temperate intermediate beaches (Table 8, Fig. 17). By contrast, terrestrial species were richer in temperate than in the other two regions (Table 8, Fig. 17). Crustaceans and polychaetes did not show any significant pattern.

Although marine species richness was not significantly different among the three latitudinal groups (Table 8), there was a visible trend of increasing richness towards the tropics (Fig. 17), and a suspected significant difference between tropical and temperate beaches. A T-test between these two regions confirmed the higher marine species richness of intermediate tropical beaches (t = 2,147, P < 0.048, DF = 15).

5.3.3.4. Dissipative beaches

Only one dissipative beach was found in the tropics, i.e. in southeast Madagascar (Fig. 4, Chapter 2). Thus, the latitudinal comparisons were made between subtropics and temperate beaches. A MANOVA with all measures of species richness was not significant (Wilk's Lambda = 0.07, Rao's R = 6. 15, P < 0.082). Dropping the two variables that did not differ between regions, i.e. crustacean and terrestrial species richness, and performing the MANOVA with the four remaining significant variables yielded a significant model (P < 0.006) with a Wilk's lambda close to 0, meaning perfect discrimination of the two regions by the variables in the model (Table 9).

Table 9. MANOVA comparison of species richness on dissipative beaches among latitudes

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test		
0.08	14.00	4	5	0.006			
Dependent variable	Mean square effect	Mean square error	F (DF: 1.15)	P-level	Temperate		Tropical
Marine species richness	126.51	8.56	14.8	0.005	13.57	<	21.33
Polychaete species richness	22.01	1.05	21.01	0.002	2.43	<	5.67
Mollusc species richness	5.18	0.46	11.17	0.01	1.43	<	3
"other" species richness	4.00	0.26	15.29	0.004	0.286	<	1.67

Thus subtropical dissipative beaches were richer in marine, polychaete, mollusc, and “other” species than their temperate counterparts (Table 9, Fig. 17).

5.3.4. Relationship between physical factors and species richness

A summary of the correlations between all physical factors and the measures of species richness is given in Table 10.

Most if not all measures of species richness showed significant correlations with several physical factors. New factors not included before in sandy beach analyses were the water table depth, the width of the intertidal beach, saturation and surf zone widths and the Beach Deposit Index (BDI).

Dean’s morphodynamic index was significantly correlated with all measures of species richness except terrestrial, polychaete and “other” species richness, corroborating the results of the previous section that dissipative beaches harbour more species than reflective ones. However several other single factors such as grain size, slope, beach and saturation widths had a better correlation with species richness indicating that species may perceive the environment in a in a way not completely described by Dean’s index. The Beach State Index (BSI) performed only marginally better than Dean’s but still had lower correlations with all measures of species richness in comparison to single physical factors.

The best correlations of most measures of species richness, except terrestrial and “other” species, were with the Beach Deposit Index or BDI. The highest correlation in this study was between relative marine species richness and BDI (Fig. 18). This index increases from beaches with steep slopes and coarser sands to beaches with flat slopes and finer sands in a gradient that resembles that from reflective to dissipative beaches (see Chapter 4). In fact reflective beaches had on average a significantly lower BDI (30) than intermediate (96) and dissipative (185) ones (ANOVA $F = 31$, $DF = 2, 49$, $P \ll 0.001$). This index can not only describe the change in slope and sand particle size from reflective to dissipative beaches but also the change of both variables within reflective and intermediate beach types. Thus BDI can account for changes in species richness within beach types that are insensitive to Dean’s index.

Table 10. Correlations between physical and biological variables for the 52 beaches analysed. Values in italics indicate correlations significant different from zero ($P < 0.05$).

Parameter	BDI	BSI	Dean's	1/slope	Beach width (m)	Sand size (mm)	Water table depth (cm)	Wave height (cm)	Wave period (s)	Surf zone width (m)	Saturation width (m)	Swash length (m)	Temperature (°C)	Salinity* (‰)
Marine Species	***0.62***	***0.37***	***0.32***	***0.49***	***0.36***	***-0.49***	***-0.40***	-0.08	-0.20	0.08	***0.45***	0.24	***0.35***	0.11
Relative species richness	***0.71***	***0.50***	***0.47***	***0.65***	***0.60***	***-0.57***	***-0.52***	-0.24	0.16	***0.37***	***0.45***	***0.36***	-0.09	***0.34***
Total Species	***0.60***	***0.32***	***0.28***	***0.49***	***0.43***	***-0.48***	***-0.32***	0.01	0.02	0.23	***0.41***	0.22	0.11	0.15
Terrestrial species	0.07	-0.02	-0.01	0.08	0.21	-0.07	0.15	0.16	***0.39***	***0.29***	0.02	0.03	***-0.39***	0.09
Polychaete species	***0.35***	0.13	0.05	0.20	0.09	***-0.34***	***-0.29***	-0.19	-0.21	-0.09	0.26	0.02	0.22	0.17
Crustacean species	***0.59***	***0.37***	***0.34***	***0.54***	***0.47***	***-0.47***	***-0.38***	0.07	0.02	0.25	***0.42***	***0.29***	0.21	0.16
Mollusc Species	***0.48***	***0.35***	***0.35***	***0.36***	0.19	***-0.42***	***-0.39***	-0.11	***-0.36***	-0.02	***0.36***	0.19	***0.45***	0.02
Other Species	0.21	0.14	0.14	0.13	0.0	0.05	0.12	-0.18	***-0.35***	-0.09	0.11	0.04	*0.31*	-0.25

* n = 48

In brief, marine species richness seems to increase towards beaches with flatter slopes having wider intertidal and saturation zones, with longer and wider swashes, finer sands and shallower water tables. It also increases towards beaches with a higher water temperature, i.e. subtropical and tropical beaches.

Controlling for the influence of the total pool of species within each biogeographical region through the calculation of the relative marine species richness (beach species richness / regional species richness), improved the correlations with all factors mentioned above, indicating that latitude plays a role in determining species richness on sandy beaches. A corollary to this was the lack of correlation between the relative species richness and temperature (Table 10).

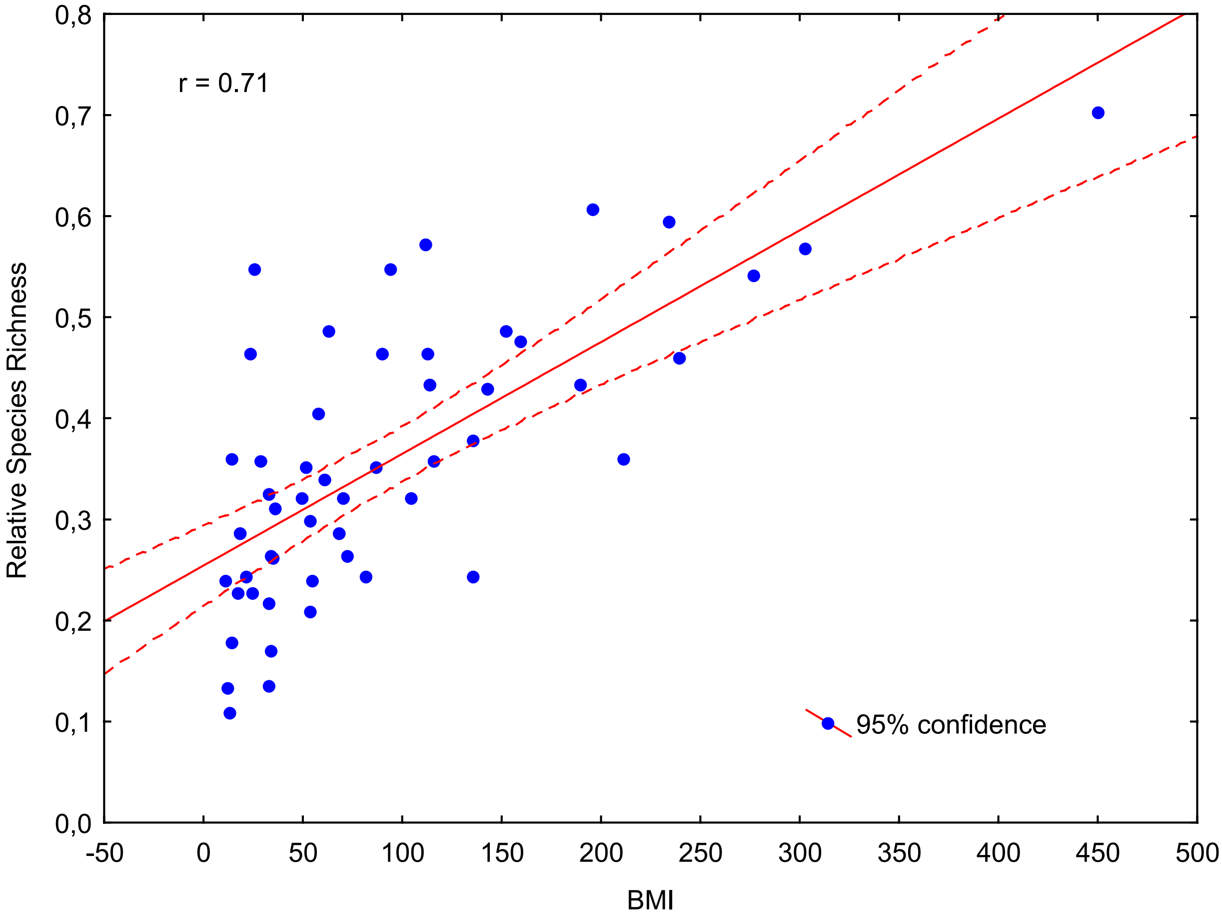

Figure 18: Regression between relative marine species richness (beach marine species richness / region species richness) and the Beach Deposit Index. RSR = 0.25431 + 0.00111 * BMI (r = 0.71, P << 0.01, n = 52)

Although total species richness (marine + terrestrial) followed a trend similar to the marine species, it will not be further considered here since it includes terrestrial species that seem to respond differently to the physical factors (Table 10). For example, contrary to marine species, terrestrial species richness was positively correlated to wave period and surf zone width and negatively related to temperature, corroborating the trend of the regional pool that shows they achieve higher diversities in temperate areas.

Polychaete richness was significantly related only to Beach Deposit Index (BDI), grain size and water table depth, increasing on beaches with flatter slopes, finer sands (higher BDI) and shallower water tables.

Crustaceans and molluscs followed the same trend as for marine species, increasing towards beaches with flatter slopes, wider intertidal and saturation zones, with longer and wider swashes, finer sands and shallower water tables. Molluscs exhibited no significant relation to beach width or swash length. Molluscs and “other” species were additionally richer on beaches with shorter wave periods. Again molluscs and “other” species were more diverse on warmer beaches, while crustaceans were not, corroborating the trend of increase towards the tropics for molluscs.

5.3.5. A test of the Beach Deposit Index

As mentioned in the previous section, the species richness data collected here fit the BDI model better than any other physical factors and morphodynamic indices. To test the generality of this result, correlations were performed with BDI and species richness for 47 beaches from the literature and these were compared with the fits achieved by the other physical factors and/or morphodynamic indices.

All correlations with species richness were significant ($P < 0.002$). BDI had the best fit ($r = 0.77$) explaining 59 % of the variance of species richness as compared with Dean’s ($r = 0.45$), slope ($r = 0.64$), grain size ($r = - 0.68$) and the beach state index ($r = 0.68$).

5.4. Discussion

5.4.1. Beach type comparison

The hypothesis that dissipative beaches harbour on average more species than reflective ones is confirmed here, not only for the total number of marine species on a beach, but also for taxonomic groups such as crustaceans and molluscs, which comprise most of the beach species. These results agree with patterns found on beaches distributed worldwide, including South Africa, USA and Chile (McLachlan, 1990; Jaramillo and Gonzalez, 1991; McLachlan et al., 1993), Uruguay (Defeo et al., 1992), Brazil (Borzone et al., 1996) and Australia (McLachlan et al., 1996a; Hacking, 1997; 1998). Also the fact that dissipative beaches in this study harboured the highest percentage of species from the total regional species pool lends support to the swash exclusion hypothesis of McLachlan et al. (1993). According to this hypothesis, the harsh swash climate of the steep coarse sand reflective beaches, with short and fast swashes, seems to exclude most of the species that can otherwise feed and move better in the longer and gentler swashes of the flatter and finer grained dissipative beaches. Indeed the total number of marine species, crustaceans and molluscs increased towards beaches with flatter slopes, wider intertidal and saturation zones, with longer and wider swashes, finer sands and shallower water tables (Table 10). The role of water table depth on macrofaunal richness has not been assessed in previous studies. A shallower water table increases the water content of the sand pores (McLachlan and Turner, 1993) facilitating both burrowing, respiration and possibly buffering temperature changes.

The community-morphodynamic coupling recorded on large spatial scales such as those studied here and by the above mentioned authors seem not to hold over temporal scales (Jaramillo et al., 1996; 2001) or at the population level (Gómez and Defeo, 1999), where factors intrinsic to the population dynamics of each species seem to take over (Defeo, 1996). For example, the correlation between species richness and beach width suggests that the amount of living space seems to limit the number of species on sandy beaches. This might imply that saturation levels in species diversity and possibly population abundance can be reached on beaches despite their highly physically dynamic environment. Physical factors may therefore not be able to keep population levels below the carrying capacity of the beach at all times and biological interactions may then increase in importance (Bruce and Soares, 1996). The differential preference of beach isopods for a certain sand size alone and in the presence of congeneric species in laboratory experiments (Defeo et al., 1997; Nel, 2000) supports the hypothesis that small-scale distributional patterns such as intertidal zonation are not only influenced by abiotic factors but also by biological interactions. Negative interactions between resident adults and its settling larvae have also being suggested (Soares et al., 1996) and demonstrated (Defeo and Alava, 1995; Schoeman and Richardson, 2002) to explain distributional patterns of adults and juvenile clams on sandy beaches. Also, female-male competition seems to be the best explanation for a counter-gradient latitudinal increase in size of males of *Emerita brasiliensis* towards tropical beaches (Defeo and Cardoso, 2002). A negative temporal correlation between abundances of the sandy beach filter feeders *Donax hanleyanus* and *Emerita brasiliensis* on the same beach has been suggested to be a result of intraguild competition (Cardoso and Veloso, 2003). Thus, the idea that beach species are controlled by few physical factors, only because they live in a simple environment, which is itself physically controlled, seems not to explain all the variations in population abundances of individual species on temporal and smaller spatial scales.

In this study, not only did the width of the saturation zone increased from reflective to dissipative beaches (see Chapter 4) but it also explained a higher percentage of marine species variance than Dean's index alone (Table 10). This gives support to the hypothesis that the predictable increase in number of species towards dissipative beaches reflects the incorporation of sublittoral species into the intertidal zone (Borzone et al., 1996). The presence or absence of sediments saturated with water imposes a physical limitation on the presence of a particular sublittoral species in the intertidal but not on the total number of species that can extend their distribution to the intertidal. If the number of species is constrained by living space, then the increase of marine species with an increase in saturation zone width supports the hypothesis of saturation levels in species diversity on beaches. Saturation levels may then be controlled by interactions between biological factors, such as competition for living space (Croker and Hatfield 1980; Grant, 1981; Defeo et al., 1997), competition for food (Bruce and Soares, 1996) or production of food (McLachlan and Romer, 1990) and abiotic forces such as morphodynamics (McLachlan, 1990; Brazeiro, 2001).

The autoecological hypothesis has been suggested as one of the leading paradigms on sandy beach ecology (McLachlan, 2001). It states that in physically controlled environments such as sandy beaches, the community structure is nothing more than the sum of the responses of each individual species to the physical environment. In this study several groups of species responded in different ways. For example, polychaete species richness did not show a significant increase towards dissipative beaches. Instead it was correlated only with variables related to the beach deposit, such as the Beach Deposit Index, grain size and water table depth. Similarly, molluscs and "other" species were the only ones exhibiting a negative correlation with wave period, suggesting higher species richness in wave fetch limited environments, such as bays and beaches fronted by coral reefs. Terrestrial species richness was not correlated with morphodynamic indices such as Dean's, BSI or BDI. They nevertheless showed an increase with wider surf zones and with longer period waves, probably reflecting a higher availability of uprooted kelps and longer periods of permanence stranded undisturbed on the drift line.

The fact that the best correlations with most measures of species richness were with the Beach Deposit Index indicates that the number of species that beaches can accommodate responds to the environment in a manner not completely described by the existent morphodynamic indices such as Dean's or the Beach State Index. At least two reflective beaches had higher species richness (temperate 16 (Appendix 5) and tropical 19 (Appendix 2) marine species) than previously found. This was due to finer sediments and a slope break on the temperate beach, or to mixing coarse and fine sediments on the tropical beach. Also, several low energy intermediate beaches had 1) either a break in slope, with a steep high tide slope comprised of coarse sands, and a flat low tide slopes comprised of fine sands, or 2) only a flat slope with fine sands. These beaches had higher species richness than predicted by correlations with Dean's or the Beach State Index.

The Beach State Index had a lower performance in this study in comparison to single physical factors because all beaches presently sampled had maximum tidal amplitudes of less than 2.1 m. The Beach Deposit Index, on the other hand, was capable of accounting for the changes in slope and sand size without the increase in wave energy or in tidal amplitude predicted by Dean's or the Beach State Index respectively. The Beach Deposit Index is not only capable of describing the change in slope and sand size from reflective to dissipative beaches, but also the change of both variables within reflective and intermediate beach types. It can additionally account for changes in slope and sand of meso- and macrotidal beaches. For example, the best correlations between BDI and species richness along a morphodynamic spectrum of increasing wave energy and tidal amplitude with the 47 beaches from the literature corroborate the present results. BDI can, therefore, account for changes in species richness within beach types that are insensitive to Dean's and it also improves the fit of increasing species richness towards macrotidal beaches. Since the Beach Deposit Index is an integrated measure of all hydrodynamic forces acting on the beach deposit, the increase in species richness from steep profiles with coarse sands to flat profiles with fine sands can thus be analysed both along wave energy and tidal gradients.

The present paradigm explaining patterns of macrofaunal diversity, abundance and biomass on sandy beaches has relied heavily on post-settlement processes influencing mainly adults (Giménez and Yanicelli, 2000; McLachlan, 2000; Brazeiro, 1999, 2001). Population ecologists seem to have been the only ones discussing the possible effect of the recruitment of larvae on the adult populations (Veloso, 1993; Santos, 1994; Donn, 1987; Defeo and Alava, 1995; Defeo, 1996, Schoeman and Richardson, 2002). Although several factors, such as nearshore hydrodynamics, the topography and substratum features (such as grain size, sorting and organic content), may affect settlement/recruitment processes, the role of these factors and processes in understanding recruitment dynamics have not yet been adequately assessed on sandy beaches (Defeo, 1996).

If the higher diversity of sandy beach organisms on a certain beach is linked to the successful settlement and recruitment of their larvae to the adult population, it seems that flat, fine sand beaches with a high BDI would offer the best settlement environment. The flatter slopes and finer sediments provide a boundary layer close the bottom with a smooth bed and laminar flow, in contrast to the turbulent flow of steep slopes with coarse sands (Elfrink and Baldock, 2002). The smooth bed creates a buffer and viscous layer above the bottom where flow velocities are almost zero, thereby favouring deposition of fine grains and also larval settlement (Hall, 1994). Larvae can be more successful in settling on flat slopes with this flow regime not only because of lower horizontal and vertical flow velocities but also because fine sediments have higher cohesion due to the greater pore dilatancy, and higher sediment binding by organic matter, microbial mucous and macrofaunal pellets (Snelgrove and Butman, 1994). This ensures the attachment of the larvae to the sediment and provides them with food. Additionally the slower, longer and thicker swash on flat slopes (McArdle and McLachlan, 1992) may increase the buffer and viscous layer, providing a greater chance to settle on the bottom.

According to Snelgrove and Butman (1994) the presence of finer sediments indicates a non-turbulent flow. Thus in reflective beaches with a steep slope but fine sands, the bottom flow environment may be more benign to settling larvae than on coarse sand beaches. Beaches with mixed sand would present mixed flow regime. This, added to the higher stability of flat slopes with fine sands in comparison to steep slopes with coarse sands (Wright and Short, 1984; Brazeiro, 2001), would maximise the survival of the recruits on beaches with high BDI values. Thus the more benign flow environment of flat sand beaches may provide, not only a better settling environment to larvae, but it might also enhance the survival of the recruits to adulthood by providing them with more time to move, burrow and feed in the longer and gentler swashes (McLachlan, 1990). This probably explains the higher species richness found in this study for crustaceans, molluscs and polychaetes on intermediate and dissipative beaches with flat slopes and finer sands.

The significant correlations between all measures of beach richness and several physical factors, including the Beach Deposit Index, suggest that species richness is controlled in a multifactorial way in two hierarchical levels: first by the successful settlement of larvae onto the beach and second by the survival of the recruits to reproductive adulthood. This hypothesis awaits further testing.

5.4.2. Latitudinal comparison

An increase in species richness from temperate towards subtropical and tropical beaches occurred in this study on both regional (biogeographical) and within-habitat levels, i.e. for each beach morphodynamic type. Remarkably, this result is also significant when clumping different beach types per region, subtropical and tropical beaches being on average richer in total number of marine species, molluscs and polychaetes. Thus the higher species diversity on tropical and subtropical beaches reflects the larger species pool available in these areas. This may indicate an evolutionary control of species richness on sandy beaches not only in a biogeographical but also on a local (habitat) scale.

Some taxa, such as crustaceans, did not show this trend on a regional or habitat scale. This seems to be explained by the differential response of members of the Crustacea to latitude, with species richness of decapods increasing (Dworschak, 2000; Macpherson, 2002), but of isopods and amphipods decreasing (Abele, 1982; Jaramillo, 1987; Vincent and Clarke, 1995) towards the tropics. Contrasting with the pattern presented by most beach species, terrestrial species richness was higher in the cold waters of temperate areas, probably associated with the distribution of their food - habitat, i.e. kelp wrack (Santelices, 1989; Soares, 1994; Mann, 2000).

High tropical diversity was also recorded for mesotidal beaches in Australia (McLachlan et al., 1996a; Hacking, 1997), Thailand (Dexter, 1996) and Oman (McLachlan et al., 1998). The trend of increasing species richness along tidal gradients (McLachlan et al., 1993) makes it difficult to compare the present results for microtidal beaches with those of mesotidal beaches studied in Australia, Thailand or Oman. In Australia the increase of species richness towards the tropics is confounded by the covariance of tide range and latitude (Hacking, 1997). Therefore, latitudinal comparisons of beaches within the same tidal range and beach morphodynamic state are warranted in Australia. The results presented here show that tropical and subtropical microtidal beaches are on average richer than their temperate counterparts, this trend occurring for reflective, intermediate and dissipative beaches. This contradicts the results of the global analyses done by Dexter (1992), who failed to detect higher diversities on tropical beaches using data from the literature. Since dissipative beaches are more common in temperate and reflective in tropical regions (Chapter 4), her results probably reflect inter-habitat rather then latitudinal differences in species richness (see also McLachlan et al., 1996a).

The pattern of increase in macrofaunal diversity towards tropical areas has also been found in other intertidal soft-bottom communities such as tidal flats (Reise, 1991) and estuaries (Atrill et al., 2001), but not for subtidal communities (Warwick and Ruswahyuni, 1987; Alongi, 1990; Kendall and Aschan, 1993; Gray, 2002). The idea that tropical benthic environments are harsher than temperate ones (Moore, 1972; Alongi, 1990; Dexter, 1992) seems to be more valid for subtidal communities, which may experience higher disturbances such as mudslides from big river outflows (Macpherson, 2002), and anaerobic conditions due to higher BOD (biological oxygen demand) in the less oxygenated subtidal deposits (Alongi, 1990).

All beach types showed a significant increase in species richness from temperate to subtropical and/ or tropical regions. These results were clearer for dissipative beaches, i.e. higher MANOVA Wilk's Lambda and lower significance levels, than for intermediate and reflective beaches. The higher homogeneity of slope and sand size on dissipative beaches among latitudes are probably responsible for these results. The sand size variation within a beach type was nevertheless detected by the Beach Deposit Index, which explained a greater percentage of the variance in species richness among beaches in comparison with Dean's, BSI or other physical factors (Table 10). Molluscs were the only taxonomic group that increased significantly towards tropical regions for all beach types, indicating the great bauplan adaptability of this group to colonize most beach habitats (Soares et al., 1998) and morphodynamic types (McLachlan et al., 1995). The higher diversity of marine species with calcareous skeletons towards warmer temperatures is related to the less costly metabolism of calcium carbonate in tropical areas (Vermeij, 1987; Clarke and Crame, 1997; Soares et al., 1998). Species richness of polychaetes and the minor group "other" increased towards the subtropics and tropics for both intermediate and dissipative beaches, a trend also found in tidal flats (Reise, 1991).

The latitudinal gradient of increasing species diversity towards tropical regions is a recurrent pattern found for many terrestrial (Rhode, 1992; Gaston, 2000) and marine taxa (Ormond et al., 1997; Roy et al., 1998; Macpherson, 2002). Explanations for this pattern abound in the literature and may involve equilibrium processes (e.g. niche partition, competition, predation, productivity), or non-equilibrium processes, e.g. intermediate disturbance, climatic stability, species-area relationship, size-ranges, effective evolutionary time and thermodynamics (Pianka, 1966; Rhode, 1992; Rhode, 1999; Allen et al., 2002).

The fact that species number increases with area and that tropical regions occupy a much larger area of the globe than temperate regions, led some authors to suggest that area is the most important factor controlling species diversity (Rosenzweig, 1995). According to this theory, a larger area with a more homogeneous climate would increase the range of the distribution of the species and its probability to be transected by physical barriers. This would increase speciation rates through vicariant processes. The colonization of a larger area would also promote a larger network of metapopulations, decreasing the probability of extinction of the species. The increase in marine species richness with beach width lends support to the possibility of reaching saturation levels at an ecological small spatial scale, but not at the biogeographic evolutionary scale required by the species-area theory. Moreover, beaches comprise 40 % of the coasts worldwide (Bird, 2000), but prevail in mid-latitude areas where sand is more abundant (Hayes, 1967; Dexter, 1992; 1996).

The increase in species richness in several marine (Roy et al., 1998) and terrestrial (Pianka, 1966) taxa with higher temperatures of the tropics could indicate an indirect relationship with productivity, i.e. species richness-energy hypothesis (Wright et al., 1993). Although marine species richness is positively correlated to temperature for the studied beaches, higher productivity on sandy beaches is a common feature of temperate high-energy beaches, where blooms of surf zone diatoms occur (McLachlan and Erasmus, 1993; Brown and McLachlan, 1990; Bate et al., 1990; McLachlan et al., 1996b). A negative correlation between species richness of coastal stomatopods, decapods and chlorophyll concentrations on the west Atlantic Ocean (Macpherson, 2002) suggests that high productivity may in fact inhibit diversity (see Rosenweig and Abramsky (1993) for an explanation to terrestrial environments). The same author noticed a decrease in fish and decapods species richness in the east Atlantic Ocean at the two West African upwelling areas. A decrease in species number in eutrophic environments is well documented (Rhode, 1992). It is therefore not clear which is the causative and which is the affected factor in the relationship between productivity and diversity.

Large scale controlled experiments such as ECOTRON have shown that richer communities exhibit higher rates of primary production and respiration (Kareiva, 1994). Rich dissipative (Brown and McLachlan, 1990) and intermediate (Cardoso and Veloso 2003) sandy beach communities seem to lend support to the hypothesis of positive feedback control between diversity and productivity - everything else being controlled, a more diverse community will have a high productivity, which will in turn support a high species diversity (diversity-trophodynamics hypothesis). However, this interaction may explain only a small within-region scale variation of diversity-productivity, and it is not intended to explain large scale geographical variations of species richness such as the latitudinal gradient, where too many factors are known to vary (Rhode, 1992).

Larger population densities have been related to wider geographical distribution in both terrestrial (Gaston and Blackburn, 2000) and beach species (Brazeiro, 1999). Also, there seems to be a gradient of increasing body size towards temperate areas, i.e. Bergman's rule, for terrestrial (Cardillo, 2002) and marine beach species (Poulin, 1995; Poulin and Hamilton, 1995; Soares et al., 1998; Fonseca et al., 2000; Defeo and Cardoso, 2002, Cardoso and Defeo 2003). Body size is correlated with fecundity for beach species (De Ruyck et al., 1991; Defeo and Gómez, 2000; Fonseca et al., 2000; Defeo and Cardoso 2002), increasing the probability of dispersal. In the studied beaches, crustaceans showed a significant increase in mean body weight (Chapter 7) and abundance (Chapter 6) from the tropics to the temperate regions. Thus it is possible that denser populations of the larger temperate beach crustaceans may have a wider geographical distribution reaching tropical areas. This seems to be true for the isopod *Excirolana braziliensis* and the mole crab *Emerita brasiliensis*, which occur from temperate to subtropical and tropical beaches (Gianuca, 1983; Defeo and Cardoso, 2002; Cardoso and Defeo in press, Chapter 6 and 7). The same pattern occurs for *Excirolana braziliensis* and the mole crab *Emerita analoga* on the coast of Chile (Jaramillo, 1982; Brazeiro, 1999, Herreras, 2001). This suggests that at least part of the increase of species richness towards tropical beaches may be explained by the inclusion in the tropics of those temperate species that have wide ranges of distribution. This lends partial support to the Rapoport's rule (Stevens, 1989), which states that temperate animals, because of their broad tolerance to the more widely fluctuating climatic conditions of mid-latitudes, have a wider latitudinal range that can be extended to the tropics, while the converse is not true. No consensus has being reached so far towards the validity of this hypothesis, with as many studies finding the patterns as not (Rhode, 1992; 1999).

The fact that the tropical beaches had on average higher species richness and lower wave energy than temperate beaches may indicate a relationship between diversity and environmental stability. The stability-time hypothesis (Sanders, 1968) states that higher diversities will be reached in more stable, less physiologically stressful and more physically benign environments. This hypothesis may explain the increase in species richness from steeper reflective to flatter dissipative beaches. However, Madagascar is not necessarily climatically stable, since its coast is impinged annually by tropical hurricanes, and the frequency of this disturbance on a certain part of the coast seems to be unpredictable (Davies, 1980) in the lifetime scale of most beach organisms, i.e. one-year scale. Despite this major unpredictable disturbance factor, Madagascar has the highest regional pool of species, along with the calm tropical coast of Bahia in northeast Brazil.

Temperature seems to be the best predictor for the increase in species richness towards the tropics (Rhode, 1992; Roy et al., 1998, Atrill et al., 2001; Macpherson, 2002). Since this variable covaries with many other factors along the latitudinal gradient such as area, measures of productivity, e.g. evapotranspiration, climatic variation etc, it is difficult to ascertain which factor, or suit of factors, is responsible for the species richness trend. The most parsimonious model may be the direct influence of higher temperatures on the metabolic kinetics of animals. A model assuming that the flux of energy through populations is temperature invariant can successfully predict the increase in species richness for terrestrial, aquatic and marine taxa along latitudinal and elevation gradients based only on the influences of temperature on the biochemical kinetics of organismal metabolism (Allen et al., 2002). Thus, higher metabolic rates in tropical beach organisms would decrease generation times and accelerate mutation rates in individuals. This would ultimately accelerate evolutionary and speciation rates, increasing species richness on tropical beaches. This greater “effective evolutionary time” (sensu Rhode, 1992; 1999) also seems to explain higher diversities on tropical estuarine flats (Atrill et al., 2001) and in pelagic, coastal and shelf communities of the Atlantic Ocean (Macpherson, 2002).

It is tempting to link this idea with the hypothesis that highly phenotypically plastic beach animals show less necessity for genetic evolutionary change than less plastic ones (Soares et al., 1999). Assuming that temperate animals may extend their distribution to tropical regions (Stevens, 1989), higher temperatures might accelerate mutation rates (Rhode, 1992, Allen et al., 2002) and break down the adapted genome of these phenotypically plastic individuals. This new genetic variation could then be worked upon by evolutionary forces, such as selection and genetic drift, contributing additionally to the increase in species richness towards tropical areas. This hypothesis warrants further theoretical scrutiny and testing.

6. Macroecological comparison of macrofaunal abundances among latitudes and beach morphodynamics

6.1. Introduction

Although the understanding of patterns of distribution and abundance of organisms is considered one of the main objectives of ecology (Krebs, 1994), the analysis of latitudinal gradients in abundance has not attracted as much attention as the patterns of biodiversity. Nevertheless, two patterns are well documented in the literature: a decrease in population densities towards the tropics and the increase in geographical ranges with higher abundances (Gaston and Blackburn, 2000). Higher species packing (Pianka, 1966) or higher patchiness (Price, 1991) has been suggested to explain reduced population abundances in tropical in comparison with temperate latitudes. Several hypotheses have been suggested to explain the relationship between animal abundance and its geographical range, such as sampling artefacts; niche breadth; geographical distribution; resource availability and vital rates (Gaston and Blackburn, 2000).

Predictable patterns of increase in total abundance of macrobenthic communities from reflective to dissipative beach types have been observed on many coasts worldwide (McLachlan, 1990; Jaramillo and Gonzalez, 1991; Defeo et al., 1992; McLachlan et al., 1993; Borzone et al., 1996, Hacking, 1997). In some cases the increase seemed to be linked not only to beach type but also to latitude for macrotidal beaches in Australia (McLachlan et al., 1996a; Hacking, 1997). No such comparison has been made involving only microtidal beaches in tropical, subtropical and temperate regions.

It has been suggested for sandy beaches that there is no difference in macrofaunal densities between tropical and temperate regions (Dexter, 1992). There is, however, some expectation that benthic populations would attain higher abundances on temperate than tropical beaches (McLachlan 1990; McLachlan et al., 1993, McLachlan, 2001). As with species diversity, no within-habitat tests, i.e. comparing beaches of the same morphodynamic type, of abundance for tropical and temperate beach communities have yet been performed.

If the knowledge of the latitudinal distribution of community abundances are scant on sandy beaches, much less is know for individual species and populations. Beach clams of the genus

Donax have been suggested to be super-adapted and therefore to represent model organisms to be used in beach comparisons (Alongi, 1990). Although *Donax* is one of the most typical beach inhabitants in tropical regions, colonizing virtually all beach types (McLachlan et al., 1995; 1996a), only 5 % of the species occur in temperate areas (Ansell, 1983). Cirolanid isopods of the genus *Excirolana*, on the other hand, not only occur from temperate (Jaramillo, 1982; De Ruyck et al., 1992) to tropical beaches (Dexter, 1976; Fonseca et al., 2000) but also can occupy all beach levels (Dexter, 1976; Jaramillo et al., 1996) and morphodynamic types (Defeo et al., 1997). Additionally, it is also the dominant organism in 35 % of the beaches in many parts of the world (Dexter, 1992). It is therefore the ideal taxon to be used in latitudinal and morphodynamic comparisons.

The objectives of this chapter are to test the following hypotheses:

1- macrofaunal density and total abundance increase from reflective to dissipative microtidal beaches on a geographical macroscale scale;

2- temperate microtidal beaches harbour higher animal abundance than tropical beaches;

3- temperate microtidal beaches support higher macrofaunal abundance than tropical beaches of the same morphodynamic type

4- abundances of isopods of the genus *Excirolana* increase towards dissipative beaches and temperate regions

Additionally, it will be tested whether physical forces associated with beach morphodynamics, such as wave height, period, grain size, etc, and oceanographic variables such as temperature and salinity, can explain the variability in abundance of the community and of taxonomic groups such as crustaceans, polychaetes and molluscs in the southern hemisphere.

6.2. Material and methods

6.2.1. Field data

(Please see Chapter 2)

6.2.2. Statistical treatment

Means of the following biological variables per beach were calculated according to beach type and latitudinal region: total macrofaunal density (individuals per square meter); total macrofaunal abundance (individuals per linear meter); abundance per taxonomic group, i.e. terrestrial (insects, arachnids and myriapods); polychaete, crustacean, mollusc as well as species grouped as "other" (i.e. nemerteans, echinoderms, sipunculids, oligochaetes, etc); and of cirolanid isopods of the genus *Excirolana*. This group was chosen since they represent the dominant species in terms of numbers of individuals on sandy beaches (Dexter, 1992) and also because they were the only genus represented in all biogeographical regions and beach types sampled in this study. In this study abundance, the total number of individuals per running meter (a 1 m wide strip of the transect), i.e. ind.m^{-1}, was estimated by integrating the area under the curve of average density per station along the transects. Dominance was calculated as the percentage of the total number of individuals of each taxonomic group in relation to the total numbers of individuals in each beach community.

In order to test the hypothesis that temperate beaches are on average richer in macrofaunal abundance than tropical ones, the five biogeographic areas sampled were grouped into tropical (Madagascar and Bahia), subtropical (Paraná) and temperate regions (south-central Chile and West Coast of South Africa). To test the hypothesis that dissipative beaches are richer than reflective ones, beaches were grouped as reflective, intermediate and dissipative. Differences between regions and beach types in the mean density and abundance values for each group were tested separately using one-way MANOVAs (Multivariate Analysis of Variance). A two-way MANOVA was not possible because reflective beaches were absent in the subtropical region, making the design incomplete to test for factor interactions (Hair et al., 1992). Also to test if community and taxonomic abundance for the same morphodynamic type differ between latitudes, one-way MANOVAs were done for each beach type, i.e. reflective, intermediate and dissipative. The Newman-Keuls *a posteriori* test of multiple means range was used to identify which group of regions and beach types differed significantly. The logarithmic (x+1) transformation was applied to the data to satisfy the MANOVA assumption of homogeneity of variances, tested by the Cochran C test (Zar, 1984).

The Pearson Product Moment correlation index was also calculated to assess the relationships between the community and taxonomic abundances and the physical factors (Dean's; Beach State Index (BSI); 1/slope; intertidal beach width; grain size; wave height; wave period; surf zone width; water temperature; water salinity; swash length; saturation zone width; water table depth and the BDI (Beach Deposit Index)). Dean's BSI and BDI were calculated using equations 1.1 (Chapter 1), 2.1 (Chapter 2) and 5.1 (Chapter 5) respectively.

6.3. Results

6.3.1. Dominance

Crustaceans dominated the fauna numerically on 75 % of the 52 beaches sampled, dominating an equal number of beaches in tropical and temperate regions (85% of each group). In subtropical beaches (10), they dominated only in 50 % of the beaches, while polychaetes dominated the other 50 %. Unexpectedly, molluscs dominated numbers only on 2 tropical beaches receiving wrack (4 % of the total), and terrestrial species expectedly dominated 2 temperate beaches (4 % of the total). Polychaetes were much less important out of the subtropics, dominating only 2 temperate beaches (4 % of the total), and no tropical beaches. The most widespread taxon was cirolanid isopods of the genus *Excirolana*, which occurred on 96 % of all sampled beaches, being dominant on 25 % of the beaches, mostly in the tropics and subtropics. Here, they contributed on average with 45 % of the total community abundance. Talitrid amphipods of at least three genera dominated on 29 % of the beaches (6 tropical and 7 temperate). Other groups which were numerically dominant on some beaches were: spionid polychaetes of the genus Scolelepis*,* dominating on 7 beaches (4 subtropical, 2 subtropical, 1 temperate); hippid suspension-feeders such as *Emerita analoga*, dominating 3 temperate beaches; and cirolanid isopods of the genus *Eurydice*, dominating 3 temperate beaches in South Africa. Donacid molluscs, despite having the status of being the most typical beach organism, dominated on only 2 beaches (1 tropical, 1 temperate) despite their wide distribution. They did not occur in Chile, where their niche was filled by *Emerita analoga* in the intertidal and by the bivalve *Mesodesma donacium* in the subtidal.

6.3.2. Beach type comparisons

Grouping the 52 beaches of all latitudes into reflective, intermediate, and dissipative rendered significant differences in macrofaunal density and abundance between beach types. The Wilk's lambda value was high and the MANOVA significant (Table 11), with only 3 variables not differing significantly among beach types.

Thus, total macrofaunal density and abundance, and abundance of crustaceans, molluscs and Excirolana increased significantly from reflective to dissipative beaches (Table 11 and Fig. 19). On the other hand, abundances of polychaete, terrestrial and "other" species were not significantly different among beach types, due to high intra-beach type variance, possibly caused by latitudinal differences. They nevertheless showed a trend to increase towards dissipative beaches (Fig. 19).

6.3.3. Latitudinal comparisons

6.3.3.1. General trends

Grouping the 52 beaches of all morphodynamic types into temperate, subtropical and tropical beaches yielded significant differences in macrofaunal density and abundance among latitudes. The variables tested could perfectly discriminate beaches in different latitudinal groups, yielding a highly significant MANOVA model ($P < < 0.0001$), with a high Wilk's lambda and Rao's R (Table 12). Only abundance of "other" species did not differ significantly between latitudes.

Total macrofaunal density was on average significantly higher on temperate beaches than on tropical and subtropical beaches. Total macrofaunal abundance was also higher on temperate and subtropical than on tropical beaches (Table 12, Fig. 20). The response of individual faunal groups did not follow the same trend. While crustaceans and *Excirolana* abundances

Table 11: MANOVA comparison of macrofaunal density and abundance on 52 beaches among beach types disregarding beach morphodynamic types.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test			
0.24	5.40	16	84	0.0				
Dependent variable Log (x + 1)	Mean square effect	Mean square error	F (DF 2, 49)	P-level	Reflective (R)	Intermediate (I)	Dissipative (D)	Interpretation
Total Density (ind.m^{-2})	1.77	0.21	8.21	0.0008	1.90	2.20	2.62	R=I<D
Total Abundance (ind.m^{-1})	5.00	0.28	17.91	<0.001	3.30	3.93	4.50	R<I<D
Crustaceans (ind.m^{-1})	6.13	0.32	19.00	<0.001	3.00	3.72	4.32	R<I<D
Molluscs(ind.m^{-1})	8.12	1.07	7.58	0.001	0.91	1.87	2.38	R<I=D
Polychaetes (ind.m^{-1})	1.57	1.22	1.29	0.28^{NS}	2.17	2.56	2.82	-
Excirolana (ind.m^{-1})	7.77	0.84	9.20	<0.001	1.94	3.01	3.20	R=I<D
Terrestrial species (ind.m^{-1})	1.05	1.01	1.03	0.36^{NS}	1.72	1.73	2.22	-
"other" species (ind.m^{-1})	0.66	1.16	0.57	0.57^{NS}	0.76	1.04	1.16	-

< or > ($P < 0.05$); = ($P > 0.05$); NS ($P > 0.05$); - not tested.

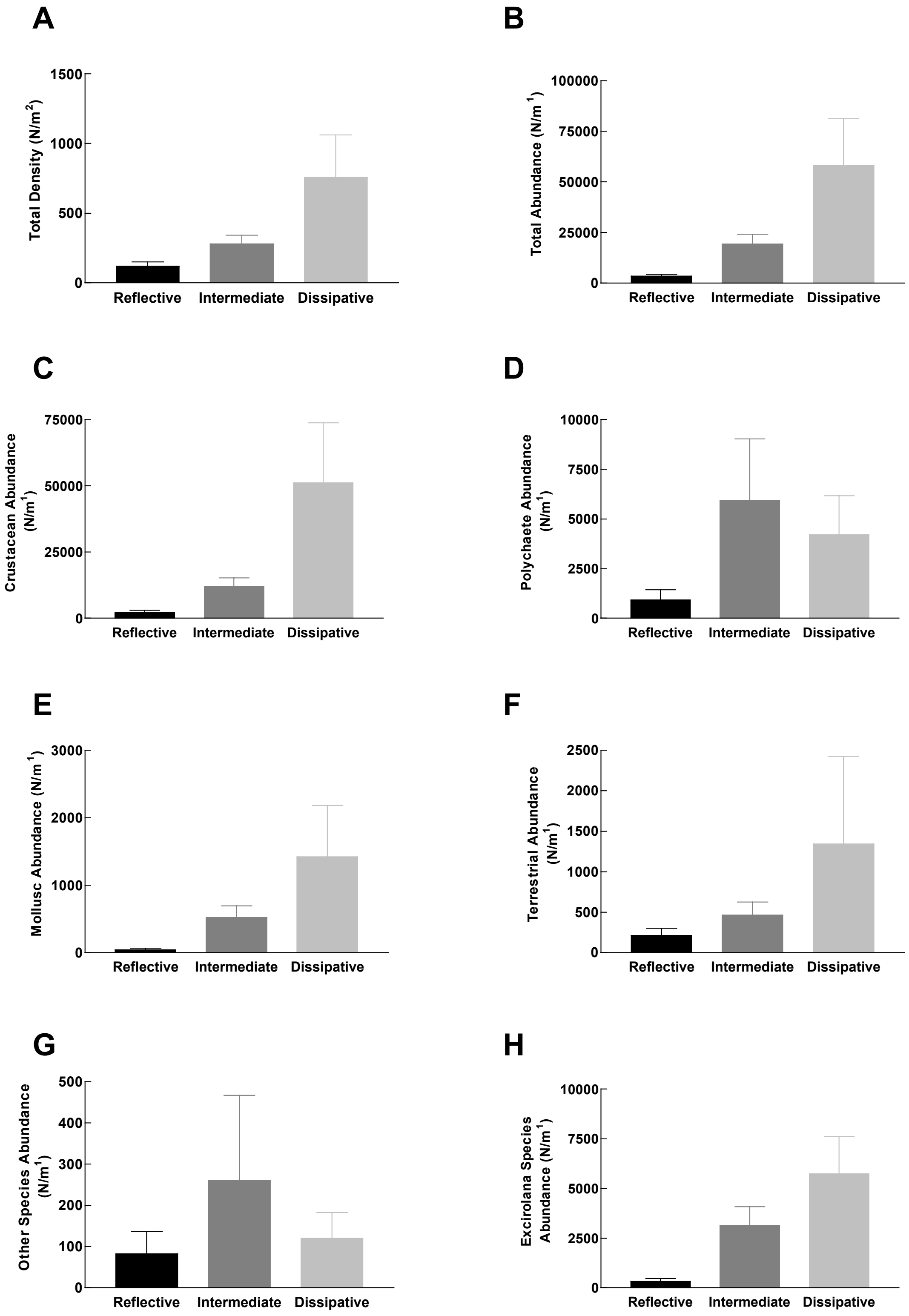

Figure 19: Total macrofaunal density and abundance of the community and taxa groups among beach types disregarding latitudes. Reflective (n = 17), Intermediate (n = 24), Dissipative (n = 11)

Table 12: MANOVA comparison of macrofaunal density and abundance on 52 beaches among temperate, subtropical and tropical regions disregarding beach morphodynamic types.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test			
0.22	5.91	16	84	0.0				
Dependent variable Log (x + 1)	Mean square effect	Mean square error	F (DF 2, 49)	P-level	Temperate (Temp)	Subtropical (Sub)	Tropical (Trop)	Interpretation
Total Density (ind.m^{-2})	1.77	0.21	8.24	<0.001	2.49	2.14	1.91	Temp>Sub=Trop
Total Abundance (ind.m^{-1})	4.26	0.31	13.72	<0.001	4.27	3.94	3.37	Temp=Sub>Trop
Crustaceans (ind.m^{-1})	5.54	0.35	16.05	<0.001	4.13	3.56	3.11	Temp>Sub>Trop
Molluscs (ind.m^{-1})	7.10	1.11	6.37	0.003	1.19	2.65	1.66	Temp<Sub>Trop
Polychaetes (ind.m^{-1})	6.20	1.03	6.02	0.005	2.01	3.57	2.55	Temp<Sub>Trop
Excirolana (ind.m^{-1})	9.58	0.77	12.44	<0.001	3.17	3.31	1.99	Temp=Sub>Trop
Terrestrial species (ind.m^{-1})	8.08	0.73	11.14	<0.001	2.51	1.35	1.38	Temp>Sub=Trop
"other" species (ind.m^{-1})	0.11	1.18	0.09	0.91^{NS}	1.05	1.05	0.91	-

< or > ($P < 0.05$); = ($P > 0.05$); NS ($P > 0.05$); - not tested.

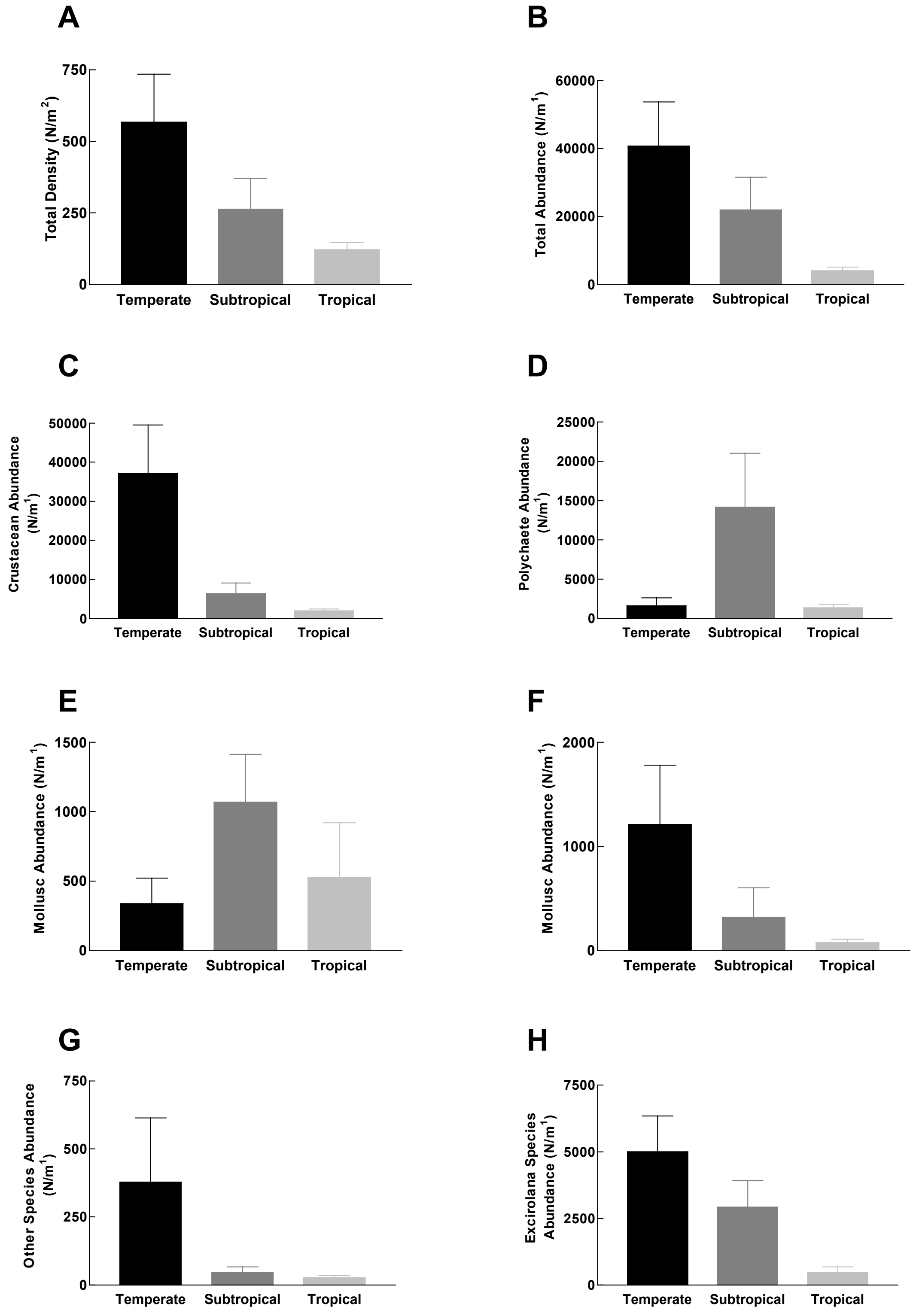

Figure 20: Total macrofaunal density and abundance of the community and taxa groups among latitudes disregarding beach types. Temperate (n = 21), Subtropical (n = 10), Tropical (n = 21)

were greater on temperate than tropical beaches, polychaetes and molluscs had greater abundances on subtropical beaches (Table 12, Fig. 20). Terrestrial species had greater abundances on temperate beaches, probably reflecting their association with kelp wrack (Table 12, Fig. 20).

6.3.3.2. Reflective beaches

Since no reflective beach was sampled in the subtropics, the latitudinal comparison is restricted to temperate and tropical regions. The analysis with all eight measures of faunal density and abundances yielded a MANOVA model with low discrimination between groups (Rao's 3.80, $P < 0.04$), since 6 of these variables did not differ significantly among latitudes, i.e. total macrofaunal density and abundance, crustacean, polychaete, *Excirolana*, and "other" species abundances ($P > 0.05$). The model with the two significant variables, i.e. mollusc and terrestrial abundances, improved the discrimination between tropical and temperate reflective beaches, with a higher Rao's R value ($P < 0.013$, Table 13). Thus molluscs were more abundant on tropical reflective beaches, while terrestrial species were more abundant on temperate reflective beaches (Table 13, Fig. 21).

Table 13: MANOVA comparison of macrofaunal abundance of 17 reflective beaches between temperate and tropical regions.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test		
0.54	5.95	2	14	0.013			
Dependent variable Log (x + 1)	Mean square effect	Mean square error	F (DF 2, 49)	P-level	Temperate		Tropical
Molluscs (ind.m^{-1})	4.00	0.50	7.50	0.015	0.19	<	1.21
Terrestrial species (ind.m^{-1})	3.13	0.50	6.20	0.025	2.39	>	1.44

< or > ($P < 0.05$).

6.3.3.3. Intermediate beaches

Intermediate beaches were the predominant beach type in all latitudes. The analysis with all abundance measures did not produce a significant model ($P = 0.07$) due to three variables that did not differ significantly among latitudes, i.e. polychaete, mollusc and "other" species. The

MANOVA analysis with the remaining five variables yielded a very significant model with high discrimination between latitudes (P < 0.02, Table 14).

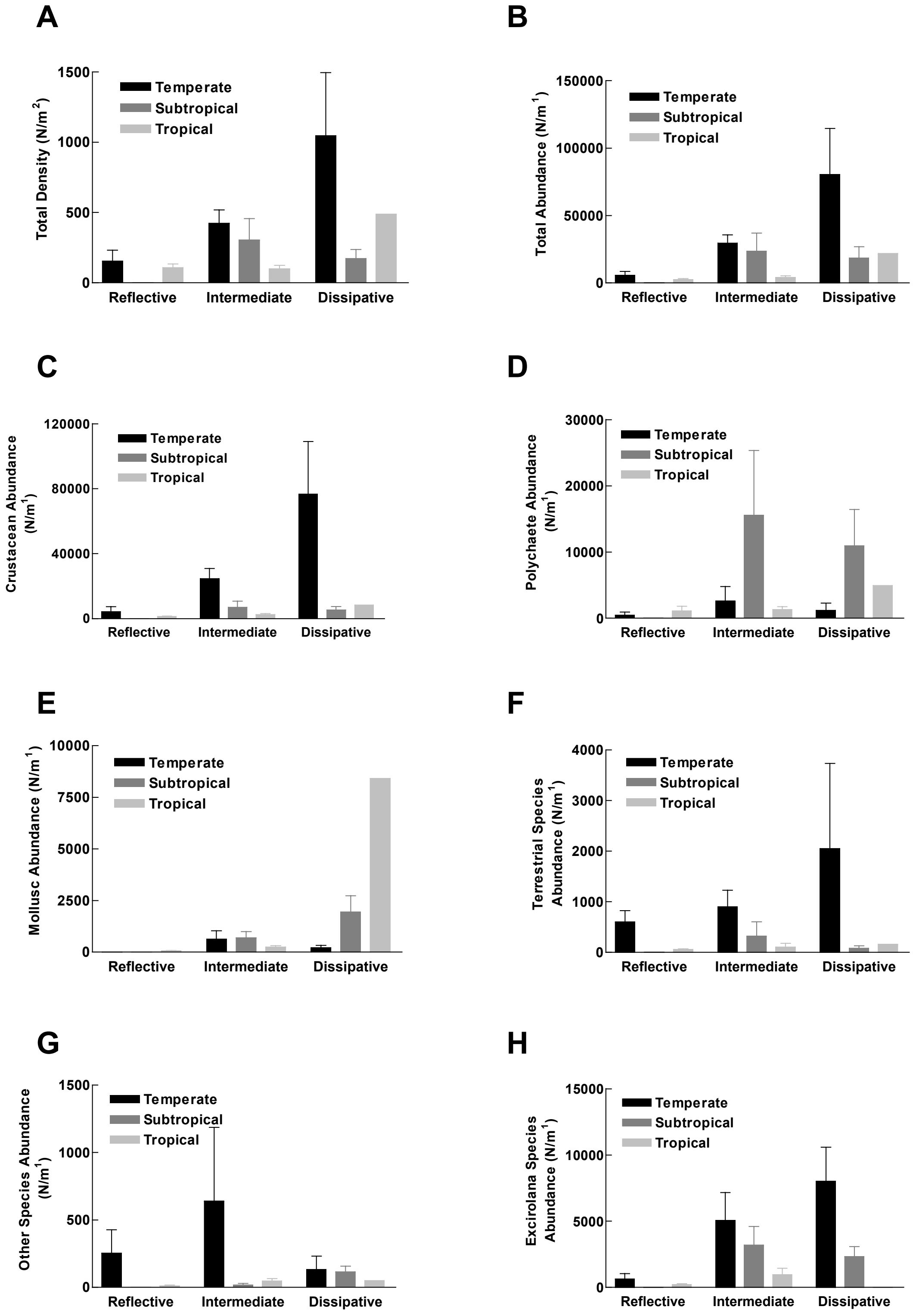

Figure 21: Total macrofaunal density and abundance of the community and taxa groups among latitudes per beach type.

Table 14: MANOVA comparison of macrofaunal density and abundance on 24 intermediate beaches between temperate, subtropical and tropical regions.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test			
0.31	2.67	10	34	0.016				
Dependent variable Log (x + 1)	Mean square effect	Mean square error	F (DF 2, 49)	P-level	Temperate (Temp)	Subtropical (Sub)	Tropical (Trop)	Interpretation
Total Density (ind.m^{-2})	0.74	0.18	4.19	0.03	2.50	2.15	1.91	Temp>Trop
Total Abundance (ind.m^{-1})	1.42	0.23	6.31	0.007	4.34	3.88	3.53	Temp>Trop
Crustaceans (ind.m^{-1})	1.85	0.18	10.12	0.0008	4.21	3.53	3.32	Temp>Sub=Trop
Excirolana (ind.m^{-1})	2.52	0.47	5.39	0.013	3.43	3.31	2.41	Temp=Sub>Trop
Terrestrial species (ind.m^{-1})	4.39	0.94	4.68	0.02	2.51	1.36	1.18	Temp>Sub=Trop

> (P < 0.05); = (P > 0.05).

Thus temperate intermediate beaches had on average significantly greater total macrofaunal densities and abundances, and also higher crustacean, Excirolana and terrestrial species abundances than beaches in subtropics or tropics (Table 14, Fig 21).

6.3.3.4. Dissipative beaches

Due to the virtual absence of dissipative beaches in the tropics (Madagascar had one), the latitudinal comparisons were made between subtropical and temperate regions. A MANOVA with all measures of species richness was not significant ($P = 0.38$). Dropping the three variables that did not differ between regions, i.e. total macrofaunal abundance, terrestrial species and "other" species abundances, yielded a significant model ($P < 0.014$) with a Wilk's lambda close to 0.1 and with a very good discrimination between temperate and subtropical dissipative beaches (Table 15).

The trends were not uniform for all tested variables. Subtropical dissipative beaches had higher polychaete and mollusc abundances, while temperate dissipative beaches had higher total macrofaunal densities and crustacean abundances (Table 15, Fig. 21).

Table 15: MANOVA comparison of macrofaunal density and abundance on 10 dissipative beaches between temperate and subtropical regions.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test		
0.11	9.88	4	5	0.014			
Dependent variable Log (x + 1)	Mean square effect	Mean square error	F (DF 1, 8)	P-level	Temperate		Tropical
Total Density (ind.m^{-2})	1.05	0.19	5.51	0.047	2.83	>	2.12
Crustaceans (ind.m^{-1})	2.26	0.19	12.00	0.008	4.68	>	3.64
Molluscs (ind.m^{-1})	3.52	0.38	9.18	0.016	1.84	<	3.13
Polychaetes (in ind.m^{-1})	4.38	0.57	7.71	0.024	2.30	<	3.75

< or > ($P < 0.05$).

6.3.4. Relationship between physical factors, and macrofaunal density and abundance

A summary of the correlations between all physical factors and macrofaunal densities and abundances is given in Table 16.

All density and abundance measures showed significant correlations with several, if not all, physical factors. New factors not included before in sandy beach analyses were the water table depth, the width of the intertidal, saturation and surf zones and the Beach Deposit Index (BDI).

Dean’s morphodynamic index had significant and positive correlations with all measures except terrestrial and polychaete abundances. Thus dissipative beaches had higher macrofaunal densities and abundances than reflective ones in all latitudes. The Beach State Index (BSI) performed only marginally better than Dean’s index. However, single physical factors hold better correlations with density or abundance than Dean’s or BSI. Generally, hydrodynamic factors linked to productivity, such as wave height, period and surf zone width had the highest correlations. Thus, total macrofaunal density, abundance, crustacean, *Excirolana* and terrestrial species abundances increased with increasing wave heights, periods and surf zone widths. Polychaete, mollusc and “other” species abundances were not correlated with these factors and instead seem to better correlated with factors associated with the beach deposit. Therefore factors, such as grain size, slope and water table depth, were all significantly correlated with abundances of all marine groups but not with terrestrial and “other” species. Beach width was also correlated with all abundance measures except the abundance of polychaetes and molluscs. Factors related to the swash, such as the swash length, or to the interaction between swash and beach deposit, such as saturation width, were also important in explaining abundance variations for most marine groups.

The Beach Deposit Index, or its log transformation, had high or the highest correlations with all marine species abundance measures. The best correlations of polychaete and mollusc abundance were with BDI, suggesting a possible link between this factor and efficiency of larval settlement of these taxa on flat beaches with fine sands. The highest correlation in this study (r = 0.75) was between total macrofaunal abundance and BDI (Fig. 22). This index increases from beaches with steep slopes and coarser sands to beaches with flat slopes and finer sands (see Chapter 5). BDI complements Dean’s index and accounts for the explanation of higher percentages of variation in abundance for most groups and especially for polychaetes.

Table 16. Correlations between physical factors and density-abundance variables for the 52 beaches. Values in italics indicate correlations significantly different from zero (P < 0.05).

Parameter Log (x+1)	BDI	Log BDI	BSI	Dean's	Slope	Beach width (m)	Sand size (mm)	Water table depth (cm)	Wave height (cm)	Wave period (s)	Surf zone width (m)	Saturation width (m)	Swash length (m)	Temperature (°C)	Salinity* (‰)
Total density (ind.m^{-2})	***0.44***	***0.57***	***0.45***	***0.47***	***0.53***	***0.43***	***-0.52***	***-0.34***	***0.50***	***0.46***	***0.61***	0.06	***0.28***	***-0.47***	0.23
Total abundance (ind.m^{-1})	***0.61***	***0.75***	***0.63***	***0.61***	***0.71***	***0.69***	***-0.62***	***-0.44***	***0.59***	***0.55***	***0.68***	***0.31***	***0.49***	***-0.57***	***0.38***
Crustacean species (ind.m^{-1})	***0.50***	***0.67***	***0.63***	***0.60***	***0.63***	***0.68***	***-0.54***	***-0.32***	***0.69***	***0.65***	***0.73***	***029***	***0.54***	***-0.60***	***0.36***
Polychaete species (ind.m^{-1})	***0.50***	***0.41***	0.27	0.25	***0.37***	0.17	***-0.44***	***-0.38***	-0.11	-0.21	0.01	0.26	0.07	0.27	0.09
Mollusc Species (ind.m^{-1})	***0.52***	***0.48***	***0.50***	*0.45*	***0.45***	0.25	*-0.49*	***-0.37***	0.05	-0.18	0.07	***0.34***	***0.32***	0.24	0.05
Terrestrial species (ind.m^{-1})	0.26	0.25	0.13	0.18	0.27	***0.40***	-0.16	-0.07	***0.29***	***0.47***	***0.43***	0.16	0.17	***-0.54***	0.22
"other" species (ind.m^{-1})	***0.32***	0.24	0.26	***0.28***	0.27	***0.33***	-0.12	-0.27	-0.01	*-0.08*	0.07	***0.40***	***0.39***	-0.05	0.02
Excilorana (ind.m^{-1})	***0.32***	***0.46***	***0.44***	***0.31***	***0.42***	***0.58***	***-0.43***	-0.24	***0.48***	***0.45***	***0.43***	0.23	0.26	***-0.47***	***0.37***

*n = 48

Abundances of all taxonomic groups, except polychaetes, molluscs and "other" species, increased significantly with decreasing water temperatures, i.e. towards temperate beaches (Table 16). Total macrofaunal abundance was the only variable that correlated with all 14 physical factors, including salinity. Salinity was also correlated with crustacean and *Excirolana* abundances.

In summary, total community density and abundance, and crustacean and *Excirolana* abundances increased towards beaches with flatter slopes, wider intertidal and saturation zones, with longer and wider swashes, finer sands and shallower water tables. Polychaetes and molluscs increased in abundance towards beaches with flat slopes, smaller grain sizes, and shallower water tables. "Other" species increased in abundance towards less reflective beaches with a greater swash length, beach and saturation width, and higher BDI.

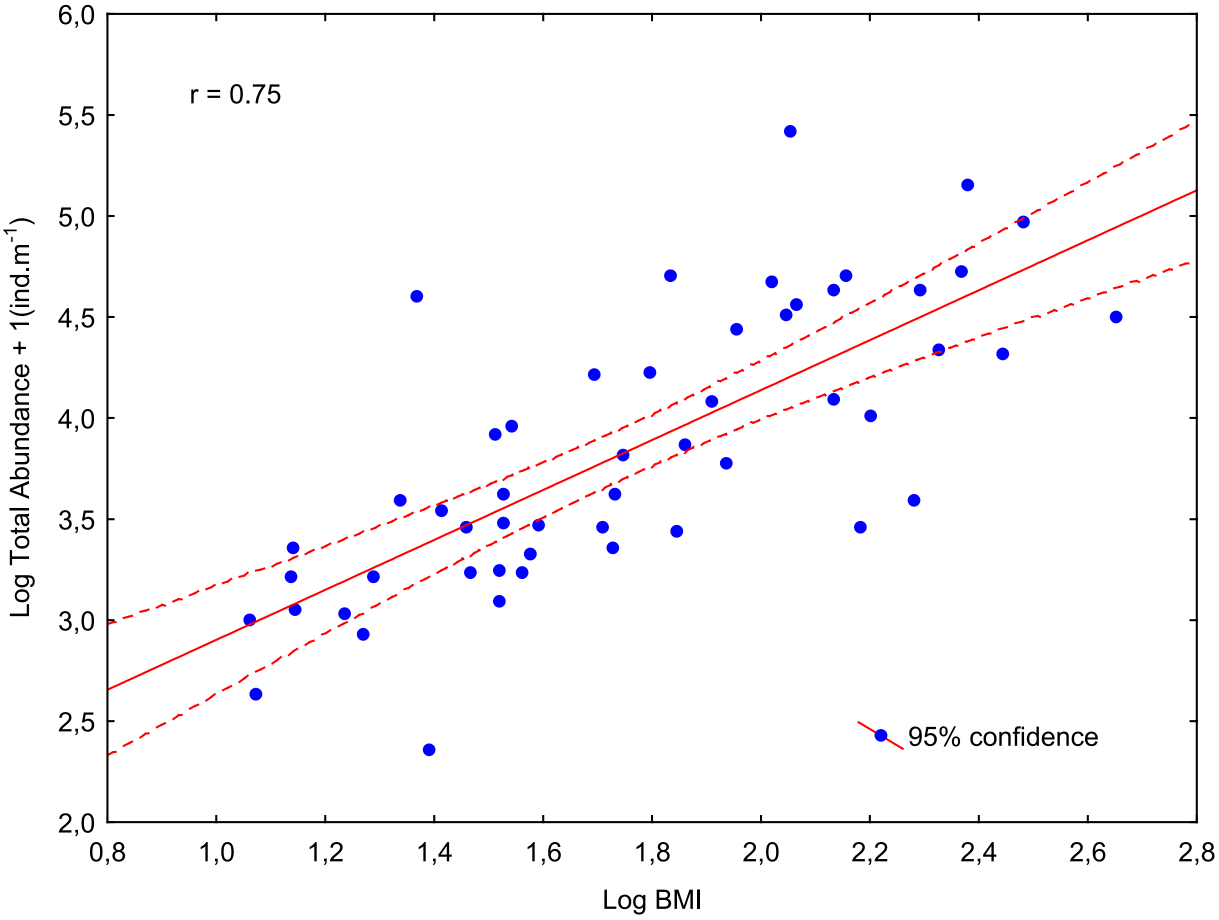

Figure 22: Regression between total macrofaunal abundance and the Beach Deposit Index for 52 beaches. Log (N + 1) = 1.6667 + 1.2359 * Log BMI (r = 0.75, P << 0.01, n = 52).

6.4. Discussion

6.4.1. Beach type comparison

The results of the present study confirm the hypothesis that dissipative beaches support denser and more abundant macrobenthic communities than reflective beaches, with higher abundances of crustaceans and isopods of the genus *Excirolana* and as well as terrestrial species. This pattern is therefore valid in a geographical macroscale comparison between temperate, subtropical and tropical regions. Although trends of increasing total macrofaunal abundances towards dissipative beaches seem to be a predictable pattern on several microtidal coasts worldwide (McLachlan, 1990; Jaramillo and Gonzalez, 1990; Defeo et al., 1992; McLachlan et al., 1993; Borzone et al., 1996), both swash control and swash exclusion hypotheses attempt to explain mainly species richness patterns (see McLachlan 1990 and McLachlan et al., 1993). At least two non-exclusive mechanisms can be at work: 1) higher abundances might be the result of higher productivity of dissipative beaches (Brown and McLachlan, 1990), thereby increasing the carrying capacity of the beach and/or 2) the less turbulent water flow on flat beaches with finer sand sizes promoting greater settlement rates and survival of juveniles into adulthood and better feeding conditions (Chapter 5). The highest correlations of total macrofaunal, crustacean and *Excirolana* abundances with surf zone characteristics (wave height, period and surf zone width) and with the properties of the beach deposit (BDI, slope and grain size) lend support to these hypotheses. On higher energy dissipative beaches both surf zone variables and beach deposit properties are interconnected, probably interacting synergistically to increase macrofaunal abundances. However, on low energy intermediate micro and macrotidal beaches (see Hacking, 1997), where surf zone productivity is apparently low, the increase in macrofaunal abundance could be better explained by higher larval settlement success and survivorship. These environments have a wider saturation zone decreasing desiccation related stresses and therefore developing more diverse and abundant communities (Chapter 5, McLachlan et al., 1996a; 1998; Dexter, 1996; Hacking, 1997).

Polychaete and mollusc abundances did not differ significantly between beach types, but showed a trend of increase towards dissipative beach types (Fig. 19). This probably reflects the high intra-beach type variance due to latitudinal differences. Higher correlations of polychaete and mollusc abundances with BDI rather than with Dean’s parameter or wave height suggests that their larval settlement may be more successful on low energy beaches with fine sands. Abundances of terrestrial species seem not to be related to beach types but rather to wider surf zones and the availability of uprooted kelp brought by bigger waves with longer periods.

Faunal responses to morphodynamics seem not to be uniform at the population level, with some studies finding the same patterns as for community abundances (Jaramillo and McLachlan, 1993, Defeo and Cardoso, 2002) while others fail to do so (Jaramillo et al., 1996; 2001). Over temporal scales, factors related to demographic processes, such as stock-recruitment relationships and other density-dependent factors (Defeo and Alava, 1995; Schoeman and Richardson, 2002), and settlement dynamics (Defeo, 1996) seem to blur the effects of morphodynamics on the dynamics of resident populations.

Beach studies investigating the spatial patterns of abundance distribution for individual species have invoked different factors according to the scale analysed. Studies over larger spatial scales invoked oceanographic influences (Donn, 1987), intensity of physical disturbances (Soares et al., 1996), or morphodynamic influences (Donn et al., 1986, Santos, 1991; Giménez and Yannicelli, 2000), whereas studies over small spatial scales invoked biological interactions (Croker and Hatfield, 1980; Bruce and Soares, 1996; Defeo et al., 1997; Nel, 2001).

It is clear that the identification of ecological patterns and responsible mechanisms is associated with the scale at which the ecological problem is tackled (Wiens et al., 1986; Wiens, 1989; Gaston and Blackburn, 2000). It is therefore necessary to disentangle the relationship between scale and mechanism on sandy beaches. Morphodynamics and other density-independent factors, such as disturbances, seem to work at the community level and larger spatial scales, i.e. alongshore distribution, inter beach types and biogeographical comparisons. By contrast, demographic factors and other density-dependent factors, such as competition and predation, seem to be more important at temporal scales in the order of magnitude of species life cycles and at small spatial scales, such as vertical distribution in the sand column and horizontal distribution along the tidal gradient (zonation).

The fact that several physical factors related to surf zone (and possibly productivity), swash processes and beach deposit characteristics hold higher correlations with total macrofaunal and taxonomic abundances than Dean's parameter indicates the multifactorial control of this community attribute. However, not all taxonomic groups responded to the same suit of physical factors, or at the same magnitude, i.e. similar correlations, as the abundance for the whole community, i.e. total macrofaunal abundance. Thus the hypothesised multifactorial nature of the responses of sandy beach macrofauna to the physical environment at larger spatial scales, observed in this study, and to the biological environment at temporal or smaller spatial scales, observed in the literature, indicates that sandy beach community structure is an emergent property and not simply the sum of each individual species responses to the physical environment as proposed by the autoecological hypothesis (McLachlan, 2001).

6.4.2. Latitudinal comparison

The hypothesis that temperate beaches had higher total macrofaunal densities and abundances in comparison with tropical beaches was confirmed in this study, even when possible differences in beach morphodynamics were not taken into account. This trend was not uniform for all taxonomic groups, with crustaceans, cirolanid of the genus *Excirolana* and terrestrial species following the same pattern as the community, while polychaetes and molluscs were more abundant on subtropical beaches. The latitudinal comparison controlling for beach type yielded the same results as the general trends analysis disregarding beach type differences. The only difference was that molluscs and polychaetes increased in abundance towards tropical and/or subtropical beaches.

The pattern of increasing macrofaunal abundances in soft-sediment communities towards temperate regions has been observed for tidal flats (Reise, 1991), and also for abyssal plains (Thurston et al., 1998). For sandy beaches, however, no differences between latitudes have been recorded in a literature review (Dexter, 1992), most probably reflecting the widely varying errors associated with the different sampling methods used by the different authors.

The only studies that compared macrofaunal communities along latitudinal gradients with the same sampling methods were done in Australia (McLachlan et al., 1996a; Hacking, 1997). They concluded that macrotidal tropical beaches had higher abundances than temperate microtidal beaches. Since tide range covaries with latitude, the greater abundances could have been the result of inter-habitat (meso- microtidal) rather latitudinal differences.

In the present study reflective, intermediate and dissipative temperate beaches had higher total densities and/or abundances than their subtropical and tropical counterparts. Thus, the latitudinal trends are valid at both regional and habitat level. These trends were, however, not uniform when looking at the taxonomic level. Terrestrial species were more abundant on reflective and intermediate temperate beaches than on their tropical/subtropical counterparts. Crustaceans were more abundant on temperate intermediate and dissipative beaches than tropical/subtropical beaches. Isopods of the genus *Excirolana* were also more abundant on temperate than tropical intermediate beaches. Molluscs and polychaetes were the only group that had the reverse pattern. Molluscs had higher abundances on tropical reflective and subtropical dissipative beaches than on their temperate counterparts. Likewise, polychaetes were more abundant in subtropical than temperate dissipative beaches.

Higher productivity in temperate areas has been suggested to explain higher abundances of macrobenthos in abyssal plains (Thurston et al., 1998) and sandy beaches (McLachlan et al., 1993). Although the cold temperate areas presently studied had very high productivity levels (Bally, 1986; McLachlan et al., 1993, Soares et al., 1997) productivity alone cannot explain why the abundances of molluscs and polychaetes were higher on tropical and subtropical beaches.

Assuming that species achieve higher abundances in the climatic regions where they first evolved, and to which they are consequently better adapted, one would expect a positive correlation between number of species and abundances in any taxonomic group. The fact that both molluscs and polychaetes had a parallel increase in species richness at regional and habitat levels (Chapter 5) and abundances towards tropical and subtropical beaches, and also that beach molluscs of the genus *Donax* are more diverse in tropical areas (Ansell, 1983, Chapter 5), supports this idea. In general, molluscs have higher diversities in tropical regions due to a less costly calcium carbonate metabolism (Vermeij, 1987). Temperate species in this study, such as *Donax serra* along the West Coast of South Africa and *Mesodesma donacium* in Chile, have their highest abundances in the sublittoral (Jaramillo et al., 1994, Soares et al., 1996), with only juveniles appearing in the intertidal. Also, Chile and the West Coast of

South Africa had very few polychaete species in the intertidal. In fact in this study polychaetes dominated mostly in the subtropical beaches (50%), being dominant in temperate regions only on two low energy beaches. Polychaetes are generally very abundant in low energy environments such as tidal flats (Reise, 1991), macrotidal tropical beaches (Dexter, 1996, McLachlan et al., 1996a) and protected beaches (Dexter, 1992). The highest correlations of polychaete abundance with the BDI in the present study suggest that the flow environment in the benthic boundary layer (Chapter 5) possibly controls adult abundance through the rates of larval settlement and successful recruitment.

It has been suggested that populations in tropical regions would be sparser and with narrower niches due to tighter species packing per unit of area/energy (Pianka, 1966, Gaston and Blackburn, 2000). This seems to be the case for terrestrial environments (Johnson, 1998; Gaston and Blackburn, 2000). The higher diversities associated with lower abundances in tropical tidal flats (Reise, 1991) and in the sandy beaches studied here lend support to this hypothesis.

Other patterns related to density or population sizes have been the geographic range-abundance relationship (Johnson, 1998). It states that larger population densities will promote a wider geographical distribution due to a larger energy consumption requirement (Gaston and Blackburn, 2000). This pattern seems to be widespread in a variety of taxa, regions and spatial scales in terrestrial (Gaston and Blackburn, 2002) and marine environments (Brazeiro, 1999). In this study, *Excirolana* dominated in numbers in 25 % of the beaches, with one of the highest mean abundances recorded at the geographical macroscale (i.e. 2979 ind.m^{-1}). This genus was the most ubiquitous, occurring on 96 % of the 52 beaches studied, in all latitudes and beach types. It achieved its highest abundances (i.e. 20842 ind.m^{-1}) on those temperate beaches that were associated with the largest mean body sizes of this genus (Chapter 7). In Chapter 5 it was suggested that higher abundances associated with larger body sizes and therefore higher fecundity could explain the wider distribution of temperate taxa in tropical regions. The results for the widely distributed Excirolana lend support to this hypothesis, as do trends reported for many other beach crustaceans, such as *Excirolana braziliensis*, and the mole crabs *Emerita brasiliensis*, and *Emerita analoga*, all occurring from temperate to subtropical and tropical beaches (Jaramillo, 1982; Gianuca, 1983; Brazeiro, 1999; Contreras; 2001; Defeo and Cardoso, 2002).

In conclusion, latitudinal patterns of beach macrofaunal abundances seem to be the result of factors working at two hierarchical levels: 1) at the evolutionary level, where higher abundances are achieved in regions where the species first evolved and is therefore better adapted and 2) at an ecological level, where productivity rates are higher (total community, crustaceans and terrestrial abundances), or where the settlement environment is more benign (molluscs and polychaetes).

7. Latitudinal and morphodynamic patterns of macrobenthic biomass and body size on sandy beaches in the southern hemisphere

7.1. Introduction

Biomass is one of the most important properties of communities and populations. Biomass is added and taken from populations through demographic processes of birth and death, immigration and emigration. This, in addition to biotic interactions such as predation and parasitism (Mouritsen and Poulin, 2002), regulates the flows of energy and materials through ecosystems (Mann, 2000).

Since there is a direct relationship between biomass and productivity in many taxa in the sea (Tumbiolo and Downing, 1994) it is possible to infer, from their biomass, the importance of populations or communities in the energy flow of the ecosystem.

Coastal ecosystems are among the most productive in the sea (Mann, 2000). Notwithstanding, latitudinal patterns of biomass distribution are not well known for such systems. Only a few trends have been observed, with biomass increasing towards temperate regions for rocky shores and soft-bottom communities (Ricciardi and Bourget, 1998).

Patterns of increasing community biomass across beach morphodynamic types have been recognised worldwide and have been attributed to surf process (McLachlan, 1990; Jaramillo and Gonzalez, 1991; Defeo et al., 1992; McLachlan et al., 1993; Hacking, 1997). However, latitudinal comparisons are almost non-existent. The only comparison was done on the east Australian coast where tidal range covaries with latitude (McLachlan et al., 1996a; Hacking, 1997). Comparisons among microtidal beaches controlling for beach type differences in the tropics and temperate regions are non-existent.

Body size is another important ecological variable that has been extensively studied for terrestrial (Gaston and Blackburn, 2000) and marine systems (Marquet et al., 1990). Several patterns have been observed with body size (Gaston and Blackburn, 2000), the most important being the trend of increase towards higher latitudes for many endo- and ectotherm taxa (Atkinson, and Sibly, 1997). On sandy beaches, body size variations in different beach types (McLachlan et al., 1995) or beach habitats (Soares et al., 1998) have been suggested to be adaptive. Furthermore, latitudinal variations in body size have also been observed for sandy beach populations (Fonseca et al., 2000; Defeo and Cardoso, 2002), although no patterns have been recorded for higher beach taxa such as crustaceans, polychaetes or molluscs. Cirolanid isopods of the genus *Excirolana* not only dominate in numbers on beaches in many parts of the world, but are also the most ubiquitous beach species (Dexter, 1992). However, little is known about geographical patterns of biomass for this important taxon.

The objectives of this chapter are to test the following hypotheses:

1- Community biomass per square and linear meter increase from reflective to dissipative microtidal beaches on a geographical macroscale;

2- Temperate microtidal beaches on average harbour higher animal biomass than tropical beaches;

3- Temperate beaches support richer macrofaunal biomass than tropical beaches of the same morphodynamic type

4 – Mean individual body sizes of the macrofauna increase from reflective to dissipative microtidal beaches

5- Mean individual body sizes of the macrofauna decrease from temperate to tropical microtidal beaches for each beach type

6- Total biomass and mean body size of isopods of the genus *Excirolana* increase towards dissipative beaches and temperate microtidal regions

Additionally it will be tested whether physical forces associated to beach morphodynamics, such as wave height, period, grain size, etc, and oceanographic variables, such as temperature and salinity can explain the variability in the biomass of the community and that of individual taxonomic groups (crustaceans, polychaetes and molluscs), as well as mean individual body size in the southern hemisphere.

7.2. Material and methods

7.2.1. Field data

(Please see Chapter 2)

7.2.2. Statistical treatment

Means of the following biological characteristics per beach were calculate according to beach type and latitudinal region: average community biomass - biomass per square meter ($g.m^{-2}$); total community biomass – biomass per linear meter ($g.m^{-1}$); total biomass per taxonomic group, i.e. terrestrial (insects, arachnids and myriapods), polychaetes, crustaceans, molluscs and species grouped as "others" (i.e. nemerteans, echinoderms, sipunculids, oligochaetes, etc); and of cirolanid isopods of the genus *Excirolana*. This genus was chosen since it represents the most widespread taxon in the present study and worldwide (Dexter, 1992).

For this study total community biomass, total animal weight in grams per running meter (a 1 m wide strip of the transect), i.e. $g.m^{-1}$, was estimated by integrating the area under the curve of average biomass per station along the transect.

Biomass dominance was calculated as the percentage of the total mass of individuals of each taxonomic group in relation to the total mass of individuals in each beach community. Mean individual body size was calculated for each taxonomic group and for *Excirolana* spp. as the ratio of total group biomass : total group abundance and expressed in milligrams per individual.

In order to test the hypothesis that temperate beaches harbour higher biomass than tropical ones the five biogeographic areas sampled were grouped in tropical (Madagascar and Bahia), subtropical (Paraná) and temperate regions (south-central Chile and West Coast of South Africa). To test the hypothesis that dissipative beaches are richer in biomass than reflective ones, beaches were grouped as reflective, intermediate and dissipative according to Wright and Short (1984) classification. Differences between regions and beach types in biomass for the community and all taxa were tested separately using one-way MANOVAs (Multivariate Analysis of Variance). A two-way MANOVA was not possible because reflective beaches were absent in the subtropical region, making the design incomplete to test for factor interactions (Hair et al., 1992). Also, to test if community and taxa biomass on beaches in the same morphodynamic type differ between latitudes, one-way MANOVAs were done for each beach type, i.e. reflective, intermediate and dissipative. Separate one-way ANOVAs were done for each taxonomic group and for *Excirolana* to compare differences in mean body sizes between beach types and between latitudes, due to different degrees of freedom between groups (number of samples in each they occurred). The Newman-Keuls *a posteriori* test of multiple means range was used to identify which group of regions and beach types differed significantly. The logarithmic (x+1) transformation was applied to the data to satisfy the MANOVA assumption of homogeneity of variances, tested by the Cochran C test (Zar, 1984). In case this assumption was not met after data transformation, the non-parametric equivalent of ANOVA, Kruskal-Wallis H test, was applied to double-check the results of the univariate ANOVAs.

The Pearson Product Moment correlation was also calculated to assess the relationships between biotic variables (the community and taxa biomass, and also mean individual body size) and abiotic variables (Dean's; Beach State Index (BSI); 1/slope; intertidal beach width; grain size; wave height; wave period; surf zone width; water temperature; water salinity; swash length; saturation zone width; water table depth and the Beach Deposit Index (BDI)).

7.3. Results

7.3.1. Dominance

Crustaceans dominated the macrofaunal biomass on 65 % of the 52 beaches sampled, dominating in less tropical (62 %), than temperate (67 %) or subtropical (70 %) beaches. Molluscs were the second group, dominating in 27 % of all beaches. They dominated the biomass in only 30 % of the tropical and 20 % of the subtropical beaches. On temperate beaches molluscs exhibited regional differences. They dominated the biomass in 60 % of the West Coast beaches of South Africa, but none in Chile. This was due to the impoverished mollusc fauna of Chile, where the beach clam *Mesodesma donacium* occurs mainly in the subtidal. On the West Coast of South Africa, juveniles and subadults of the largest species of

Donax, i.e. *Donax serra*, and the predator-scavenger surf gastropod *Bullia laevissima* were responsible for the biomass dominance. Species of the genus *Donax* dominated in biomass in only 15 % of the beaches, mostly in the West Coast of South Africa (5 beaches) and in only three subtropical beaches in Madagascar and North Brazil.

Hippid suspension-feeders of the genus *Emerita* dominated the biomass on 33 % of the beaches, being the top biomass contributor on all 11 beaches sampled in Chile. They contributed on average 72 % or 1144 $g.m^{-1}$ of the total community biomass on those beaches.

Although the most widespread taxon was the cirolanid isopod genus *Excirolana*, occurring on 96 % of all sampled beaches, they dominated the biomass of only two beaches (one tropical; the other temperate). They were, however among the top three biomass contributors on 39 % of all beaches in all latitudes to which they contributed on average with 15 % or 13 $g.m^{-1}$ of the total community biomass. Talitrid amphipods of at least three different genera dominated the biomass on only 10 % of the beaches (four tropical and one temperate). Both polychaetes and "other" species were much less important, dominating only on two beaches each (4 % of the total).

7.3.2. Beach type comparison

Significant differences in average and total community biomass, as well as for taxonomic groups occurred among reflective, intermediate, and dissipative beaches disregarding latitudinal effects. The MANOVA was highly significant ($P < 0.01$), with only four variables not differing significantly among beach types (Table 17).

Average and total community, crustacean, and *Excirolana* biomass increased significantly from reflective to dissipative beaches (Table 17 and Fig. 23). The differences for molluscs, polychaete, terrestrial and "other" species biomass were not significant ($P > 0.05$). Only the variable average community biomass remained heterogeneous after data transformation (Table 17), but the Kruskal-Wallis test confirmed the results of the univariate ANOVA (Kruskal-Wallis $H = 7.72$, $DF = 2, 52$; $P < 0.02$). Mean individual body size showed no significant differences among beach types for any group (Fig. 24).

Table 17. M ANOVA comparison of community and taxa biomass among beach types on 52 beaches disregarding latitude.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test			
0.45	2.59	16	84	0.025				
Dependent variable Log (x + 1)	Mean square effect	Mean square error	F (DF 2, 49)	P-level	Reflective (R)	Intermediate (I)	Dissipative (D)	Interpretation
Average community biomass ($g.m^{-2}$)*	1.54	0.21	7.35	0.002	0.25	0.43	0.92	R=I<D
Total community biomass ($g.m^{-1}$)	6.46	0.52	12.32	<0.001	1.17	1.84	2.55	R<I<D
Crustaceans ($g.m^{-1}$)	6.86	0.65	10.51	<0.001	0.91	1.46	2.35	R=I<D
Molluscs ($g.m^{-1}$)	0.82	0.50	1.65	0.20^{NS}	0.36	0.74	0.75	-
Polychaetes ($g.m^{-1}$)	0.33	0.18	1.83	0.17^{NS}	0.35	0.53	0.66	-
Excirolana ($g.m^{-1}$)	2.03	0.21	9.48	<0.001	0.26	0.75	0.99	R<I=D
Terrestrial species ($g.m^{-1}$)	0.11	0.10	1.09	0.35^{NS}	0.12	0.25	0.29	-
"other" species ($g.m^{-1}$)	0.10	0.25	0.39	0.68^{NS}	0.16	0.30	0.26	-

< or > (P<0.05); = (P>0.05); NS (P>0.05); - not tested.*heteroscedastic

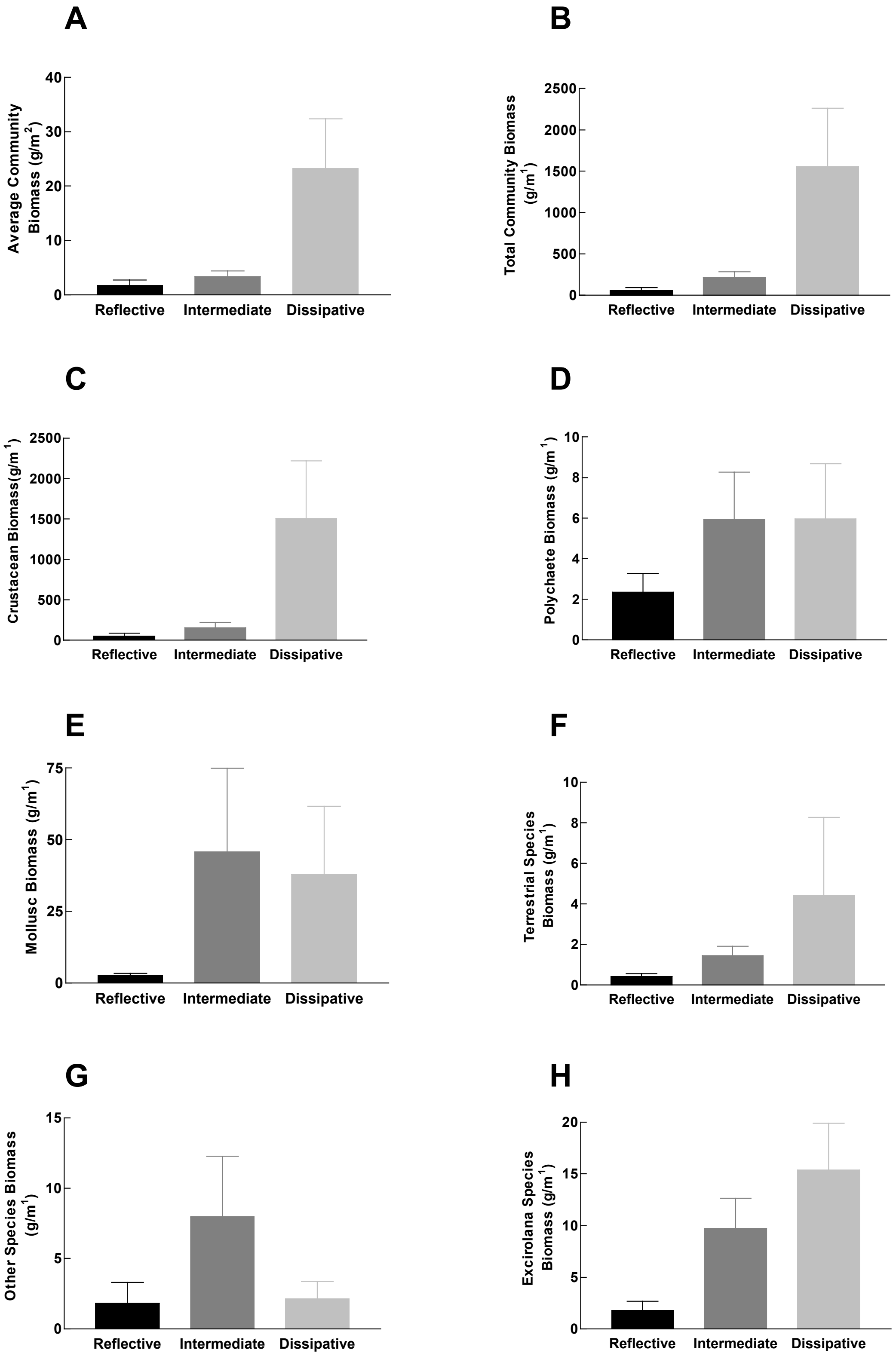

Figure 23: Average faunal biomass in each beach type on 52 beaches. Reflective (n = 17), Intermediate (n = 24), Dissipative (n = 11).

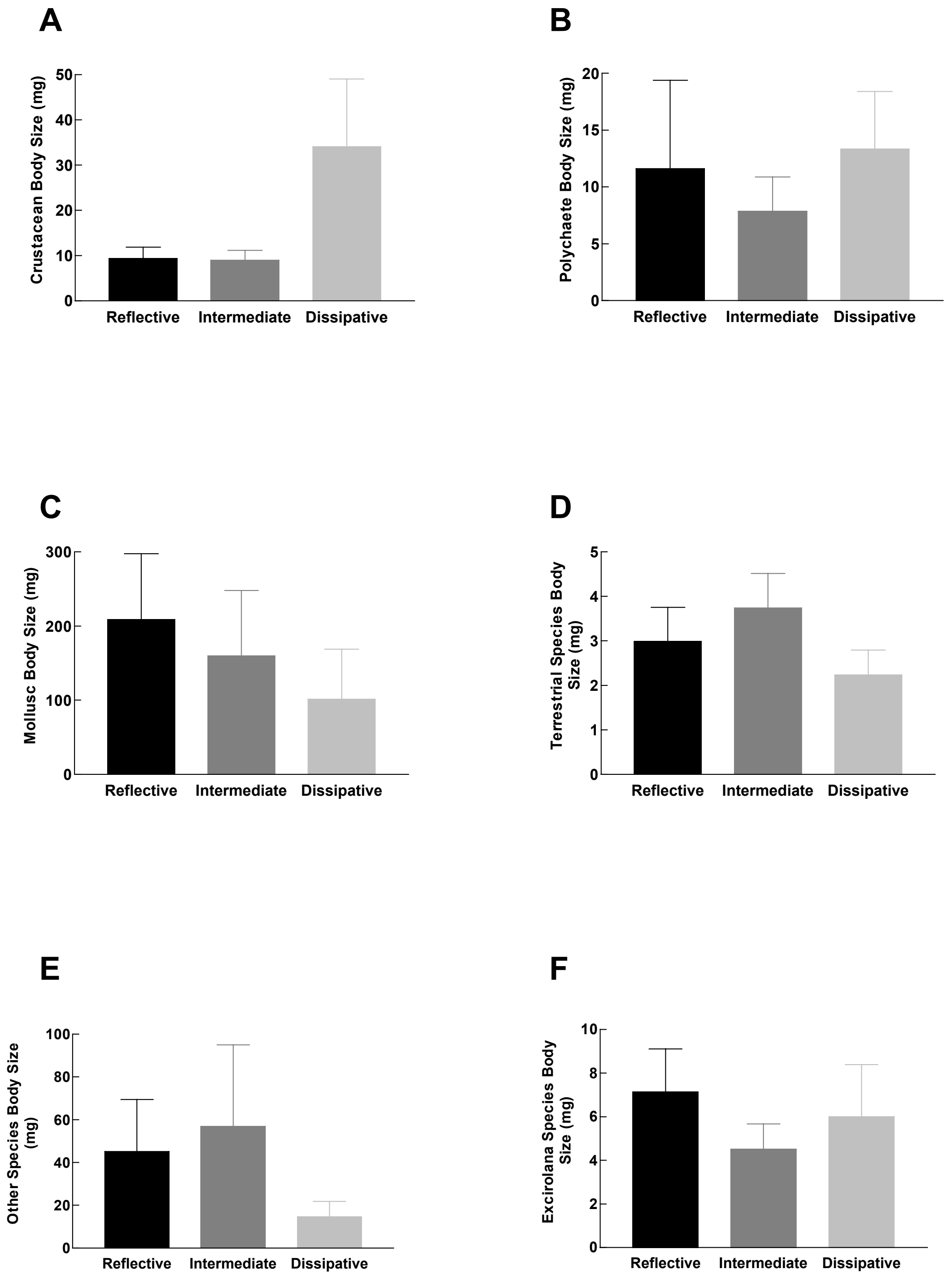

Figure 24: Mean faunal body size in each beach type on 52 beaches. Reflective (n = 17), Intermediate (n = 24), Dissipative (n = 11).

7.3.3. Latitudinal comparison

7.3.3.1. General trends

Grouping the 52 beaches of all morphodynamic types into temperate, subtropical and tropical beaches yielded significant differences in community and taxa biomass among latitudes. The variables tested could perfectly discriminate beaches in different latitudinal groups with a highly significant MANOVA model ($P = 0$), and a high Wilk's lambda and Rao's R (Table 18). Only mollusc, polychaete and "other" species biomass did not differ significantly between latitudes.

Biomass variances of some groups were still heterocedastic after data transformation (Table 18). However the Kruskal -Wallis test confirmed the results of the univariate ANOVAs, with all variables differing significantly among latitudes, i.e. average community biomass ($H = 24.71$, $DF = 2, 52$; $P < 0.0$), total community biomass ($H = 24.87$, $DF = 2, 52$; $P < 0.0$), crustacean biomass ($H = 20.89$, $DF = 2, 52$; $P < 0.0$), *Excirolana* biomass ($H = 31.48$, $DF = 2, 52$; $P < 0.0$), terrestrial species biomass ($H = 16.51$, $DF = 2, 52$; $P < 0.003$).

Thus average and total community biomass, crustacean, *Excirolana* and terrestrial species Biomass was on average significantly higher on temperate than on tropical and subtropical beaches (Table 18, Fig. 25).

7.3.3.2. Mean body size

The individual ANOVAs detected significant body size differences among latitudes for all but mollusc, terrestrial and "other" species (Table 19). Mean body size variances were still heterocedastic after data transformation for polychaete and *Excirolana* spp. The Kruskal - Wallis test confirmed the results of the univariate ANOVAs, with mean body sizes of polychaetes ($H = 13.94$, $DF = 2, 49$; $P < 0.0009$) and *Excirolana* spp. ($H = 19.88$, $DF = 2, 50$; $P < 0.0$) varying significantly among latitudes.

Table 18: MANOVA comparison of community and taxa biomass among 52 temperate, subtropical and tropical beaches disregarding morphodynamics.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test			
0.23	5.26	16	84	0.025				
Dependent variable* Log (x + 1)	Mean square effect	Mean square error	F (DF 2, 49)	P-level	Temperate (Temp)	Subtropical (Sub)	Tropical (Trop)	Interpretation
Average community biomass (g.m^{-2})	3.08	0.15	21.06	0	0.90	0.20	0.19	Temp>Sub=Trop
Total community biomass (g.m^{-1})	10.03	0.38	26.50	0	2.51	1.49	1.16	Temp>Sub=Trop
Crustaceans (g.m^{-1})	10.01	0.52	19.09	<0.0001	2.21	1.20	0.86	Temp>Sub=Trop
Molluscs (g.m^{-1})	0.11	0.53	0.21	0.81^{NS}	0.66	0.69	0.54	-
Polychaetes (g.m^{-1})	0.49	0.17	2.82	0.069^{NS}	0.56	0.69	0.34	-
Excirolana (g.m^{-1})	4.62	0.11	42.62	0	1.12	0.58	0.19	Temp>Sub>Trop
Terrestrial species (g.m^{-1})	0.62	0.08	7.40	0.002	0.40	0.12	0.074	Temp>Sub=Trop
"other" species (g.m^{-1})	0.34	0.24	1.44	0.25^{NS}	0.37	0.062	0.21	-

> (P<0.05); = (P>0.05); NS (P > 0.05); - not tested.*all heterocedastic

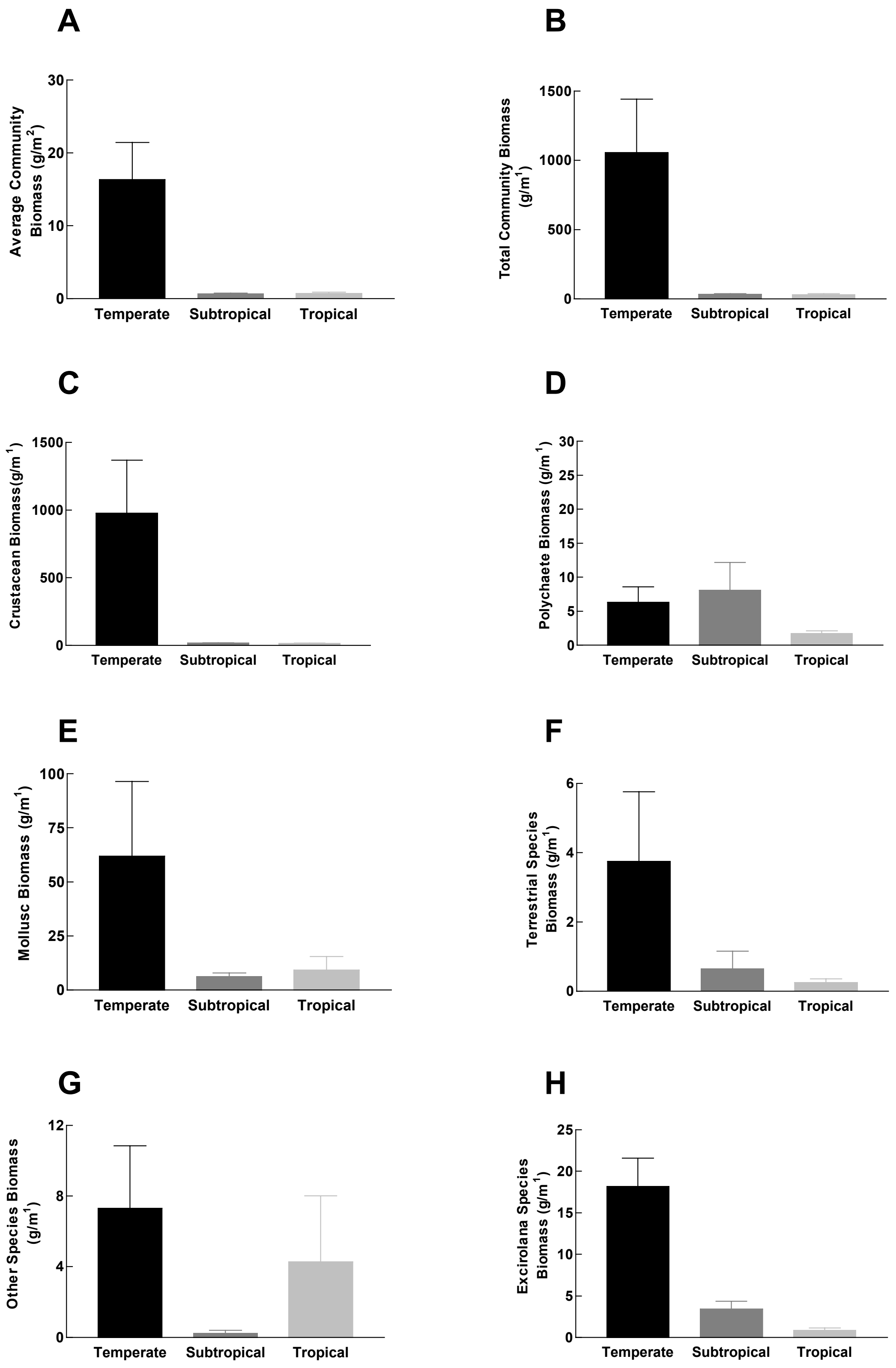

Figure 25: Average faunal biomass per region for 52 beaches. Temperate (n = 21), Subtropical (n = 10), Tropical (n = 21).

Thus, mean body sizes of crustaceans, polychaetes and isopods of the genus *Excirolana* were significantly larger on temperate than subtropical and tropical beaches disregarding beach types (Table 19, Fig. 26).

7.3.3.3. Reflective beaches

No reflective beach was sampled in the subtropics, thus the latitudinal comparison is restricted to temperate and tropical regions. The analysis with all eight measures faunal biomass yielded a MANOVA model with a high discrimination between groups (Wilk's = 0.12), with 4 variables showing no significant difference between latitudes, i.e. crustaceans, molluscs, polychaetes and "other" species. From the remaining four variables three were still heterocedastic: average community, *Excirolana* spp. and terrestrial biomass. The Kruskal - Wallis test was not significant for those variables ($P > 0.05$). They, nevertheless, showed a tendency to higher mean biomass in temperate latitudes (Table 20, Fig. 27)

Total community biomass was the only homoscedastic variable exhibiting latitudinal significant differences, and it increased from tropical to temperate reflective beaches (Table 20, Fig. 27).

Mean faunal body size followed the same trend as biomass, increasing towards temperate reflective beaches for crustaceans, *Excirolana*, molluscs and polychaetes (Table 21, Fig. 28). This variable had a heteroscedastic variance for polychaetes and the differences between latitudes were not confirmed by the Kruskal Wallis test ($P > 0.05$)

7.3.3.4. Intermediate beaches

Intermediate beaches were the dominant beach type in all latitudes. The analysis with all biomass measures produced a MANOVA model with low significance ($P = 0.048$); dropping the three variables that did not vary significantly among latitudes, i.e. polychaete, mollusc and "other" species biomass, yielded a very significant MANOVA model with high discrimination between latitudes ($P < 0.04$, Table 22). From the remaining variables only

Table 19: ANOVAs testing for mean body size differences of the fauna among latitudes disregarding morphodynamics.

Dependent variable						Newman-Keuls test			
Log (x + 1)	Mean square effect	Mean square error	DF (1, x)	F	P-level	Temperate (Temp)	Subtropical (Sub)	Tropical (Trop)	Interpretation
Crustacean body size (mg)	0.90	0.18	49	4.99	0.01	1.12	0.74	0.74	Temp>Sub=Trop
Mollusc body size (mg)	1.40	0.75	39	1.87	0.17^{NS}	1.68	0.99	1.48	-
Polychaete body size (mg)*	1.96	0.18	46	10.82	<0.001	1.07	0.50	0.47	Temp>Sub=Trop
Excirolana body size (mg)*	1.00	0.094	47	10.64	<0.001	0.88	0.37	0.57	Temp>Sub=Trop
Terrestrial species body size (mg)	0.08	0.08	43	1.01	0.37^{NS}	0.57	0.40	0.52	-
“other” species body size (mg) *	0.98	0.50	24	1.96	0.16^{NS}	1.19	0.47	1.14	-

> (P<0.05); = (P>0.05); NS (P > 0.05); - not tested.*all heteroscedastic

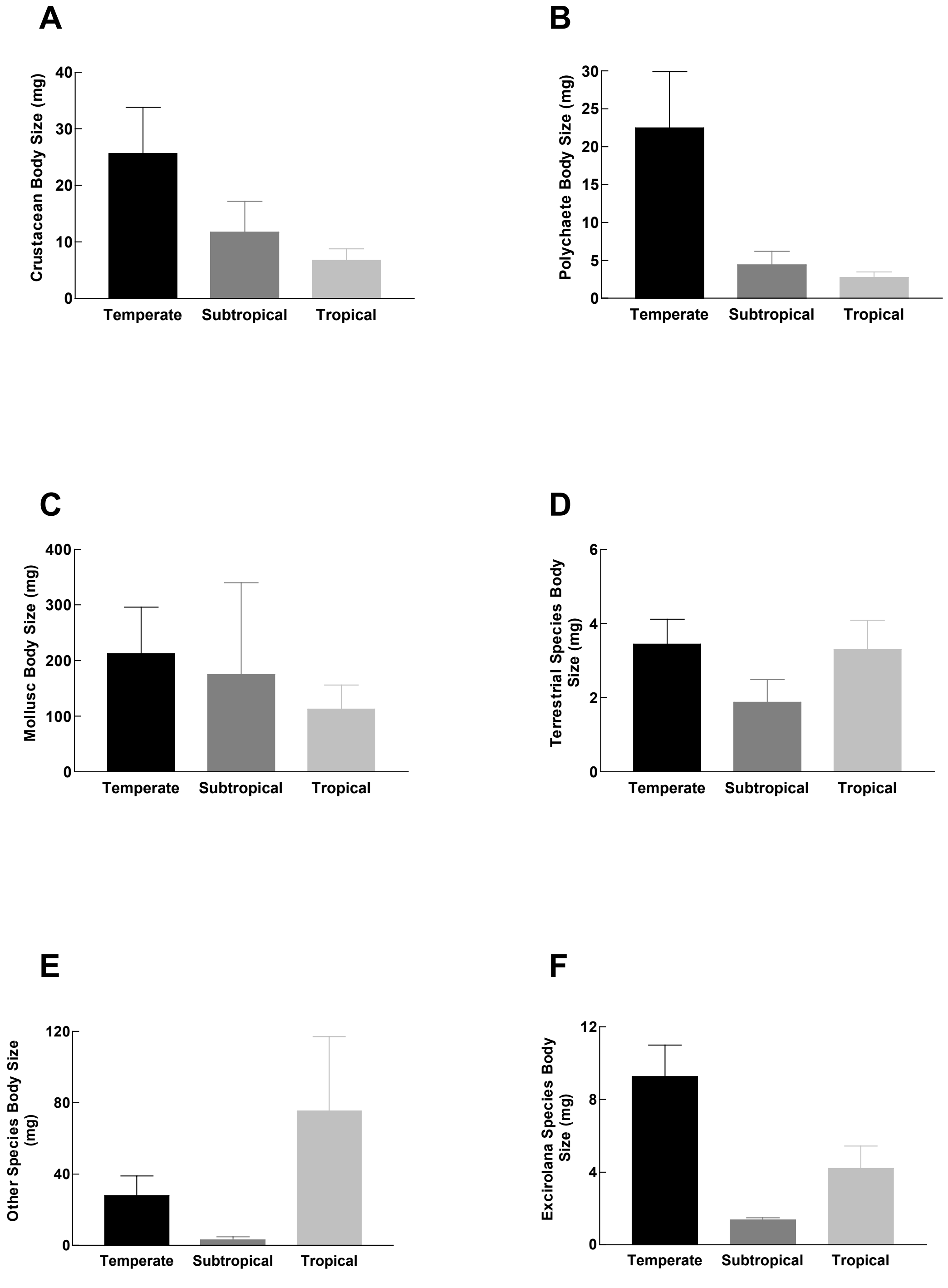

Figure 26: Mean faunal body size per region for 52 beaches. Temperate (n = 21), Subtropical (n = 10), Tropical (n = 21).

Table 20: MANOVA comparison of community and taxa biomass for 17 reflective beaches between temperate and tropical regions.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test		
0.12	7.27	8	8	0.006			
Dependent variable Log (x + 1)	Mean square effect	Mean square error	F (DF 2, 15)	P-level	Temperate		Tropical
Average community biomass (g.m^{-2})*	0.27	0.08	3.57	0.08	0.45	>	0.17
Total community biomass (g.m^{-1})	1.73	0.25	6..83	0.02	1.66	>	0.96
Crustaceans (g.m^{-1})	1.54	0.36	4.27	0.057^{NS}	1.38	-	0.72
Molluscs (g.m^{-1})	0.26	0.15	1.74	0.21^{NS}	0.17	-	0.44
Polychaetes (g.m^{-1})	0.23	0.13	1.79	0.20^{NS}	0.53	-	0.28
Excirolana (g.m^{-1})*	0.92	0.06	14.16	0.002	0.62	>	0.11
Terrestrial species (g.m^{-1})*	0.62	0.014	10.38	0.006	0.27	>	0.065

(P<0.05); = (P>0.05); NS (P > 0.05); - not tested.*all heterocedastic

Table 21: Mean faunal body size comparisons for 17 reflective beaches between temperate and tropical regions.

Dependent variable						Newman-Keuls test		
Log (x + 1)	Mean square effect	Mean square error	DF (1, x)	F	P-level	Temperate		Tropical
Crustacean body size (mg)	0.50	0.09	15	5.18	0.037	1.13	>	0.77
Mollusc body size (mg)	401259	52497	9	7.64	0.022	812	>	148
Polychaete body size (mg)*	1.10	0.21	14	5.47	0.035	1.10	>	0.48
Excirolana body size (mg)	0.50	0.11	14	4.69	0.048	1.06	>	0.64

(P<0.05); = (P>0.05); NS (P > 0.05); - not tested.*all heteroscedastic

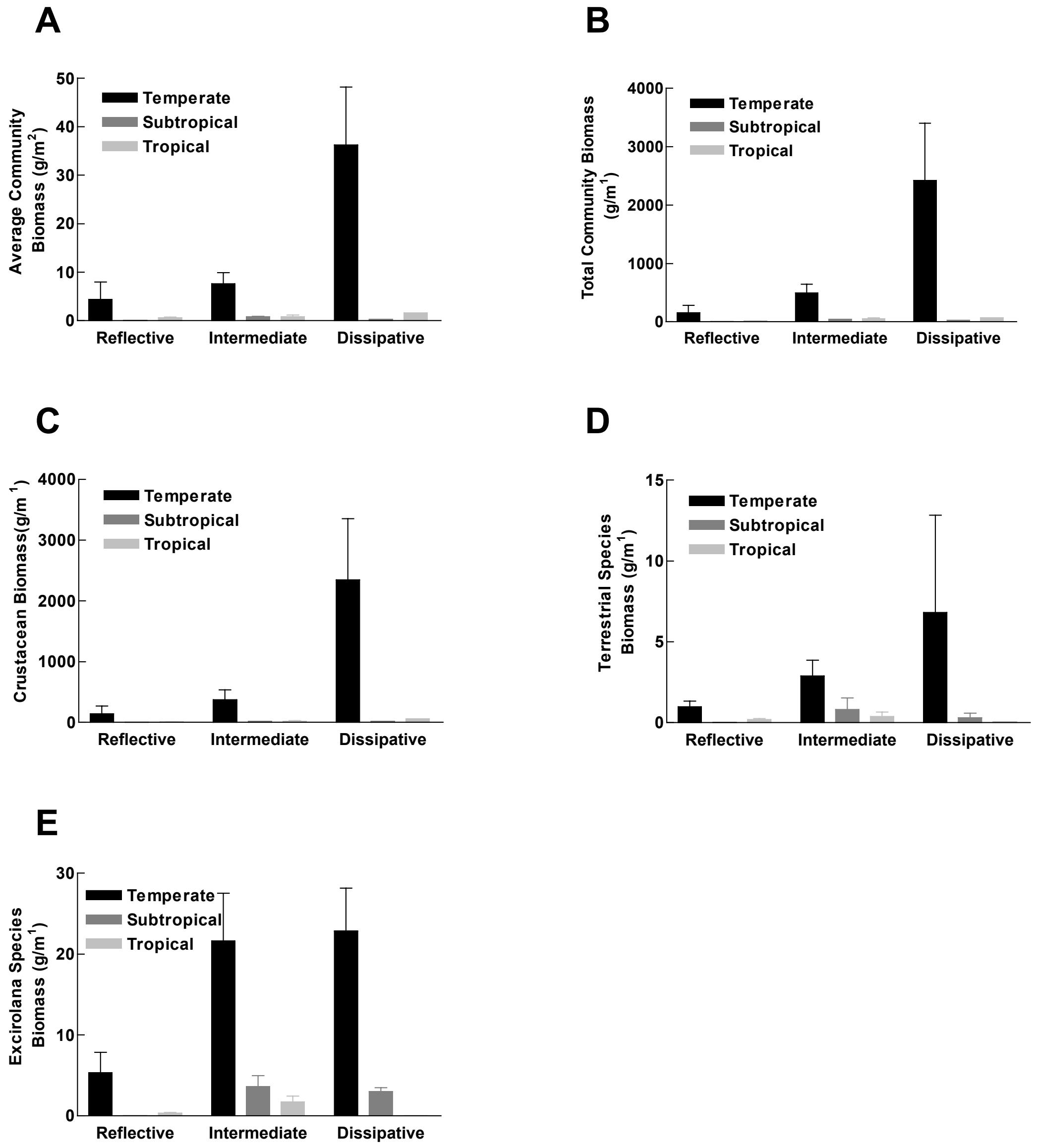

Figure 27: Average faunal biomass per beach type in each latitudinal region.

average community biomass was still heterocedastic after log-transformation. A Kruskal-Wallis test nevertheless confirmed the result of the univariate ANOVA that average community biomass was significantly different on intermediate beaches among different latitudes (H = 12.80, DF = 2, 24, P < 0.02).

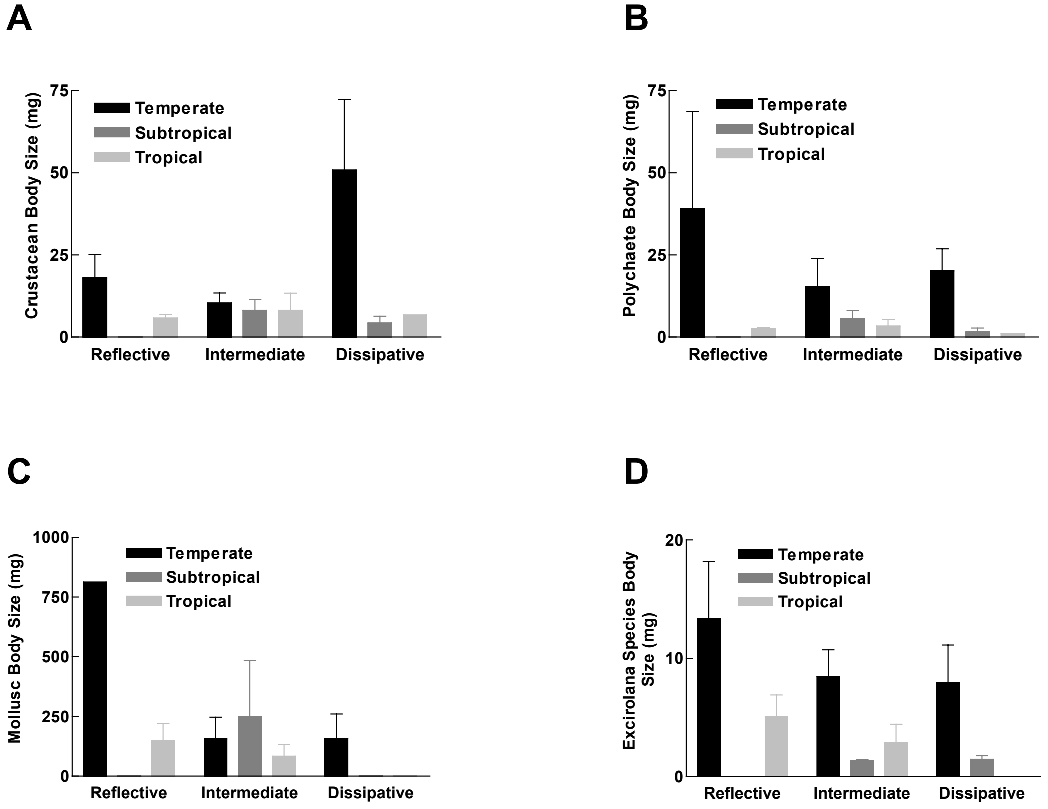

Figure 28: Mean faunal body size per beach type in each latitudinal region.

Similarly, *Excirolana* mean body size varied significantly among latitudes (F = 4.79, DF = 2, 21, P < 0.02). Although this variable was heterocedastic, the Kruskal-Wallis test confirmed the ANOVA result (H = 13.22, DF = 2, 24, p < 0.01).

Thus temperate intermediate beaches had significantly higher average and total community, crustacean, *Excirolana* and terrestrial biomass (Table 22, Fig 27). It had also the largest *Excirolana* along the latitudinal gradient (Fig. 28)

7.3.3.5. Dissipative beaches

The latitudinal comparisons were made only between subtropical and temperate regions since only one dissipative beach was found in the tropics (Madagascar). A MANOVA with all measures of species richness was not significant (P = 0.34). Dropping the four variables that did not differ between regions, i.e. polychaete, mollusc, terrestrial and "other" species

Table 22: MANOVA comparison of faunal biomass between 24 intermediate temperate, subtropical and tropical beaches.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test			
0.26	3.32	10	34	0.004				
Dependent variable Log (x + 1)	Mean square effect	Mean square error	F (DF 2, 21)	P-level	Temperate (Temp)	Subtropical (Sub)	Tropical (Trop)	Interpretation
Average community* biomass (g.m^{-2})	0.93	0.072	12.81	<0.001	0.79	0.24	0.20	Temp>Sub=Trop
Total community biomass (g.m^{-1})	3.08	0.25	12.40	<0.001	2.49	1.53	1.37	Temp>Sub=Trop
Crustaceans (g.m^{-1})	3.14	0.35	9.02	0.002	2.10	1.20	0.95	Temp>Sub=Trop
Excirolana (g.m^{-1})	2.00	0.09	22.15	<0.0001	1.25	0.58	0.32	Temp>Sub=Trop
Terrestrial species (g.m^{-1})	0.35	0.083	4.21	0.03	0.47	0.13	0.10	Temp>Sub=Trop

> (P<0.05); = (P>0.05);*all heterocedastic

biomass yielded a significant model ($P < 0.0044$) with a Wilk's lambda close to 0, and a high discrimination between temperate and subtropical dissipative beaches (Table 23). Average community and total crustacean biomass had heterogeneous variances. The Kruskal-Wallis test, however, confirmed the ANOVA results for both, i.e. average community ($H = 5.73$ DF = 1, 10, $P < 0.02$) and crustacean ($H = 5.74$ DF = 1, 10, $P < 0.02$) biomass.

Temperate dissipative beaches had higher average and total community, crustacean and *Excirolana* biomass (Table 23, Fig. 27). Also, mean individual body sizes of polychaetes ($F = 8.24$, DF = 1, 10, $P < 0.02$) and molluscs ($F = 6.11$, DF = 1, 10, $P < 0.02$) were significantly larger on the temperate dissipative beaches (Fig. 28). Although this last variable was heteroscedastic, the Kruskal-Wallis test confirmed the ANOVA result ($H = 5.73$, DF = 1, 10 $P < 0.01$).

Table 23: MANOVA comparison of faunal biomass on 10 dissipative beaches between temperate and subtropical regions.

Wilk's lambda	Rao's R	DF 1	DF 2	P-level	Newman-Keuls test		
0.07	16.39	4	5	0.0044			
Dependent variable* Log (x + 1)	Mean square effect	Mean square error	F (DF 1, 8)	P-level	Temperate		Tropical
Average community biomass ($g.m^{-2}$)*	3.30	0.23	14.12	0.006	1.35	>	0.095
Total community biomass ($g.m^{-1}$)	6.52	0.22	30.00	<0.001	3.15	>	1.38
Crustaceans ($g.m^{-1}$)*	6.35	0.59	10.74	0.011	2.93	>	1.19
Excirolana ($g.m^{-1}$)	1.05	0.07	15.40	0.004	1.30	>	0.60

> (P<0.05)* heterocedastic

7.3.4. Relationship between physical factors, macrofaunal biomass and mean body sizes

A summary of the correlations between all physical factors and macrofaunal biomass is given in Table 24.

All biomass measures showed significant correlations with several physical factors. Although factors such as sand size, beach slope and width and the Beach Deposit Index had significant correlations with biomass, factors related to surf zone processes and therefore possibly to productivity, such as wave height, period and surf zone width, held the highest positive correlations with average and total community biomass, and also with crustacean, *Excirolana* and terrestrial biomass. The BSI was, like Dean's and the BDI, outperformed by surf zone variables.

Polychaete biomass values were not related to surf zone processes, but rather to the properties of the beach deposit increasing with flatter slopes, finer sands, shallower water tables and probably less turbulent flows, i.e. higher BDI (Table 24). Molluscs had a slight trend of increase in biomass towards more dissipative beaches with wider swashes and saturation zones. "Other" species also increased in biomass on wider beaches with wider swash and saturation zones. Dean's parameter was correlated with most biomass measures, but at lower correlations than other individual or composite (BDI) factors. Beach width explained biomass variances of all groups except molluscs, having the highest fit with *Excirolana* biomass. Most of the biomass measures, except for molluscs, polychaetes and "other" species, had high correlations with temperature. Thus, average and total biomass of the community, crustaceans, terrestrial species and *Excirolana* significantly increased with lower temperatures, i.e. towards temperate regions.

The body sizes of terrestrial and "other" species were not significantly correlated with any physical factor measured. On the other hand, the mean body size of polychaetes, crustaceans and *Excirolana* were significantly larger at lower water temperatures. Besides temperature, factors linked to surf zone processes, and possibly productivity, explained part of the variation of body size in crustaceans and polychaetes. The body size of molluscs seems to increase towards steeper slopes, coarser sands, with shorter swash periods and more turbulent flows (BDI), all of which are features of a reflective environment.

Table 24. Correlations between physical factors, faunal biomass and mean body size for the 52 beaches analysed. Values in italics indicate correlations significantly different from zero ($P < 0.05$).

Parameter Log (x + 1)	Log BDI	BSI	Dean's	1/slope	Beach width (m)	Sand size (mm)	Water table depth (cm)	Wave height (cm)	Wave period (s)	Surf zone width (m)	Saturation width (m)	Swash length (m)	Temperature (°C)
Average community ($g.m^{-2}$)	***0.31***	0.34	***0.34***	0.24	***0.30***	***-0.29***	-0.12	***0.66***	***0.61***	***0.62***	-0.08	***0.30***	***-0.66***
Total community ($g.m^{-1}$)	***0.50***	***0.49***	***0.46***	***0.42***	***0.53***	***-0.41***	***-0.29***	***0.72***	***0.67***	***0.67***	0.16	***0.47***	***-0.74***
Crustaceans ($g.m^{-1}$)	***0.46***	***0.44***	***0.44***	***0.43***	***0.48***	***-0.33***	-0.25	***0.72***	***0.68***	***0.67***	0.05	***0.41***	***-0.68***
Polychaetes ($g.m^{-1}$)	***0.47***	***0.35***	***0.33***	***0.39***	***0.30***	***-0.45***	***0.36***	0.15	0.09	0.20	0.27	0.27	-0.22
Molluscs ($g.m^{-1}$)	0.19	***0.31***	***0.28***	0.11	0.18	-0.22	-0.16	0.07	-0.09	0.05	***0.31***	***0.31***	-0.07
"other" species ($g.m^{-1}$)	0.14	0.22	0.18	0.09	***0.33***	-0.16	-0.07	0.09	0.10	0.11	***0.40***	***0.38***	-0.14
Terrestrial species ($g.m^{-1}$)	***0.28***	0.14	0.11	***0.29***	***0.40***	-0.18	-0.04	***0.34***	***0.47***	***0.41***	0.08	0.18	***-0.45***
Excirolana spp. (g/m^{1})	***0.48***	***0.48***	***0.41***	***0.44***	***0.60***	***-0.41***	-0.13	***0.66***	***0.69***	***0.64***	0.20	***0.46***	***-0.77***
Crustacean body size (mg)	-0.0	0.02	0.06	-0.01	0.01	0.06	-0.07	***0.43***	***0.38***	***0.28***	-0.26	0.06	***-0.45***
Polychaete [1] body size (mg)	0.11	0.17	0.14	0.01	0.14	-0.18	-0.06	***0.43***	***0.36***	***0.31***	-0.11	0.23	***-0.60***
Mollusc [2] body size (mg)	***-0.38***	-0.27	-0.22	***-0.38***	-0.11	***0.42***	0.28	-0.09	-0.06	-0.17	-0.04	-0.06	-0.21
"other" species [3] body size (mg)	-0.01	0.01	-0.02	-0.06	0.16	-0.09	0.09	0.07	0.24	0.09	0.28	0.14	-0.03
Terrestrial species[4] body size (mg)	0.01	-0.05	-0.16	0.03	0.26	0.05	-0.09	-0.03	-0.01	-0.07	0.24	0.06	-0.12
Excirolana spp. [5] body size (mg)	0.01	0.01	0.06	-0.09	0.03	-0.13	0.20	0.02	0.11	0.08	0.15	0.24	***-0.36***

[1] (n = 49), [2] (n = 41), [3] (n = 27), [4] (n = 46), [5] (n = 50)

7.4. Discussion

7.4.1. Beach type comparison

The hypothesis that dissipative beaches have higher biomass of community and taxonomic groups than reflective beaches is supported in this study for community, crustaceans and cirolanid isopods of the genus *Excirolana*. This is a geographical macroscale trend involving beaches in three major climatic regions of the southern hemisphere. The highest correlations of biomass for these groups were, however, with surf zone variables, such as wave height, and period and with surf zone width. This suggests that it is not the morphodynamic processes of wave transformation of the beach profile through the swash that controls faunal biomass, but rather productivity in the water column generated by surf zone processes. McLachlan et al. (1981) showed that rich macrofaunal communities on high energy intermediate and dissipative beaches are maintained by blooms of surf zone diatoms, adapted to exploit and maximise production in highly turbulent surf zones. These blooms would not only be generated by high waves but would also be kept in the beach ecosystem by vertical and horizontal currents generating circulation cells in the surf zone. Additionally the nutrients coming from the continental run-off and also regenerated by the biomass rich fauna would feedback the production of surf zone diatoms. This, associated with high POM generated by the beach macrofauna (Soares et al., 1997) and enriched by the microbial loop (Brown and McLachlan, 1990) could support higher faunal biomass and production than low energy reflective beaches. Although some dissipative beaches on the West Coast of South Africa are not supported by surf diatoms (Bally, 1987) they are part of a rich detritus-driven trophic chain, fuelled by POM and DOM derived from kelp uprooted from the nearby kelp beds by big waves (Soares et al., 1997). Mollusc and polychaete biomass differences were not significant between beach types most probably because of their stronger relations with the beach deposit features, i.e. grain size, slope and flow environment (BDI) in the case of polychaetes, or with swash processes in the case of molluscs.

The higher association of macrofaunal biomass with wave height than with Dean's morphodynamic index was also observed on beaches in South Africa, Chile and USA (McLachlan, 1990; McLachlan et al., 1993; Jaramillo and McLachlan, 1993). In contrast, an increase in biomass was observed towards lower energy tropical macrotidal beaches in Australia (Hacking, 1997; but see McLachlan et al., 1996a). This is probably due to the dominance by polychaetes, which are associated more with the benthic boundary layer processes (see BDI correlations and Chapter 5, 6) in these depositional environments.

The biomass of species not controlled by swash processes, such as terrestrial species, did not differ significantly between beach types. Instead, this biomass was positively related to surf zone processes indicating the probable association between larger waves and surf zones and uprooted kelp.

Although the mean body size of the faunal groups tested here did not differ between beach types, there was a significant trend of increasing mollusc sizes towards steeper slopes with coarser sands and more turbulent and shorter swashes. This contrasts with the suggestion that smaller body sizes of beach clams towards reflective beaches would be an adaptation to burrow faster and escape predation (McLachlan et al., 1995). Since these authors compared only a small number of selected bivalves, with the smaller species being from the tropics and the larger being from temperate regions, size might be linked to latitudinal rather than beach type differences.

Beach habitat also seems to influence size. For example, the South African beach clam *Donax serra* had larger sizes in the surf zone in comparison to the intertidal zone (Soares et al., 1998). The best test of the size-beach type relationship for beach fauna should be to measure body size changes of the same species on the same beach habitat and within the same latitudinal region along the morphodynamic spectrum. This was done for crustaceans on Chilean beaches and there was a significant increase towards dissipative beaches (Jaramillo and McLachlan, 1993), but no difference was found on the coast of California (Dugan and Hubbard, 1996). In the present study both crustaceans and polychaetes increased in size with bigger waves and wider surf zones, indicating a possible link with surf zone productivity.

There were differences in magnitude of responses of biomass and body size attributes depending on taxon and the physical factor tested. This lack of uniformity of responses of each species to the physical environment indicates that other factors might play a role in shaping community structure. Biological interactions, such as predation by fish, birds and large crabs (Brown and McLachlan, 1990), and among the macrobenthos (McDermott, 1983), may therefore be additional factors controlling biomass levels on sandy beaches.

7.4.2. Latitudinal comparison

In this study the hypothesis that microtidal temperate beaches harbour significantly larger total community and taxa biomass for crustaceans, terrestrial species and isopods of the genus *Excirolana* in comparison with microtidal tropical and/or subtropical beaches was supported both for the average beach in each latitudinal region and also when comparing beaches of the same morphodynamic type (within-habitat comparison). The significant inverse correlation between biomass of these groups and water temperature corroborates the above conclusion. Only polychaete and mollusc total biomass did not differ between latitudes, reflecting their association with the beach deposit and swash processes rather than with latitude linked surf zone productivity. The patterns of decreasing total community biomass towards tropical beaches have not been adequately tested before on sandy beaches, but showed a trend to increase from microtidal subtropical to mesotidal temperate beaches (McLachlan, 1990, McLachlan et al., 1993; Jaramillo and McLachlan, 1993). The only formal test done in Australia showed, unexpectedly, that community biomass increased from microtidal temperate to macrotidal tropical beaches (Hacking, 1997, but see McLachlan et al., 1996a). Since tide covaried with latitude it is not possible to ascertain if those differences reflect inter-habitat or latitudinal differences.

Biomass variations of soft-bottom communities with water temperature have been somehow contradictory, with some authors suggesting an increase in biomass with temperature (Tumbiolo and Downing, 1994) while other suggested a decrease (Riccardi and Bourget, 1999). These authors did not compare the same habitats or taxa, and therefore their results have confounded influences.

An increase in biomass towards temperate regions might be expected since higher productivity is associated with higher latitudes in the oceans (Levinton, 1995; Mann, 2000, Macpherson, 2002) and coasts (Bustamante et al., 1995; Mann, 2000). Total biomass is generally positively correlated to productivity (Tumbiolo and Downing, 1994). Indeed, higher biomass associated with higher productivities is found in temperate latitudes for sandy beach macrobenthos (Gianuca, 1983; Santos, 1994; McLachlan et al., 1996b; Defeo and Cardoso, 2002; Cardoso and Veloso, 2003) and also in abyssal plains (Thurston et al., 1998).

The increase in biomass from tropical and subtropical to temperate regions was consistent in each morphodynamic type, i.e. reflective, intermediate and dissipative. It demonstrates the influence of latitudinal differences on productivity of beach communities. Data on global primary production for the regions considered in this study show that the studied temperate regions were indeed richer with phytoplankton producing from 150 to > 250 mg C / m² / day. Subtropical regions produced less, around 100 to 150 mg C / m² / day, and tropical regions, around 100 mg C / m² / day (Fig. 10.6 in Levinton, 1995). Also, sandy beaches and rocky shore communities have higher primary productivity on temperate than on tropical coasts of Southern Africa (Bate et al., 1990; Bustamante et al., 1995).

No attempt was made in this study to classify feeding-guilds since sandy beach organisms are generalists and can function at two trophic levels, depending on environmental conditions (Defeo and Basted, 1990) and/or resource availability (Brown and McLachlan, 1990). Nevertheless, suspension feeders, such as the mole crab *Emerita* and Donacid and mesodesmatid bivalves, were by far the most important biomass contributors, together dominating 58 % of the beaches in all latitudes.

One of the most striking patterns in nature is the body size increase for both ecto- and endotherms towards higher latitudes, namely the Bergman's rule (Atkinson and Sibly, 1997). The latitudinal comparison disregarding the effect of beach morphodynamics showed that crustaceans, polychaetes and isopods of the genus *Excirolana* increased significantly in mean body size from tropical to temperate beaches. There were nevertheless some differences according to beach type. For reflective and dissipative beaches molluscs were also larger in temperate regions. On intermediate beaches, only *Excirolana* were larger in temperate regions. The increase in body size at lower temperatures was observed for *Donax serra* in South Africa (Soares et al., 1998), *Excirolana braziliensis* on both Atlantic (Fonseca et al., 2000) and Pacific coasts (Contreras, 2001) and *Emerita brasiliensis* in the Atlantic coast (Defeo and Cardoso, 2002). The reasons for this increase are still controversial (Atkinson and Sibly, 1997). Since beach animals have higher growth performances in temperate than tropical regions (Zuniga et al., 1985; McLachlan et al., 1996b; Defeo and Cardoso, 2002; Cardoso and Veloso, 2003), body sizes might be more affected by food productivity (Soares et al., 1997) than by temperature related metabolic constraints (Atkinson and Sibly, 1997). The significant correlations between body sizes of polychaetes and crustaceans and surf zone characteristics lend support to this hypothesis. The lack of such correlations for molluscs and *Excirolana* indicates that more information is needed to understand body size patterns on sandy beaches.

8. Beach morphodynamics and community structure – a synthesis

8.1.1. Morphodynamics

The geographic analyses of beach morphodynamics revealed two interesting patterns: the prevalence of different beach types in different latitudes; and a decrease in wave period towards reflective beaches. A new theoretical approach for the prediction of beach slopes from few morphodynamic characteristics helped to understand the complex feedback interactions between forcing and response variables in determining beach morphodynamics.

The prevalence of reflective beach types in tropical regions and dissipative types in temperate regions is related to wave climate. Low energy waves are dominant in tropical seas, whereas high-energy waves are dominant in temperate regions (Davies, 1980). The occurrence of coral reefs is also related to climate and they exist only in tropical regions. The covariation of reflective beaches and coral reefs with latitude, however, does not imply a cause-effect relationship, since several tropical reflective beaches were not fronted by coral reefs, and reflective beaches also occurred in temperate regions. It could be suggested that morphodynamics differ between reflective beaches fronted and not fronted by coral reefs. However, from all 11 physical factors measured in this study only wave period was shorter, water table shallower and beach width narrower in beaches fronted by coral reefs ($P < 0.05$). No corresponding significant difference was observed for macrofaunal communities ($P > 0.05$). Although there was no difference in wave height between beaches fronted and not fronted by coral reefs, these biotic structures surely decrease the impact of high-energy events such as tropical hurricanes in Madagascar. In North Brazil, only one of the beaches studied was partially fronted by coral reefs and no hurricanes are known to occur. Additionally, tropical beaches of east Australia (Hacking, 1997), where the great reef barrier is situated, and Oman (McLachlan et al., 1998), without reefs, have smaller waves than temperate areas due to the low wave energy climate at this latitude. Thus high energy dissipative beaches in tropical regions will be rare, but may occur on coasts with long wave fetches, such as South Madagascar and, possibly, some Pacific islands.

A theoretical equation based on the action of few forcing factors such as wave height, tide, beach width and grain size on beach geometry had good predictive power for beach slopes. However, it did not perform well on beaches with a break in slope, having a steep high tide slope with coarse sands and a flat low tide slope with fine sands. Further tests of the formula on these beaches should tackle the different slopes and associated sand sizes separately.

The beach morphometric model could predict beach slopes without considering wave period. This could imply that either this variable is not important in controlling natural beaches slopes or that it covaries with the important controlling factors. Variation in beach types on coasts with uniform sand sizes seems to depend more on wave height than the wave period regimes. On these coasts wave period seems to be associated with the geographic position of beaches and consequently with the wave fetch available for the wind to act (Borzone et al., 1996).

Beach morphodynamic models and classification were originally proposed for high-energy temperate coasts (Wright and Short, 1985), and are therefore biased towards those conditions. In addition, the morphodynamic index used to classify beach types was originally created by Dean to describe trends in beach profile erosion and accretion based on empirical relationships between wave energy, sand transport potential and slope (Carter, 1988). This index predicted higher erosion with storm waves, i.e. large waves with short periods. Since reflective beaches were classified as representing the accreting end of the beach depositional cycle, long wave periods were attributed to this beach type. In the present study, reflective beaches had shorter wave periods because they occurred in low energy wave climates, such as the tropics, and in low energy environments, such as adjacent to coral reefs, bays or islands facing the continent. Indeed, these environments with limited wave fetch have predominance of beaches in reflective states (Jackson et al., 2002).

8.1.2. Macrobenthic communities

An analysis of species richness, abundance and biomass of intertidal macrofaunal communities in five different biogeographic provinces, four coasts and three oceans revealed several consistent patterns: 1) an increase in species richness, biomass and abundance from reflective towards dissipative beach types; 2) an increase in species richness from temperate towards tropical and subtropical beaches, for the total species pool and in each beach type; 3) an increase in biomass and abundance towards temperate beaches; 4) an increase in mean body sizes of crustaceans, polychaetes, molluscs and isopods of the genus *Excirolana* in each beach type towards temperate regions. Although some of these patterns were observed previously, this is the first time latitudinal comparisons have been done controlling for tide, beach types and taxonomic differences.

Even though only swash length was measured, the analyses performed here support the contention that the more benign swash climate of dissipative beaches is conducive to more diverse and richer macrobenthic communities in both abundance and biomass (McLachlan et al., 1993). Adults and juveniles of beach macrofauna could move, burrow and feed better on flat beaches with fine sands and long, gentle swashes. High primary production in dissipative surf zones would fuel high macrofaunal standing stocks, which in turn would regenerate a great proportion of the nutrients needed by the primary producers (Brown and McLachlan, 1990). Reflective beaches would, in contrast, have impoverished communities due to greater difficulty in feeding, moving and burrowing caused by its steeper slopes, shorter and faster swashes and coarser sands. Only extremely well adapted fauna, with strong bodies capable of moving and burrowing fast in coarse sand would be able to survive in such harsh conditions. Mole crabs of the genera *Emerita* and *Hippa* (Dugan et al., 1999), isopods of the *genus Excirolana* (De Ruyck et al., 1991; Nel, 1995), and drift line talitrids (Gómez and Defeo, 1999) appear to be the best-adapted fauna on reflective beaches. Additionally, narrower or missing surf zones on reflective beaches would not generate surf zone circulation cells capable of maintaining blooms of surf zone diatoms in the beach ecosystem, thereby explaining the low standing stocks and densities found in this study on tropic and temperate reflective beaches.

The swash exclusion hypothesis (McLachlan et al., 1993) was devised to explain primarily differences in species diversity along the morphodynamic continuum. The way it is stated assumes that macrobenthic species could, at first instance, colonize all beach types, and only then most of them would be excluded from reflective beaches due to the harsher conditions imposed by their swash climate in comparison to the more benign swash climate of dissipative beaches. This hypothesis implicitly uses post-settlement processes to explain patterns of diversity on sandy beaches. Pre-settlement processes have been suggested to be important on sandy beaches (see review in Defeo, 1996), but no attempts have been made to explain how settlement may vary according to beach morphodynamics. The Beach Deposit Index proposed here suggests a possible link between slope and grain size and the success of fauna settlement though differences of water flow in the benthic boundary layer. The BDI is a dimensionless index that integrates the associated variation of slope and grain size of the beach deposit. For the beaches studied it varied from 5 to 450, increasing towards dissipative conditions, i.e. flat slopes and fine sands. However, low energy intermediate beaches with flat low tide slopes and fine sands, and reflective beaches with fine sands, can also support highly diverse communities. This variation in species richness, associated with the presence of flat slopes and fine sands, was detected by BDI. BDI could therefore explain the highest variation in species richness along the wave gradient of the 52 beaches studied here (Chapter 5, Fig 16) and also for 47 beaches from the literature varying along wave and tidal gradients (Chapter 5).

It is proposed here that higher species richness on flatter beaches with fine sands is explained by higher larval settlement success. The smooth bed of flatter slopes and finer sediments produces boundary layers with laminar flows and thicker viscous layers, where flow velocities are closer to zero, thereby being conducive to larval settlement. In contrast, steep slopes with high water percolation through coarser sands would generate thinner boundary layers with turbulent, high velocity vertical and horizontal flows (Elfrink and Baldock, 2002). This environment would not be conducive to successful settlement for most polychaete and mollusc larvae with low body densities. Probably only high body density larvae, such as those of decapod crustaceans, could successfully settle under these turbulent and unstable flow environments. This creates a link between benthic-pelagic processes and probably explains the higher species richness on flat fine sand beaches.

At the macroecological spatial scale analysed here, communities from tropical, subtropical and temperate beaches respond primarily to the physical environment. Indeed, a multivariate discriminant analysis performed with 10 beach community attributes can correctly classify 92% of the beaches identified as reflective, intermediate and dissipative (Table 25). This is a remarkable discrimination of physically classified beach types by biological attributes. The response of communities to the physical environment, however, seems to be complex and multifactorial. Not all members of the community responded to the same factor or suit of factors in the same way, showing that different taxa might be controlled by different factors. This is also valid when comparing the different community attributes. For example, species richness increased, but abundance, biomass and body size decreased towards the tropics. Again the patterns differed depending on the taxa.

The increase in both regional species richness and habitat species richness, in each beach type, towards tropical areas seems to be a result of the higher speciation rates in this region experienced by many beach taxa. The correlation of higher speciation rates with higher temperatures can be explained by the acceleration of metabolic processes, decreasing generation lengths and increasing mutation rates and natural selection. However, latitudinal gradients in species richness are not unidirectional and may be also influenced by historical and ecological factors. For example, some taxa, such as terrestrial species, had higher species richness in temperate regions and these were associated with the presence of stranded kelp. Stranded kelp may increase species richness on sandy beaches on a local scale not only by providing food subsidy (Soares et al., 1997), but also by increasing habitat heterogeneity on the drift line (Soares, 1994). On the other hand, stranded kelp may decrease species richness of the intertidal beach by disturbing feeding and movement of typical sandy beach organisms (Soares et al., 1996).

Because open oceanic reflective beaches were absent in the Subtropical region sampled here, two separate one-way MANOVA analyses were performed in this study for each community and taxonomic group variable analysed (species richness, abundance and biomass). It could be suggested that a two-way MANOVA considering only Tropical and Temperate regions (i.e. excluding the Subtropical region) and beach type (i.e. reflective, intermediate and dissipative) could reveal interactions between latitudinal and beach type factors invalidating the present results. Conversely, absence of significant interactions would support the interpretation of main effects made here. Indeed such analyses revealed significant latitudinal (Wilk's Lambda = 0.09; Rao's R = 1.92; DF = 40, 34; $P < 0.03$) and beach type (Wilk's Lambda = 0.12; Rao's R = 6.09; DF = 20, 17; $P <<< 0.001$) differences for all variables analysed and no significant interaction between latitude and beach type (Wilk's Lambda = 0.14; Rao's R = 1.39; DF = 40, 34; P = 0.17). The results of the one-way MANOVAs performed in this study, and also the univariate T-tests considering only tropical and temperate regions, can be considered valid and robust, supporting the patterns obtained in this thesis.

Table 25: Multiple discriminant analysis of beach types by community biological descriptors for 52 beaches

DF	Eigenvalue	Canonical R	Wilk's lambda	Chi-square	Degrees of freedom	P-level
1	2.39	0.84	0.25	61.37	20	<0.0001
2	0.17	0.38	0.85	7.02	9	0.64

Factors	Factor loading Root 1	Factor loading Root 2	F - value	P - level
Marine species richness	0.22	-0.10	2.97	0.06^{NS}
Relative species richness	0.40	-0.28^{3}	9.61	<0.001
Crustacean species richness	0.26	-0.16	3.93	0.03
Mollusc species richness	0.20	-0.14	2.49	0.09^{NS}
Total Density ($ind.m^{-2}$) ^{a}	0.36	-0.33^{2}	8.22	<0.001
Total Abundance ($ind.m^{-1}$) ^{a}	0.55^{2}	-0.18	17.91	<0.001
Crustaceans ($ind.m^{-1}$) ^{a}	0.57^{1}	-0.15	19.03	<0.001
Molluscs ($ind.m^{-1}$) ^{a}	0.36	0.09	7.58	<0.001
Total community biomass ($g.m^{-1}$) ^{a}	0.45^{3}	-0.25	7.29	0.002
Crustaceans biomass ($g.m^{-1}$) ^{a}	0.40	-0.46^{1}	10.51	<0.001

Beaches Observed as	Classified as Reflective	Intermediate	Dissipative	Percentage correct
Reflective	17	0	0	100
Intermediate	1	21	2	87.5
Dissipative	0	1	10	90.9
Total	18	22	12	92.3

$^{1}, ^{2}, ^{3}, ^{4}$ factor loading importance order in each root ; ^{a} log (x + 1), ^{NS} (P > 0.05)

The patterns revealed here were observed at a geographical macroscale at the level of the community and for typical beach taxa. At this scale, physical factors seem to play an important role in structuring beach communities. Evidence from the literature suggests that at smaller spatial and also at temporal scales, biological factors, such as competition, and demographic processes, such as stock-recruitment relationships, seem to play increasingly important roles. The dream of any ecologist is to build a simple but ultimately coherent theory that can explain ecological patterns at all temporal and spatial scales. Sandy beach communities, due to the simplicity of the physical environment, which is defined only by the movement of sand and water, could be the ideal ecosystem in which to build such a theory. However, like any other ecosystem, the shaping of beach communities is complex, multifactorial and hierarchical at evolutionary and ecological levels. The recognition of patterns and underlying processes on sandy beaches will be ultimately achieved only by tackling ecological phenomena at all scales and levels.

8.2. Sandy Beaches – the way forward

The objective of this study was to make a macroecological comparison of sandy beach community structure and physical factors along morphodynamic gradients and in different latitudinal regions in the southern hemisphere. For this purpose 52 beaches were sampled only once spanning from reflective to dissipative conditions and covering five biogegraphic areas, four coasts and three oceans. The hypotheses tested were exploratory and therefore accomplished the first step of macroecological studies: to test for the existence of repetitive patterns at a spatial macroscale (Gaston and Blackburn, 2000). Several working hypotheses about the possible mechanisms creating those patterns were suggested. In this section I will attempt to highlight how some hypotheses can be tested and will also discuss other research needs on sandy beach ecology.

8.2.1. Morphodynamics

As summarised by Brown (2001) and McLachlan (2001), the classification of beaches into different morphodynamic types has been very useful in developing an understanding of sandy beach ecology. The use of morphodynamic indices, such Dean's or the Beach State Index, to identify beach types has not been always successful due to the variable nature of the physical factors used in the equations. Although grain size is relatively stable on beaches (Carter, 1988), wave height and period are very variable and can change in a matter of minutes (Cowell and Thom, 1994). Also, as mentioned in Chapter 3, beach morphology, during non-storm periods, is generally the result of antecedent hydrodynamic conditions (Wright et al., 1985). Both of these factors together may introduce estimate errors of unknown magnitude when calculating beach types.

If biological communities are going to be sampled only once, the best would be to monitor daily the hydrodynamic factors for approximately seven days before the biological sampling. This should be done during high and low tides, running measurements of wave heights and periods during 20 minutes and then considering only the significant waves, i.e. the 33 % highest waves (Davies, 1980; Carter, 1988; Bird, 2000). If the study is annual, the wave and slope monitoring should be repeated monthly to additionally calculate the modal morphodynamic state of the beach studied. Beach sediments may be collected only once per month, but beach slopes should be monitored together with the wave conditions.

As mentioned in Chapter 3, the usefulness of the beach morphometric model to predict equilibrium slopes should be tested after inserting into the equation some important variables, such as wave period, beach permeability and surf and swash zone wave-bottom friction coefficients. Also, calculations should be done considering the breaks in slope in some beaches, and further laboratory and field tests should be performed to ascertain its predictive value. The daily hydrodynamic and beach slope data collected before biological sampling could then be used to test if beach slopes and fauna respond to antecedent hydrodynamic conditions (Chapter 3).

The new Beach Deposit Index (BDI) could also be used in ecological studies, since it is an integrated measure of the morphodynamic forces acting on the beach deposit and its fauna. It has the special advantage of not depending on the time-consuming monitoring of wave heights and periods. The link between the BDI and the flow environment in the benthic layer should be verified with field data. This should be done in association with geomorphologists, since measurements of field velocities in the water column of the swash zone (Archetti and Brocchini, 2002) are very difficult and highly complex to perform (see recent reviews by Butt and Russel, 2000; Elfrik and Baldock, 2002 and Longo et al., 2002).

The analyses of beach types in different latitudes in Chapter 4 revealed that tropical eastern coasts had a predominance of low energy reflective beaches, some of those fronted by coral reefs. Since the distribution of coral reefs is mainly concentrated on the east coasts of the continents (Chapter 4; Davies, 1980; Bird, 2000), it would be interesting to also investigate tropical beaches on western coasts. In the southern hemisphere, these coasts are exposed to larger westerly swells (Davies, 1980), a lower sea-surface temperature, due to north-flowing currents branching from the circum-Antarctic west drift current, and also to cold waters upwelled from the bottom of the sea (Shannon, 1985). It would be interesting to know the beach morphodynamic types occurring under these conditions and the community structure of the beach fauna to contrast with the present results. Dissipative tropical beaches were rare on the coasts studied here, probably due to the low wave energy climate and also due to lack of fine sand input on the coast. Therefore, conditions favouring the development of dissipative beaches in tropical regions, such as beaches close to large rivers bringing fine sand to the coast, i.e. the Sergipe coast with the São Francisco River in northeast Brazil, should be also investigated.

The discussion of morphodynamics has so far been concentrated only on the intertidal beach. However, it is well known that the morphology of the intertidal beach is the result of, and interacts with, the surf zone dynamics (Carter, 1988). It would then be extremely important to perform morphological and sedimentological measurements not only on the intertidal but also in the surf zones, as outlined before, and to calculate indices such as the surfing scale parameter (see Borzone et al., 1996) to have a complete picture of beach morphodynamics.

8.2.2. Macrobenthic communities

The results obtained in this study are related to the methodology used. They are meso- (intra-region) and macroscale (inter-region) comparisons concerning only inter-beach type and inter-regional spatial patterns in species richness, abundance, biomass and body size. According to Wiens (1989), biogeographical studies have a particular sampling scheme designed to cover as many points as widely separated as possible to cover a large spatial scale – in the case studied this would be one transect sampled only once per beach in several different types of beaches per region and in several regions. Thus a large spatial cover is gained at the cost of losing resolution at a small spatial scale, i.e. many transects on one beach and over time. Because of the large scale, studies, such as performed here, can be interpreted at ecological and evolutionary scales (Wiens et al., 1986; Wiens, 1989). Most of the hypotheses advanced here comprise those scales.

Three new species were discovered during this study: the spionid polychaete *Scolelepis vazaha* in Madagascar (Eibye-Jacobsen and Soares, 2000) and the cirolanid isopods *Eurydice kensley*i and *Eurydice barnardi* on the west coast of South Africa (Bruce and Soares, 1996). At least three more new species of Malagasy cirolanids and one of Baiano (from northeast state of Bahia in Brazil) ophelid polychaete were present and are waiting to be described. I predict that more research in the tropics will uncover many more new species, increasing its already high species richness.

In this study, species richness and abundance were better correlated with the Beach Deposit Index, in comparison to other physical factors suggesting that processes occurring at the scale of the benthic boundary layer may influence larval and juvenile settlement. Measurements and observations in the swash zone are very difficult to do but are not impossible. For example, Frouin et al. (1998) filmed the behaviour of an abundant new species of *Scolelepis* on high-energy reflective beaches on French Tahiti. In order to test the hypothesis that larvae of macrobenthic species settle more successfully on flat slopes with fine sands than on steep slopes with coarse sands, both field and laboratory experiments should be done. On each beach, meroplankton can be sampled in the surf zone and swash water column during the run-up and run-down of each swash, and abundances in the water column can be compared to abundances of freshly settled larva and juveniles in the sediment. This could be done under varying regimes of wave energy during the recruitment period in the area to test each species larval settling competence. Larvae could then be brought from the field to the laboratory to be tested in flume tanks (Snelgrove and Butman, 1994) if they can better withstand current flows in fine sands in comparison with coarse sands.

An increase in species richness, abundance and biomass from temperate to tropical regions was observed here only on eastern tropical coasts. The same comparison should be done including the higher energy west tropical coasts, since they are less affected by coral reefs. Also tropical beaches close to large rivers should be sampled to see the effects of the input of fine sands on morphodynamics and how this affects the fauna in the tropics in comparison to beaches in areas with coral reefs. The effect of coral reefs on community structure should also be tested. In the same tropical area, beaches in the same morphodynamic state fronted and non-fronted by coral reef should be compared.

The results obtained here did not test for latitudinal gradients on the same coast. The hypothesis that the increase of species richness in the tropics was the result of the inclusion of widely distributed temperate species can only be tested by comparing tropical and temperate beaches on the same coast. Therefore a similar study to the one done here should be performed along the same coast, controlling for tidal and morphodynamic influences.

It has been suggested that upwelling areas in the tropics distort latitudinal diversity gradients of coastal benthic communities (Macpherson, 2002) probably due to decreasing sea surface temperatures. This could be tested for sandy beach fauna by comparing tropical beaches within and outside, both north and south, of upwelling cells. Recent comparisons on the north coast of Chile did not detect any differences (Jaramillo et al., 2001). Such comparisons should also be done in other upwelling tropical coasts such as found in Oman, Cabo Frio (in Rio de Janeiro), Senegal and India.

Productivity has not been measured in this study, but maps of primary productivity (Dring, 1982; Levinton, 1995) indicate that the tropical coastal areas studied here are less productive than their temperate counterparts. This pattern is also confirmed by the fact that primary production on sandy beaches and rocky shores around the Southern African coasts is higher in the temperate in comparison with the tropical coast (Bate et al., 1990; Bustamante et al., 1996). Since nothing is known about phytobenthos production on sandy beaches, a careful study should be carried out comparing primary and secondary production in the water column and sediments in tropical and temperate regions.

Although not directly addressed in this study, ecological sampling design on beaches has been widely discussed lately (Jaramillo et al., 1995; James and Fairweather, 1995; Cardoso and Veloso, 1997; Defeo et al., 2001). The area per beach sampled here ranged from 3.3 to 4.5 m^2, being large enough to sample more than 90 % of the species on dissipative beaches (Jaramillo et al., 1995). On intermediate subtropical beaches in Brazil a total area of 2 m^2 is large enough to sample 90 % of the fauna (Cardoso and Veloso, 1997). However, the discussion on the number of transects per beach and the distribution of stations per transect has been more contentious than that regarding area (James and Fairweather, 1995; Defeo and Rueda, 2001). Since beach fauna distribution, like most benthic organisms, is patchy, the most appropriate sampling design is a grid of stations regularly distributed from high to low tide spring. The number of grids along the beach would depend on along-shore variability in beach morphology and on the research question. This design has been successfully applied to only two sandy beach studies (Bally, 1983; Giménez and Yannicelli, 2000), which identified different controlling factors at different spatial scales. The grid cell sampling design would additionally eliminate the problem of autocorrelation, common in organisms that are distributed along environmental gradients (Legendre, 1993). The grid sampling design can be analysed by powerful geostatistical methods such as kriging, which can calculate auto and cross-correlations and lag differences between species abundances and biomass and morphological features such as cusps horns and bays (Giménez and Yannicelli, 2000).

The sandy beach ecosystem, however, comprises the intertidal beach and surf-zone. There is intense exchange of materials between these compartments, in the form of nutrients, organisms and sand, and also energy in the form of wave turbulence (McLachlan et al., 1981; Carter, 1988). Borzone et al. (1996) have sampled beaches intertidally and subtidally across the entire morphodynamic spectrum. They observed an increase of saturation zone width from reflective to dissipative beaches followed by an increase of subtidal species on the intertidal. Therefore they concluded that the increase in species richness along the morphodynamic gradient is due to the inclusion of inner-surf zone fauna into the lower intertidal beach. Following this result, it could be stated that the intertidal macrobenthic community structure of intermediate and dissipative beaches is more dependent on the surf zone community structure than on reflective beaches due to greater morphodynamic interaction between these two compartments on the former beaches (Wright and Short, 1994, Carter, 1988). The greater link of both biological and morphodynamic environments on intermediate and dissipative beaches makes these beaches constitute a true ecosystem depending more on internal than external inputs of energy and material (McLachlan et al., 1981; Brown and McLachlan, 1990). Reflective intertidal beaches would therefore depend more on external inputs of energy and materials, not constituting true ecosystems (Brown and McLachlan, 1990). To test this hypothesis, future studies should sample both intertidal and subtidal parts of the beach along the complete morphodynamic spectrum (Borzone et al., 1996).

From the perspective of conservation, it should be noticed that unexpectedly low relative species richness was observed on highly dissipative beaches within tourist areas such as Strandfontein (38 %) on the west coast of South Africa, and Prainha (48 %) on the southeast coast of Brazil (Appendix 5). It is not yet clear whether trampling affects beach fauna (Jaramillo et al., 1996b; Moffet et al., 1998), but more research should be done, since there is an increasing recreational pressure on beaches of the southern hemisphere (De Ruyck et al., 1995; 1997a; 1997b). Future studies should also encompass highly impacting experiments such as football games on the saturation, retention and dry sand zones, performed daily during the summer season to mimic tourist user patterns.

According to the results presented here (Chapters 3; 4; 5; 6 and 7) both intertidal sandy beach community structure (species diversity, abundance and biomass) and environmental settings (beach slope, grain size, wave height and period) differed significantly according to beach morphodynamic type. Thereby, in order to account for the influence of morphodynamics, it is of utmost importance that beach type is controlled for in any ecological or environmental impact study. The lack of control of morphodynamic influence may be the reason why many previous studies could not detect the impact of nourishment (Hayden and Dolan, 1974; Gorzelany and Nelson, 1987; Rakocinski et al., 1996). The few impact studies that accounted for morphodynamic influences had mixed results with some detecting (McLachlan, 1996; Peterson et al., 2000; Schoeman et al., 2000) and others not detecting (Jaramillo et al., 1996; Jaramillo et al., 2002) any significant impact. Alternatively, beach fauna, due to their high phenotypic plasticity (Brown, 1996; Soares et al., 1996; 1998; 1999) may be highly resilient to physical impacts (Jaramillo et al., 2002). This alternative hypothesis will only be appropriately tested in studies controlling for beach type and tidal influences with a higher sampling resolution (daily and weekly sampling), following the temporal trajectories of impacted and non-impacted sites over longer temporal scales than presently analysed, i.e. years.

The effect of minimum viable population sizes has been widely discussed in the terrestrial conservation literature (see review on Pimm, 1991). It is not yet known which is the minimum viable population size for beach fauna, and if this varies according to species and morphodynamic type. In this study, reflective beaches had on average lower abundance and biomass than their dissipative counterparts (Chapter 6; 7), and, in certain cases, different species composition than dissipative beaches (Appendices 2; 3; 4; 5). Tropical beaches had on average lower abundance and biomass than their temperate counterparts (Chapter 6; 7). If we apply the precautionary principle for managing beaches, it could be suggested that the communities on beaches with lower abundances and biomass, i.e. reflective and tropical beaches, could be facing a higher risk of extinction than dissipative and temperate beaches subject to a recurrent environmental and/or anthropogenic impact. Increase in coastal human populations and tourism in underdeveloped and developing countries (Brown and McLachlan, 2002), mostly in the tropics, point to the need for more detailed studies concerning the ecology and conservation of tropical beaches.

9. References

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10. Appendices

10.1. Appendix 1.

Physical characteristics of the 52 studied beaches.

Beaches	BDI	BSI	Deans	1/ Slope	Beach width (m)	Sand size (mm)	Water table depth (cm)	Wave height (cm)	Wave period (s)	Surf zone width (m)	Saturation width (m)	Swash length (m)	Temperature (°C)	Salinity ($^0/_{00}$)
Cap Est low energy	14	0,49	0,84	5	8	0,37	45	20	4,3	1	1,20	1,20	29	35
Cap Est high energy	17	0,48	0,81	7	21	0,42	66	50	10,3	1	7,50	5,00	27	20
Ampanavoana	12	0,54	0,99	7	23	0,61	127	100	10,4	50	3,60	9,00	26	25
Varingut	19	0,74	1,78	8	28	0,43	95	40	3,5	15	4,00	4,00	27	24
Fampotabe	34	0,41	0,63	9	18	0,28	97	30	12,2	1	3,20	3,20	28	20
Ampanavoana CR	34	0,45	0,74	10	15	0,31	46	5	1,5	1	1,50	1,50	28	24
Ambudi	25	0,14	0,15	14	12	0,59	51	10	7,3	1	1,00	0,00	27	20
Maroantestra	54	0,73	1,73	15	18	0,29	19	25	3,5	35	2,60	1,30	30	10
Ambinanibe	70	0,99	3,52	20	35	0,30	38	170	11,3	50	10,00	17,50	25	36
Fotobato	73	0,81	2,18	22	42	0,31	54	94	9,4	50	18,00	15,00	28	33
Baie de Singe	212	1,29	7,45	37	42	0,18	19	185	11,3	120	18,00	24,00	24	35
Tororão	19	0,60	1,12	8	30	0,45	43	60	7,8	50	10,00	5,00	23	36
Iemanjá	12	0,33	0,43	8	24	0,72	61	30	6,2	1	3,40	3,40	25	32
Ponta da Baleia	26	0,56	1,00	10	36	0,40	50	50	8,3	15	10,20	2,80	26	34
Cumuruxatiba	35	0,32	0,42	12	26	0,36	22	15	6,7	1	10,00	0,00	22	34
Zeloris	29	0,72	1,62	12	49	0,42	36	90	8,6	100	24,50	7,00	26	32
Porto Marina Hotel	29	0,32	0,42	13	32	0,47	24	20	6,5	1	16,10	4,60	25	31
Hawaizinho	39	0,67	1,41	13	49	0,34	40	80	11,2	10	28,00	7,00	23	36
Praia do Farol	38	0,72	1,62	13	56	0,35	27	80	9,4	15	36,00	12,00	26	34
Pontal do Sul	37	0,38	0,54	15	42	0,42	66	20	5,7	1	3,00	0,00	26	31
Lugar Comum	159	0,88	2,50	34	112	0,22	12	80	11,2	20	72,00	24,00	26	33
Grande SFS	22	1,00	3,64	9	38	0,43	52	200	8,5	2	8,10	8,10	19	34
Riviera	33	0,86	2,53	13	39	0,41	36	100	6,5	2	12,00	12,00	22	32
Brejatuba	54	0,81	2,21	15	49	0,29	29	100	11,3	2	14,00	17,50	22	36
Santiene	51	0,84	2,36	18	49	0,36	42	100	8,0	3	10,50	7,00	23	34
Ubatuba	87	0,92	2,90	23	49	0,27	26	100	9,3	50	10,50	10,50	21	30
Prainha	152	1,31	7,82	30	70	0,20	26	200	10,3	100	25,00	15,00	20	33
Peças	234	0,81	2,18	35	70	0,15	18	20	5,6	30	15,00	10,00	23	31
Deserta	277	1,48	11,69	40	84	0,15	10	150	8,2	100	42,00	18,00	23	34
Grande Ilha do Mel	303	0,99	3,54	44	84	0,15	24	50	9,0	50	14,00	14,00	23	32
Atami	450	1,22	6,24	55	126	0,13	5	50	6,7	50	45,00	9,00	23	35
Mailquillahue	14	0,14	0,21	12	32	0,90	5	32	11,3	1	2,30	4,60	13	36
Punta Gabiota	23	0,60	1,59	12	45	0,53	51	242	19,5	100	9,60	6,40	13	35
Alepue R	49	0,55	1,35	13	35	0,27	27	27	5,9	1	7,50	7,50	13	36
Mehuín	90	1,02	5,10	20	42	0,23	28	222	16,5	150	6,00	9,00	13	35
Chan-Chan	69	0,85	3,25	22	63	0,33	66	238	16,6	150	4,50	9,00	13	36
Pichicuyin	112	1,05	5,40	25	66	0,23	35	238	16,5	150	23,50	18,80	13	36
Ronca	113	1,02	5,09	26	70	0,24	38	219	15,5	120	15,00	15,00	14	35
Universitaria	116	1,04	5,26	27	63	0,24	33	196	13,2	120	4,50	9,00	13	34
Alepue I	105	0,93	3,96	28	84	0,28	43	258	19,0	175	12,00	6,00	13	32
Cheuque	143	1,12	6,44	32	91	0,23	34	229	13,3	70	13,00	26,00	13	36
Punta de la Barra	196	0,80	2,80	43	84	0,23	18	118	16,3	120	6,00	21,00	13	31
Slipper Bay	14	0,33	0,43	8	32	0,60	76	40	10,3	1	5,40	2,70	15	33
Velddrif	33	0,61	1,17	10	32	0,31	69	30	6,3	20	2,70	2,70	13	30
Stompneus Bay	56	0,63	1,25	11	42	0,20	60	30	11,0	1	16,50	10,50	15	33
Bloubergstrand	33	0,88	2,51	11	39	0,35	54	150	12,5	70	6,00	6,00	13	36
Britannia Bay	63	1,05	3,94	17	65	0,28	57	175	12,5	100	20,00	20,00	14	35
Spoegrivier	81	1,00	3,43	23	83	0,29	27	160	12,5	70	43,00	26,00	14	-
Strandfontein	136	1,31	7,33	26	90	0,20	16	200	12,5	100	42,00	42,00	14	-
Dwarkesboos	190	0,86	2,41	27	78	0,15	32	30	9,0	30	54,00	18,00	14	33
Groenrivier	136	1,08	4,22	33	111	0,25	54	160	12,5	80	31,00	23,20	14	-
Silwerstroomstrand	239	1,50	11,56	36	105	0,16	12	200	12,5	150	53,00	24,00	13	-

10.2. Appendix 2.

Community structure and species composition on 11 beaches of South-Central Chile. Abundance (ind)/biomass (g) per running meter.

	Mailquillahue	Punta Gabiota	Alepue R	Mehuin	Chan-Chan	Pichicuyin	Ronca	Universitaria	Alepue I	Cheuque	Punta de la Barra
Orchestia chiliensis	21/0.1546		16/0.0182	9/0.0077	14/0.0113			13/0.0120			
Orchestoidea tuberculata	1673/11.9481	13202/59.863	9187/16	1111/1.52	20735/92	5313/29.17	212963/491	3219/17.5	25956 /459	8667/56.1	25033/119
Bathyporeiapus magellanicus			122 /0.0816	3429/1.71	58/0.0268	2294/16.49	3519/1.2841	3798/1.64	2389/1.15	6613/2.5	1880/0.6204
Cheus annae				9/0.0039	14/0.0028		16/0.0092		3710/0.8654		19/0.0177
Phoxocephalopsis				19/0.0145		75/0.0315	400/0.0727	13/0.012			38/0.0236
Huarpe sp						30/0.0255				41/0.037	288/1.1
Phoxocephalidae						15/0.0015					
Amphipod 1	7/0.0021	125/0698									
Amphipod 2		62/0.0524									
Excirolana braziliensis		94/0.4745	179/0.3349	1102/3.64	4533/16.5	1419/5.19	6095/19.26	1966/5.94	1975/13.3	5545/12.6	1151/2.99
Excirolana hirsuticauda		3623/9.99	1923/6.1726	5878/9	16303/48	3275/20.64	12589/20.45	11313/18	2150/3.46	5217/10.1	5333/5.35
Excirolana monodi			122/0.4204	226/0.532		196/16.27	64/0.1409	215/0.585	2150/1.66	82/0.2201	921/10.22
Macrochiridothea setifer					14/0.0127	302/0.8405	672/12.89		32/0.1603	103/0.314	19/0.0825
Sphaeromatidae 1		10/0.0216	16/0.0150								
Sphaeromatidae 2		10/0.0185									
Emerita analoga	106/9.1518	625/71.26	4878/633.95	15240/1497	7684/700	19019/2804	12877/2118	15972/13	7420/913	23825/77	5525/335
Lepidopa chilensis				38/0.0869		15/0.0150	80/5.6466			21/0.024	153/0.3494
Oligochaeta	276/0.0680										
Euzonus heterocirrus		20334/37.57	16/0.0095	57/0.0821	115/1.44	45/0.03	144/0.3141	27/0.0533		21/0.0074	58/0.0982
Nephtys impressa			41/7.1734	19/0.1691		45/3.7734	32/0.7436	13/1.4689	16/1.0615	62/3.227	230/1.64
Hemipodus triannulatus		52/0.4539									
Scoloplos sp		10/0.0842				15/0.9996					58/0.9148
Dispio sp		21/1.0629									
Scolelepis sp		10/0.0277		9/0.0097		15/0.0450					
Boccardia sp											19/0.0883
Mesodesma donacium				28/0.1285		30/0.1626	32/0.1917	13/0.8869		62/5.19	96/1.31
Nemertinea 1											115/0.2258
Nemertinea 2	99/0.1811										
Curculionidae 1				66/0.0522							
Coleoptera 1							208/11.6		80/0.1167		
Coleoptera 2					14/0.0141		16/0.0196				
Coleoptera 3									64/0.0965		
Coleoptera 4									96/0.1292		19/0.0334
Coleoptera 5				9/0.0116							
Coleoptera 6				9/0.0097							
Phalerisidia maculata		10/0.1849			29/0.0423	15/0.0916	8894/29.36	229/1	1051/3.88	21/0.0277	652/1.32
Bledius maculipennis		10/0.0267					48/0.0508		510/0.6568		58/0.053
Bledius sp									48/0.6567		
Hymnoptera 1				132/0.0676			608/0.3418	13/0.0107			19/0.0196
Hymnoptera 2					29/0.0197		16/0.0092				
Diptera 1		10/0.0154	8/0.0095	57/0.2947	1338/8.07	91/0.0645	1072/1.0543		653/0.1914		345/2.48
Diptera 2				9/0.0386	14/0.0705		1248/0.4122	13/0.0067	80/0.0233		441/0.1963
Diptera 3							16/0.0774				
Tabanidae larvae		10/0.0134									
Diptera larvae 1	78/0.1797	1458/1.7376									
Diptera larvae 2		10/0.0010									
Diptera pupae	35/0.2283	156/0.2742			14/0.0028				111/0.0265		
Mosquitoe larvae									64/0.0265		
Hemiptera 1				188/0.2067	14/0.0071		16/0.0115				
Hemiptera 2											
Marine species richness	5	13	9	13	8	16	13	10	9	12	17
Total density (ind.m^{-2})	72	850	452	652	786	474	3634	607	653	544	492
Total abundance (ind.m^{-1})	2296	39845	16508	27645	50925	32211	261625	36820	46800	50278	42470
Average biomass (g m^{-2})	0.6805	3.9642	18.6418	34.8476	13.6413	42.9058	52.2104	23.4616	19.9882	94.2491	5.464
Total biomass (g m^{-1})	21.92	183.2	664.2	1515	865.6	2898	2713	1406	1400	7843	482.7

10.3. Appendix 3.

Community structure and species composition on 10 beaches of Bahia in Northeast Brazil. Abundance (ind)/biomass (g) per running meter.

	Tororao	Iemanjá	Ponta da Baleia	Cumuruxatiba	Zeloris	Porto Marina Hotel	Hawaizinho	Praia do Farol	Ponta do Sul	Lugar Comum
Metharpinia sp						7/0079				
Monoculodes sp				13/0.0023						
Platorchestia platensis		231/0.3068	840/1.6205		213/0.2310	1313/2.385		195/0.2597	982/2.4426	398/0.2252
Orchestia brasiliensis	188/0.4869	161/0.3404	386/0.7331		183/0.1267	7/0.0053		24/0.048	27/0.133	25/0.0462
Bathyporeiapus copacabana								37/0.0101		25/0.0051
Atylus minikoi			8/0.0043							
Chaetilia sp			8/0.0105		122/0.0274			134/0.0497		
Excirolana armata										25/0.0201
Excirolana braziliensis	297/0.4491	161/0.1706	1092/0.9852	66/0.134	386/0.2585	172/0.2397	1528/3.4523	366/0.1799	216/0.5041	4278/4.23
Excirolana carangis	22/0.0629			152/0.4274						
Eurydice sp					10/0.0043	7/0.0095				
Eurydice littoralis					10/0.0023					
Metamysidopsis neritica			277/0.1122			97/0.0277	9/0.0041	37/0.0084		
Bowmaniella brasiliensis			202/0.2297		355/0.1518	37/0.0087	93/0.0881	268/0.2662	9/0.0307	
Emerita brasiliensis		11/0.471	17/22.016		203/5.4134					497/5.81
Emerita portoricense	43/0.4269	70/1.4122	59/5.6686	20/0.2077		172/18.81	121/0.9178	49/3.5411	189/9.9598	
Lepidopa richimondi	7/0.3802		8/0.4746		10/0.4077			37/0.3575		50/0.1091
Lepidopa venusta										25/6.4827
Pinnixa patagoniensis			59/0.1216			60/0.1043	19/0.25	24/0.0501	9/0.0721	671/3.0697
Ocypode quadrata						7/0.0015				
Neocallichirus sp								12/3.1072		
Ogyrides hayi								12/0.0128		25/0.0658
Scolelepis squamata	29/0.0634	16/0.018	17/0.0321	7929/2.2291	20/0.0629	45/0.1077		110/0.1876	27/0.1542	1890/0.2042
Scolelepis sp	14/0.0065							49/0.0167		
Euzonus mamillata	7/0.0091		17/0.2045			7/0.0165		24/0.17		75/0.0298
Hemipodus rotundus	80/0.1815	268/1.108	42/0.0757	264/0.7251	51/0.0843	753/0.6258	578/1.2056	353/0.515	63/0.2125	1094/0.8965
Hemipodus olivieri			336/0.7301							
Orbinia sp	123/0.1470		8/0.0145		10/0.0094			49/0.0379		50/0.032
Scoloplos sp						22/0.0531				
Dispio sp	29/0.1		8/0.1207					98/0.8172	9/0.089	
Lumbrineris tetraura						15/0.6013				50/0.6108
Armandia sp				561/0.4628						
Magelona riojai									9/0.0189	
Lumbrineridae			8/0.0174							
Annelida			8/0.031							50/0.3496
Donax hanleyanus			8/1.0831			7/0.3773	587/126.54	12/2.3052	9/1.1651	
Donax gemmula				7/0.1065	10/0.0781			37/0.0224		448/0.1389
Tivela mactroides								12/0.4173		25/0.8357
Iphigenea brasiliana		5/4.0157			10/7.5820	15/6.4505				
Ollivancillaria uretai							19/5.7975			
Mellita quinquiesperforata			8/2.8197		51/3.7699			146/78.93		
Nemertinea		16/0.0123		73/0.039						
Aranae 1			17/0.3881		20/0.0702			37/0.4441	27/0.5424	
Aranae 2								12/0.0128		
Labiduria riparia										50/0.027
Coleoptera larvae	10/0.0514	5/0.0083		20/0.0452	20/0.0123	30/0.0353				25/0.0784
Phaleria brasiliensis		54/0.254	8/0.0371	26/0.1093	10/0.0329	119/0.5128				497/1.5348
Bledius bonaerensis				7/0.0061						
Bledius microcephalus		5/0.0022								
Diptera pupae				7/0.0043						
Diptera 1		5/0.0134								
Tabanidae larvae										25/0.5652
Insecta larvae			8/0.0096		10/0.0139		9/0.0433			25/0.0431
Ant lion										25/0.0203
Formicidae				20/0.0063	10/0.0009					
Isoptera									144/0.1257	
Marine species richness	12	10	23	11	17	15	10	23	13	20
Total density (ind.m^{-2})	30	42	98	331	38	86	71	39	42	92
Total abundance (ind.m^{-1})	854	1009	3453	9163	1715	2894	2963	2133	1720	10346
Average biomass (g m^{-2})	0.0810	0.3224	1.0282	0.1697	0.3093	0.8941	0.4004	1.8004	0.3523	0.3093
Total biomass (g m^{-1})	2.365	8.133	37.54	4.505	18.34	30.38	138.3	91.77	15.45	25.43

10.4. Appendix 4.

Community structure and species composition on 10 beaches of the West Coast in South Africa. Abundance (ind)/biomass (g) per running meter.

	Slipper Bay	Velddrif	Stompneus Bay	Bloubergstrand	Britannia Bay	Spoegrivier	Strandfontein	Dwarskesbos	Groenrivier	Silwerstroomstrand
Talorchestia		230/0.6981	107/0.4359	1286/3	1057/1.78	754/1.4976	2552/5.13		13787/22.11	
Talorchestia australis										1079/1.582
Mandibulophoxus sp						5486/3.8518	1811/1.61		11579/15.21	123/0.1814
Urothoe tumorosa										25/0.0161
Urothoe sp					15/0.0084					49/0.0161
Bathyporeia sp							515/0.2444			
Eurydice kensleyi n.sp.		15/0.0285	1514/0.925		4672/2.94	2602/4.3478	3025/4.24	1360/1.768	10552/11.76	34253/21.95
Eurydice barnardi n.sp.	9/0.0027									91136/42.14
Exosphaeroma			172/0.2851					93/0.1236		
Exosphaeroma					15/0.3334					
Tylos granulatus	18/2.8132				123/1.77	603/10.5609	494/2.77		2003/336.76	
Excirolana natalensis	560/14.2385	115/0.9884	215/3.4492	3370/12.87	2037/14.69	245/2.2565	226/3.26	261/5.65	1617/15	74/0.3054
Excirolana latipes			54/0.9		506/12.83	339/6.6549	473/8.61		719/12.92	172/5.1135
Halioplasma caecus			11/0.0165							
Niambia sp		15/0.0086	21/0.0087		61/0.0299	509/0.1164	21/0.0067		590/0.1929	
Gastrosaccus					567/2.3615	1452/11.09	1297/2.7	19/0.017	924/1.126	4855/11.8824
Gastrosaccus brevifissura										25/0.0918
Mesopodopsis slabberi		8/0.013								
Cumopsis sp					46/0.0072			261/0.0433		123/0.0413
Myodocopina								410/0.8933		
Calianassa kraussi			140/3.9795							
Magelona papilicornis			204/0.8250							
Lumbrineris tetraura			32/4.8453							
Paraonides lyra capensis					31/0.0275			75/0.0294		
Glycera convoluta					15/0.0681			19/0.0448		
Dispio magna					92/2.94			317/2.48		
Scolelepis squamata	27/00.18	107/2.5253	1944/1.130	10/0.038	291/1.84		247/2.76	279/0.204		7527/30.77
Prionospio saldanha			75/0.0217	10/0.005				75/0.0355		
Nephtys capensis			11/0.0251		521/2.68		21/0.0426	298/2.5238		147/1.64
Sigalion capensis								56/3.8111		
Cirriformia tentaculata			21/6.5075							
Sternaspis scutata			11/1.4941							
Donax serra		8/6.236		3519/141	1363/622		247/211			687/145
Bullia digitalis					322/69		41/7.43	317/14.11		245/26
Bullia laevissima								75/49		
Bullia tenuis										252.72
Nemertinea		8/0.1011	881/25.334		4978/44.6	94/2.71	700/9.9		565/59.5	221/10.83
Coelopa africana	27/0.0322									
Fuscelia capensis	18/0.0134									
Diptera pupae	311/0.3914	107/0.248	161/0.2652		138/0.1506		391/0.3274	19/0.0525	26/0.0079	539/0.2457
Diptera 1					15/0.0048					
Diptera 2					15/0.0048					
Diptera 3	9/0.0018									
Diptera 4	9/0.0027									
Diptera 5			11/0.0806							
Diptera 6			11/0.0052							
Diptera 7		8/0.0052								
Tabanidae larvae	9/0.1475		21/0.7184		15/0.3561					
Chironomidae	9/0.0027									
Mosquito larvae	391/0.5112	614/1.1067	473/0.4402	10/0.002						
Mosquito 1			11/0.0043							
Telmatogeton larvae							21/0.0179		103/0.0159	
Hymenoptera	9/0.0027					19/0.059				
Pachyphaleria capensis				10/0.113			41/0.49	19/0.3215	51/0.5154	
Acanthoscelis ruficornis							62/1.64		26/3.67	
Staphylinidae	160/0.0974	15/0.0026	140/0.0607		31/0.0179		62/0.009		26/0.0026	245/0.0712
Curculionidae			11/0.0078							
Coleoptera 1	36/0.0456		215/0.1881	10/0.018						
Coleoptera 2					15/0.0191					
Coleoptera 3	9/0.0045									
Coleoptera 4	18/0.0116									
Coleoptera 5			21/0.0494							
Coleoptera 6	18/0.0402									
Coleoptera larvae	9/0.0054		11/0.0199							
Aranae 1						19/0.1079			51/0.14	
Aranae 2									51/0.0423	
Marine species richness	4	8	16	5	18	9	14	16	9	17
Total density (ind.m^{-2})	48	42	155	196	263	143	132	50	369	1283
Total abundance (ind.m^{-1})	1652	1251	6498	8225	16942	12122	12246	3950	42670	141547
Average biomass (g m^{-2})	0.527	0.355	1.5393	3.7457	15.5462	0.5699	2.5994	1.2522	4.0272	2.9102
Total biomass (g m^{-1})	18.3663	11.9614	52.0252	157.2974	780.3133	43.2484	262.2803	81.278	478.9663	300.6145

10.5. Appendix 5..

Community structure and species composition on 11 beaches of North and Southeast Madagascar. Abundance (ind)/biomass (g) per running meter.

	Cap Est Low Energy	Cap Est High Energy	Ampanavoana	Varingut	Fampotabe	Ampanavoan a Coral Reef	Ambudi	Maroantsetra	Ambinanibe	Fotobato	Baie de Singe
*Talorchesti*a sp	248/0.4504	370/0.3531	72/0.108	800/0.89	1049/1.223	2000/1.35	13/0.0113	940/1.2		129/0.17	40/0.0418
Amphipoda sp		5/0.0015									
Diogodias platyrostris	31/0.0084	25/0.0095		68/0.0414	292/0.0804	5/0.0025	19/0.0216		919/0.3882	20/0.026	30/0.0149
Urothopsis brevicauda											620.23998
Excirolana geniculata	10/0.1154	79/0.3471	36/0.0738	6/0.0138	10/0.0804	5/0.1164	16/0.0742		15/0.0217	339/4.59	
Excirolana sp	5/0.0202										
Excirolana affinis				19/0.0157				576/0.77			
Eurydice orientalis		20/0.0214		99/0.118	972/1.092	35/0.0365	51/0.0602				
Eurydice inornata	21/0.0369								36/0.0217	10/0.025	
Eurydice indicis									175/0.3711		
Eurydice sp 1											10/0.0139
Eurydice sp 2	3/0.0036									60/0.115	7381/9.22
Tylus sp	7/0.0034										
Alloniscus	5/0.0006										
Dies monodi								4/0.0028			
Exosphaeroma estuarium				6/0.0044							
Pseudosphaeroma barnardi							3/0.0047				
Gastrosaccus madagascariensis	9/0.054	345/0.381	216/0.2076	236/0.1814	583/0.2431			63/0.0217	372/0.4595	3894/1.3	10/0.0169
Cumacea	2/0.0002										
Emerita austroafricana	19/1.38			56/0.101					357/82		80/8.74
Hippa adactyla		64/0.3381	48/0.8358	12/0.023	61/0.5834		10/0.7353		131/5.56	10/0.117	10/2.71
Philyra scabriuscula											100/34.4
Ocypode ceratophtalmus						5/14.43					
Ocypode madagascariensis									22/0.8539		
Brachyura megalop			6/0.0018					4/0.0007			
Oligochaeta				6/0.005				7/0.0032			
Annelida											30/0.404
Scolelepis williami	385/0.61	15/0.0743							58/2.5	2619/3.1	4443/4.89
Scolelepis lefebvrei	159/0.5756					1516/4.22		93/0.2652			10/0.007
Scolelepis vazaha n.sp.	137/0.1413			12/0.0094				1996/0.35		20/0.009	339/0.1971
Scolelepis squamata						165/0.6461		468/0.117			
Dispio sp	2/0.0071			6/0.0119							
Glycera tesselata							6/0.0206				
Goniadopsis incerta		10/0.1356							139/1.1	239/0.96	80/0.5753
Goniadella gracilis							3/0.0047				
Leptonereis sp						15/0.6931					
Lumbrineris sp						5/0.1814					
Armandia sp											70/0.1433
Sigalion mathilde									29/0.9151		
Psionidens indica		15/0.0125	42/0.0216	6/0.0031	26/0.0086				44/0.0325		
Donax simplex	7/0.0081								277/0.8477	50/0.089	7859/6.43
Donax faba						70/2.2866					
Donax aemulus	2/0.0028	69/2.2407		198/0.5356	15/0.1796	5/0.0005			168/3.4132		548/1.38
Donax incarnatus	80/2.2964									40/0.613	
Donax madagascariensis									7/0.1674		
Taria sp						15/5					
Atactodea glabatra						304/7	90/4.23				
Bivalvia spat								7/0.0025			
Nemertinea 2				62/0.138			3/0.0013	4/0.0011	22/0.7121	10/0.009	20/0.1682
Willeya delagensis							13/2.25				
Sipuncula				6/0.0075					7/0.017		
Apodocreedia vanderhorsti						5/0.0255					
Draculo celetus				6/0.0402							
Coleoptera 1	2/0.0021					10/0.01					
Coleoptera 2			6/0.0042								
Coleoptera 3		5/0.0015		6/0.0126							
Staphylinidae					5/0.002						70/0.0149
Tenebrionidae larvae		30/0.017	6/0.0024	12/0.014	10/0.002	5/0.0035					
Tabanidae larvae						10/0.0755					
Diptera larvae	3/0.0229							4/0.0014			80/0.0239
Ant lion											10/0.004
Hymnoptera		25/0.085			5/0.001						
Myriapoda		5/0.0015		6/0.0044							
Aranae		5/0.002									
Marine species richness	19	12	7	18	9	14	12	11	17	14	19
Total density (ind.m^{-2})	146	49	17	58	152	254	18	249	75	166	487
Total abundance (ind.m^{-1})	1137	1085	432	1630	3028	4175	227	4166	2779	7440	21845
Average biomass (g m^{-2})	0.6749	0.1758	0.0498	0.0767	0.1762	2.188	0.5712	0.1736	2.8588	0.2507	1.5542
Total biomass (g m^{-1})	5.69	3.9453	1.2552	2.1667	3.4956	36.0787	7.4123	2.7365	99.62	11.08	69.61

10.6. Appendix 6.

Community structure and species composition on 10 beaches of Paraná, Southeast Brazil. Abundance (ind)/biomass (g) per running meter.

	Grande Sao Francisco do Sul	Riviera	Brejatuba	Santiene	Ubatuba	Prainha	Pecas	Deserta	Grande Ilha do Mel	Atami
Platorchestia platensis							1319/0.9072			174/0.1619
Orchestoidea brasiliensis	336/0.2546		12/0.0215	11/0.0129	11/0.0026					
Puelche sp 2										87/0.0043
Puelche sp 1							660/0.0789	1425/0.3398	834/0.2086	232/0.0547
Phoxocephalopsis sp							49/0.0086	40/0.8114		116/0.0605
Haustorioidea						16/0.0016				
Bathyporeiapus bisetosus							1979/0.3487	237/0.0777	301/0.099	
Tholozodium rombofrontalis		9/0.003					1022/0.1539		15944/3.4744	3188/0.8302
Excirolana armata				11/0.0048	57/0.0722	402/0.8673	2721/2.3651	2018/2.7227	11541/11.3696	3768/3.9441
Excirolana braziliensis	2554/3.8219	830/1.07	1898/3.3538	2191/2.32	479/0.8312	739/1.42		20/0.0059		
Macrochiridothea giambiagiae				11/0.0049	296/0.0899	48/0.0405	115/0.0219	178/0.0395	46/0.0286	
Metamysidopsis neritica		9/0.0029	35/0.0112	151/0.0296			99/0.0125	356/0.072	46/0.0218	377/0.094
Bowmaniella brasiliensis		81/0.0408		65/0.0285	114/0.0899	32/0.0669	264/0.2109	277/0.1959	23/0.0502	232/0.0536
Emerita brasiliensis	451/28.0646	72/21.93	81/6.227	151/0.6697	68/0.2041	257/0.5991	16/0.1649		23/0.0118	29/0.0367
Lepidopa richimondi	18/1.8032		12/1.1749	11/0.0269	103/13.37	241/10.6668	33/0.9594	297/6.2262	487/13.5138	348/10.1799
Pinnixa patagoniensis									23/0.2111	696/2.8262
Brachiura juvenile and megalopa		9/0.0012					16/10			
Ocypode quadrata	9/0.1969	45/2.4	23/0.4324	22/0.1992	11/1.15	80/1.6463			46/1.0748	
Callichirus major										
Ogyrides hayi							16/0.0862		23/0.1393	58/0.5786
Scolelepis squamata		442/0.319	23/0.0232	22/0.0119	661/0.4275	273/0.1848	49199/4.2328	12130/1.3146	63175/11.7023	16666/3.2942
Euzonus furciferus			12/0.9217		2280/42.62	64/1.5194	280/1.6569	198/0.7976	116/0.6148	1855/2.972
Orbinia sp b						193/0.4337	346/0.3712		209/0.355	29/0.0195
Hemipodus olivieri	159/2.331	117/0.5154	46/0.0115	194/0.0606	80/0.1025	96/0.1374	231/0.6688	218/0.3543		522/0.56
Nephtys simoni										87/0.0951
Dispio remanei						16/0.5728	33/0.164		23/0.0949	232/1.2093
Psionidens indica	27/0.0188	18/0.0118	12/0.002	43/0.0144						
Paraonidae					34/0.014	64/0.0227		158/0.0579		29/0.0095
Oligochaeta	35/0.0094							79/0.2403		
Donax hanleyanus	230/9.1807	117/3.627	116/0.1428		1824/1.2579	48/0.1503		40/0.3402	371/1.2611	319/0.2098
Donax gemmula						273/0.1874	1646/0.5754	2117/0.7754	510/1.3345	2261/1.1748
Mesodesma mactroides							16/9.2833		46/6.3939	
Tivela mactroides		9/0.0052								29/0.0256
Hastula salleana						16/0.0547		693/6.9794	23/0.2426	
Ollivancillaria vesica				11/17.91						
Mellita quinquiesperforata										145/1.7839
Nemertinea						32/0.0356	82/0.1138	59/0.0599		29/0.0057
Ant lion									23/0.0449	
Hemiptera			12/0.0005							
Formicidae			12/0.0176						23/0.0197	
Tabanidae larvae							16/0.3076			
Phaleria brasiliensis							874/4.1898			
Bledius bonaerensis							16/0.0028			
Bledius microcephalus								20/0.0123		
Elatheridae								20/0.0157		
Coleoptera larvae	115/0.2989						115/0.0619			
Coleoptera 1										29/0.0169
Coleoptera 2							973/0.5455			29/0.0221
Labiduria riparia							33/0.0598			116/0.817
Insecta larvae								20/0.0115		
Marine species richness	9	12	11	13	13	18	22	20	21	26
Total density (ind.m^{-2})	99	46	44	60	117	40	717	231	1038	241
Total abundance (ind.m^{-1})	3933	1760	2292	2893	6020	2892	53175	20600	93858	31680
Average biomass (g m^{-2})	1.1772	0.9151	0.2352	0.4114	1.1508	0.2511	0.5941	0.2404	0.9572	0.2407
Total biomass (g m^{-1})	45.98	29.93	12.34	21.30	60.23	18.61	37.60	21.45	52.27	31.04

10.7. Appendix 7.

Publications with data from this thesis

Bruce NL, Soares AG (1996) Taxonomy and ecology of sandy beach *Eurydice* (Crustacea, Isopoda, Cirolanidae) from the West coast of South Africa. Cah.Biol.Mar. 37:77-98

Eibye-Jacobsen D, Soares AG (2000) New records of *Scolelepis* (Polychaeta : Spionidae) from the sandy beaches of Madagascar, with the description of a new species. Bulletin of Marine Science 67:571-586

Soares AG (1994) Sand beach morphodynamics and macrofaunal associations: a preliminary analysis. In: McGwynne LE (ed) White sand mussels: ecology, status and conservation. Rep. Inst. Coast. Res., Univ. Port Elizabeth, Vol 36, Port Elizabeth, p 24-26

Soares AG, McLachlan A, Schlacher TA (1996) Disturbance effects of stranded kelp on populations of the sandy beach bivalve *Donax serra* (Roding). J.Exp.Mar.Biol.Ecol. 205:165-186

Soares AG, Schlacher TA, McLachlan A (1997) Carbon and nitrogen exchange between sandy beach clams (*Donax serra*) and kelp beds in the Benguela coastal upwelling region. Mar.Biol. 127:657-664