FEATURE ARTICLE: REVIEW

Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis

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ABSTRACT: Physical and biological factors govern community and population features of sandy beach macrofauna. At the macroscale, species richness decreases from tropical to temperate beaches, and from macrotidal dissipative to microtidal reflective beaches. At the species level, life history traits are highly plastic over latitudinal gradients; large-scale variations in environmental variables modulate intraspecific phenotypic differentiation. At the mesoscale, alongshore and across-shore distributions tend to be unimodal, bell-shaped within a beach, with abundance varying from the central region to the boundaries, even though environmental gradients (wave exposure, salinity) can cause asymmetries. Zonation is highly dynamic and not sharply defined. This is attributed to short- (hourly, daily) or medium- (seasonal) term reactions to environmental conditions, passive transport and sorting by the swash (e.g. recruits), active micro-habitat selection (e.g. adults), and intra- and interspecific interactions. Across-shore distribution may become multimodal due to intraspecific segregation by sizes during recruitment. At the microscale (individual neighbourhood or quadrat scale), behavioural factors and intra-/interspecific interactions become more important as density increases. Human induced impacts also generate variability in population demography, structure and dynamics. We identify physical-biological coupling at different temporal and spatial scales, emphasizing the role of life history traits in order to assess alternative regulatory mechanisms and processes. Our synthesis suggests that: (1) biological interactions are more important regulatory agents than previously thought: in benign dissipative beaches or undisturbed sites, intra- and interspecific competition can be more intense than in reflective beaches or disturbed sites, where the populations are physically controlled; (2) supralittoral forms are relatively independent of the swash regime and show no clear response to beach type; (3) marked long-term fluctuations are noticeable in species with planktonic larvae structured as metapopulations, due to environmental disturbances and stochasticity in reproduction and recruitment.

Sandy beaches are defined by just 3 factors—tide regime, sand particle size and wave energy—and occur as a range from reflective (upper) to dissipative (lower) types. Since macrofauna show clear patterns of response to beach type, these simple environments provide a unique opportunity to explore processes controlling community and population ecology. *Photos by Dr. Andrew Short* (*University of Sydney, Australia*)

KEY WORDS: Sandy beaches · Macrofauna · Communities · Populations · Patterns · Regulation · Processes

INTRODUCTION

At the time of the first international sandy beach symposium in 1983, sandy beach research was in a transition from early, mainly qualitative studies of macrofauna ecology and ecophysiology, to quantitative work (McLachlan & Erasmus 1983). Studies on energy flow and nutrient cycling in beach ecosystems
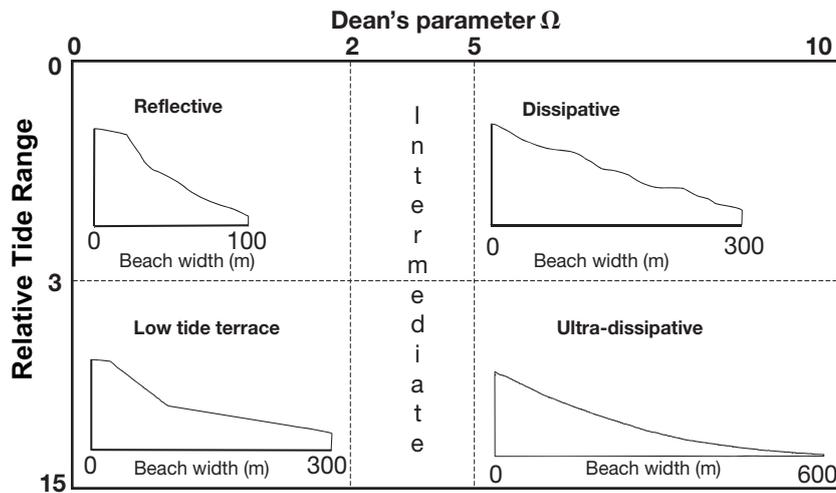
Fig. 1. Beach classification based on 2 composite indices developed for sandy shores: Dean's parameter (Ω) and the Relative Tide Range. Dissipative, intermediate and reflective domains are defined for microtidal open beaches where tide range <2 m (after Short 1996)

remained a dominant theme through the 1980s. In the 1990s most sandy beach research focused on community and population ecology. Beach research lagged far behind studies of other coastal environments, and before 1980 it lacked a body of theory to drive it, but this has steadily changed. Although they are still less studied than most other coastal systems, beaches are much better characterized in the new millennium. A significant body of knowledge has accumulated and a variety of hypotheses concerning sandy beach ecosystems and communities have been developed, so that beach studies have become increasingly theory driven. In this review we summarize the current status of community and population ecology for sandy beach macrofauna (hyperbenthos not included), focusing on key processes operating at different scales, and on how they interact to yield the patterns observed. We also refine the theory, identifying the physical-biological coupling at different temporal and spatial scales and emphasising the role of life history traits in order to assess the magnitude of alternative regulatory mechanisms.

THE BEACH ENVIRONMENT

The benthic macrofauna of sandy beaches includes representatives of many phyla, but crustaceans, molluscs and polychaetes are usually dominant and can be divided into intertidal and supralittoral forms (Brown & McLachlan 1990). Their habitat is dynamic and defined by 3 factors: tides, waves and sand. The interactions between tidal regime, wave climate and sediment type

produce a range of beach morphodynamic types which span a continuum from microtidal reflective beaches, narrow and steep, to macrotidal dissipative systems, which are wide and flat, and under conditions of large tides, grade into tidal flats (for review see Short 1996). The most accretional state is the reflective beach, formed under condition of small tides and waves and coarse sand; here there is no surf zone and wave energy is reflected back to sea from waves breaking directly on the steep beach face. In erosional or dissipative states the beach is flat and fronted by a wide surf zone, in which waves dissipate much of their energy. The dissipative state forms under conditions of large tide range, high wave energy, fine sand, and tends to be more prevalent at higher latitudes. A series of intermediate states are recognized between the above extremes (Fig. 1).

Various indices of beach type have been used by ecologists. Dean's dimensionless fall velocity (Ω), a measure of how reflective or dissipative a microtidal beach is (Short 1996), is defined as:

$$\Omega = \frac{Hb}{Ws \cdot T}$$

where Hb is breaker height (m), Ws is sand fall velocity (m s^{-1}) and T is wave period (s). $\Omega < 2$ characterizes reflective beaches, whereas $\Omega > 5$ defines dissipative ones and $2 < \Omega < 5$ characterizes intermediate beach states (Fig. 1). Essentially, Ω is a measure of the ability of the prevalent wave energy to erode sand. Another measure of beach type is relative tide range RTR = TR/Hb, where TR is spring tide range (m). RTR indicates the relative importance of tides versus waves in controlling beach morphodynamics (Fig. 1). As Ω does not take tides into account, the Beach State Index (BSI) has been used to compare beaches subject to differing tide ranges; BSI is Ω multiplied by tide range and indicates the ability of waves and tides to move sand (McLachlan et al. 1993). Soares (2003) developed the Beach Deposit Index (BDI), a composite index of beach slope and grain size. Recently, McLachlan & Dorvlo (2005) developed the beach index (BI):

$$BI = \log_{10}\left(\frac{Mz \cdot TR}{S}\right)$$

where Mz is the mean grain size (in phi units + 1, to avoid negative values), TR is the maximum spring tide range (m) and S is beach face slope (dimensionless).

Water movement over the beach face, after a broken wave (bore) collapses on the sand, is termed swash (McArdle & McLachlan 1991, 1992). In reflective beaches, waves break directly on the beach face generating harsh swash climates, i.e. dynamic, turbulent swashes with short periods, with many swashes running above the sand water saturation level, and water draining rapidly into the coarse sand. Conversely, dissipative systems have benign swashes, where much of the wave energy is consumed in the surf zone so that swashes reaching the beach face tend to be less turbulent and have longer periods; swashes seldom go above the saturated beach face so there is little drainage into the sand (McLachlan & Turner 1994). Sandy beach macrofauna experience this environment through 3 suites of physical factors: the sediment texture and movement, the swash climate, and the exposure/moisture gradient on the beach face (Brown & McLachlan 1990). Sediment texture and movement includes particle size, sorting, fluidity and accretion/erosion dynamics. Swash climate includes the swash period, speed, turbulence and water movement over and into the beach face. The intertidal gradient is the degree of aerial exposure of the sediment surface and the changing moisture content of the sand over the tidal cycle.

LARGE-SCALE VARIATIONS

The large scale, or macroscale, concerns biogeographic patterns in community and population features, including variations over beaches with different morphodynamics.

Communities

Latitudinal patterns

Matching the pattern recorded for other environments (Willig et al. 2003), species richness increases from temperate to tropical sandy beaches (Fig. 2) (Hacking 1997, McLachlan et al. 1998, Soares 2003, McLachlan & Dorvlo 2005). This contradicts the earlier pattern found by Dexter (1992), who did not take into account beach type; the above studies allowed for beach type by comparing species richness against physical variables or compound indices of beach state (e.g. BSI, Ω). Latitudinal variation in beach type is crit-
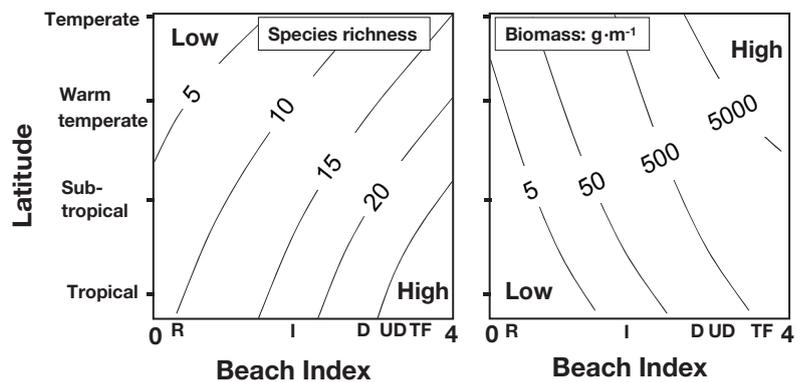

Fig. 2. Conceptual model of latitudinal variations in species richness (number of species per transect survey) and biomass (g m^{-1}) as a function of beach type, as categorized by the Beach Index. The number of species increases at low latitudes under conditions of (1) fine sands and flatter slopes, (2) benign swash climates, and (3) increasing tide range. Biomass is also highest towards tidal flats and increases from tropical to temperate sandy beaches (R = reflective, I = intermediate, D = dissipative, UD = ultradissipative, TF = tidal flat)

ical to elucidate these large patterns; tropical regions had a greater proportion of reflective beaches than subtropical or temperate regions, the latter being dominated by dissipative beaches because of higher wave energy and fine sand (Soares 2003, McLachlan & Dorvlo 2005).

Following the opposite trend, abundance and biomass increase from tropical to temperate beaches (Fig. 2), although these trends are less clear for polychaetes and molluscs than for crustaceans (Soares 2003, McLachlan & Dorvlo 2005). Greater abundance and biomass on temperate dissipative beaches could be attributed to greater food availability, due to greater productivity mainly provided by abundant benthic fauna and surf zone phytoplankton (McLachlan 1990). The presence of surf diatom accumulations has led to the definition of dissipative beaches as semi-closed ecosystems (sensu McLachlan 1980), in contrast to reflective beaches, defined as interfaces with low productivity, subsidized by organic inputs from the sea (Brown & McLachlan 1990). Whereas increased wave energy in temperate areas seems to cause increased productivity and biomass, stranded seagrass or algae (Colombini & Chelazzi 2003), or the presence of upwelling (Jaramillo et al. 2001) can also add to sand beach energetics and biomass.

Relationships with physical parameters

McLachlan (2001) identified 3 paradigms which define large scale community patterns on exposed sandy beaches: (1) the concept of overriding physical control in harsh environments, (2) the beach morphodynamic models (Fig. 1), and (3) the increase of species
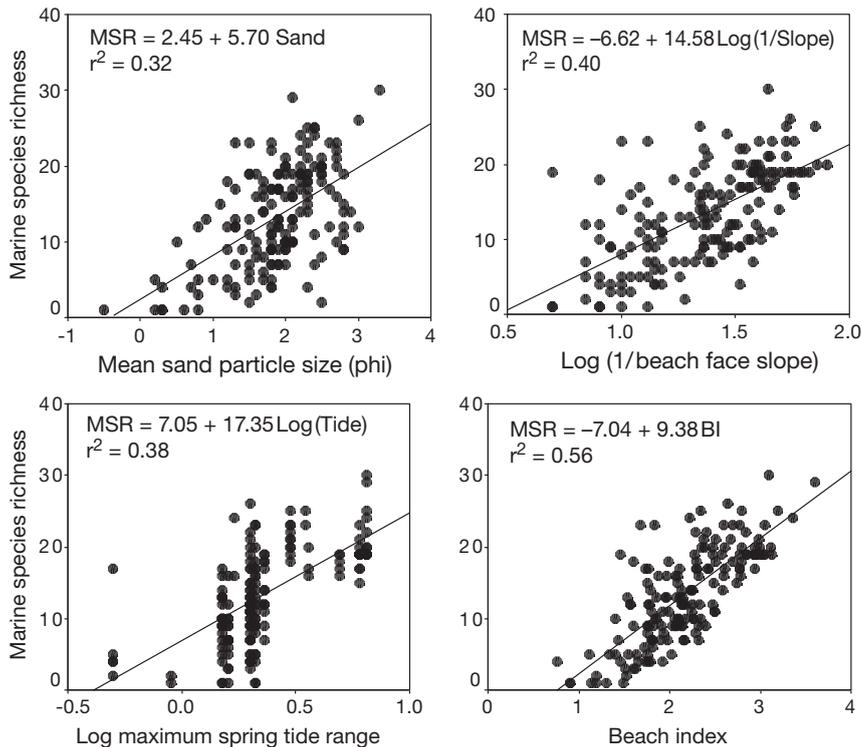
Fig. 3. Significant relationships (p < 0.01) between marine species richness, and sand particle size, beach face slope, tide range and the Beach Index (after McLachlan & Dorvlo 2005)

richness, abundance and biomass from microtidal reflective to macrotidal dissipative beaches.

Beach environments largely lack biogenic structure and are extremely dynamic in space and time. Thus, their intertidal macrofauna is considered to be physically controlled in the sense of the Autecological Hypothesis (Noy-Meir 1979). This hypothesis, as adapted by McLachlan (1990), states that sandy beaches are physically controlled environments where communities are structured by the independent responses of individual species to the physical environment, biological interactions being minimal. A main prediction of this hypothesis is the increase in community descriptors from harsh reflective to benign dissipative beaches. In agreement with this prediction, sandy beach communities increase in richness, density, total abundance and biomass from microtidal reflective beaches to macrotidal dissipative beaches (McLachlan et al. 1981, 1993, 1996a, McLachlan 1990, Jaramillo et al. 1995). McLachlan & Dorvlo's (2005) analysis of worldwide data also showed that species richness decreases with coarser sand, steeper beach face slope, and smaller tide range (Fig. 3). Increasing tide range makes beaches more dissipative (McLachlan & Dorvlo 2005), creating a vertical exposure gradient along which intertidal species establish themselves, with wave effects being secondary. Neglect of the role of

tides may be due to the fact that most workers compared regions subject to a fairly uniform tide range.

The response of abundance to changes in individual physical factors and to composite indices of beach state is exponential, being more variable than the response of species richness. Biomass, which also responds exponentially, is the most variable of the 3 community measures and seems to be related to the amount of wave energy, which may indicate productivity (McLachlan 1990, McLachlan et al. 1993, Nel 2001, Soares 2003). McLachlan & Dorvlo (2005) showed that abundance and biomass exponentially decrease with intertidal beach face slope (see also Defeo et al. 1992a, Nel 2001, Brazeiro 2001, G. Stephenson & A. McLachlan unpubl.). Slope is closely related to swash climate, which becomes less harsh as beach face slope flattens, indicated by longer swash periods, less swash activity above the effluent line, and less turbulence (McArdle & McLachlan 1991, 1992). Beach face slope is thus both a measure of the dimensions of the intertidal zone and an index of swash climate and beach type.

In the context of the Autecological Hypothesis, the pattern of species richness was explained as exclusion of species from the reflective end of the gradient of beach types by a harsh swash climate. This idea was refined as the Swash Exclusion Hypothesis (SEH: McLachlan et al. 1993), based on the finding that the swash climate which the macrofauna experience on the beach face is closely coupled to beach type (McArdle & McLachlan 1991, 1992). Exclusion of species towards the reflective end of the beach morphodynamic spectrum may be due to both harsh swash climate and coarse sands, as reflected by strong relationships between community attributes and compound indices of beach state (e.g. BI, BSI, Dean's parameter) or individual physical factors (McLachlan, 1990, Defeo et al. 1992a, Hacking 1997, Brazeiro 1999, Ricciardi & Bourget 1999, Jaramillo et al. 2000a, Nel 2001, Soares 2003, Rodil & Lastra 2004, McLachlan & Dorvlo 2005, G. Stephenson & A. McLachlan unpubl.).

The mechanisms which explain the presence or absence of species across the continuum of beach types have not been fully elucidated (McLachlan 2001). Ignoring the effects of latitude and exposure, swash climate and sand particle size define the immediate environment experienced by macrofauna, so that

increasing harshness in these factors (coarse sediment, short and turbulent swashes and accretion-erosion dynamics: the expanded SEH or Multicausal Environmental Severity Hypothesis) may exclude species from reflective systems (Alexander et al. 1993, McLachlan et al. 1995, Nel 1995, 2001, Dugan et al. 2000, Brazeiro 2001, Defeo et al. 2001, Veloso & Cardoso 2001, G. Stephenson & A. McLachlan unpubl.). Soares (2003) questioned whether the exclusion of species towards the reflective extreme was due to pre- or post-settlement processes. Defeo et al. (2001, 2003) formulated the Habitat Harshness Hypothesis (HHH), postulating that in reflective beaches the harsh environment forces organisms to divert more energy towards maintenance, resulting in lower fecundity and higher mortality. Thus, post-settlement processes may prevent some species from establishing populations on reflective beaches. We postulate that species richness is therefore mainly controlled by the physical environment on the large scale (Fig. 4). At a finer scale and under more dissipative conditions, biological factors may become more important (Defeo et al. 2003, McLachlan & Dorvlo 2005).

Populations

Latitudinal patterns

Identification of large scale patterns underpinning species' distributions in sandy beaches is often limited by the short time series of population variables, the restricted spatial coverage of most studies, and the use of different methodologies. Many studies have been based on snapshot sampling of a large number of beaches, but this does not elucidate variations in population features (Defeo 1996a).

Early studies of latitudinal patterns in sandy beach populations found large scale variations in life history traits of cirolanid isopods, notably in reproduction (Fish 1970, Jones 1970), distribution (Klapow 1970, Glynn et al. 1975, Dexter 1977), morphological and genetic variations (Weinberg & Starczak 1988, 1989, Lessios et al. 1994, Lessios & Weinberg 1994) and sediment preferences (Defeo et al. 1997). Marked variations in reproductive traits were also detected in *Emerita* species (Wenner et al. 1987, Dugan et al. 1991, 1994, Defeo & Cardoso, 2002, 2004), which were inversely related to surf zone water temperatures and positively related to food availability in dissipative systems. A review of 15 clam species from ocean beaches around the world showed that bivalves with larger individual sizes and biomass dominate dissipative beaches of temperate zones, whereas smaller species are found on subtropical reflective beaches (McLachlan et al. 1996b).
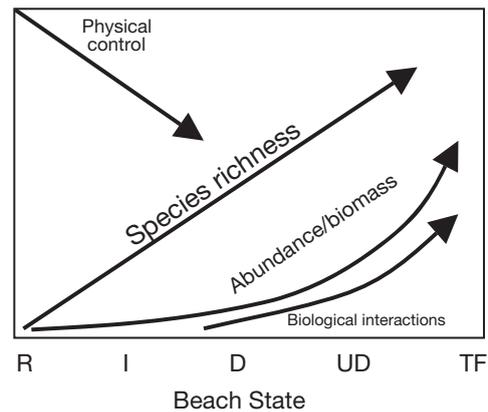

Fig. 4. General conceptual model relating biological descriptors and beach state. Species richness and abundance increase from reflective beaches to tidal flats. Towards the reflective domain, species richness is mainly controlled by the interaction of physical factors such as sand, tides, waves, and beach face slope. At a finer scale and under more dissipative conditions, biological factors become more important. (R = reflective, I = intermediate, D = dissipative, UD = ultradissipative, TF = tidal flat)

Large-scale studies, recently conducted on the mole crab *Emerita brasiliensis* (planktonic larvae) and the cirolanid isopod *Excirolana braziliensis* (ovoviviparous) in South America, showed systematic and recurrent patterns in population features within their range (Defeo & Cardoso 2002, 2004, Cardoso & Defeo 2003, 2004). The main findings were changes from temperate to tropical beaches (Fig. 5), namely increases in abundance, growth and mortality rates, reduced predominance of females, a shift from seasonal to continuous reproduction, and decreases in individual size of ovigerous females, fecundity, length at maturity, mass and longevity. Scaling of population density to body size was observed for *Emerita*, with densities and body mass ranging over more than 2 orders of magnitude. These patterns did not hold for male mole crabs, which showed increasing occurrence, individual sizes and growth intensity towards subtropical beaches, where the predominance of females was significantly lower. Moreover, the greater total densities in subtropical reflective beaches (Defeo & Cardoso 2004) contradict worldwide trends that show greater macrofauna abundance (community level) occurring in dissipative beaches (McLachlan 2001). Thus, large-scale variations in abundance were ascribed to other factors operating at larger spatial scales (e.g. temperature), whereas departures from the patterns were attributed to the response to local variations in physical (e.g. beach morphodynamics and exposure) and biological (e.g. competition) characteristics rather than to biogeographic effects (Defeo & Cardoso 2004). Asymmetries and converse latitudinal trends between sexes, cou-

pled with studies conducted from local to large spatial scales (Defeo et al. 1997, Fiori & Defeo 2005), suggest that sandy beach populations are regulated by density-dependent processes operating at the mesoscale (see below) and environmental factors acting together.

Phenotypic plasticity and genetic stasis may be characteristic of sandy beach species. Soares et al. (1998, 1999) and Laudien et al. (2003) showed no large scale genetic differentiation in the whelk *Bullia digitalis* (aplanktonic larval phase) and the surf clam *Donax serra* (planktonic larval phase) in South Africa. Both studies ascribed this to a high degree of plasticity in their behaviour, ecophysiology and morphology, which allowed them to rapidly adapt to environmental changes. The evidence provided above demonstrates that life history traits in sandy beach populations can be highly plastic over latitudinal gradients, with large scale variations in temperature and concurrent environmental variables leading to an adjustment of the phenotype–environment relationship. Plasticity may therefore lead to separate populations displaying differences in behaviour and life history patterns.
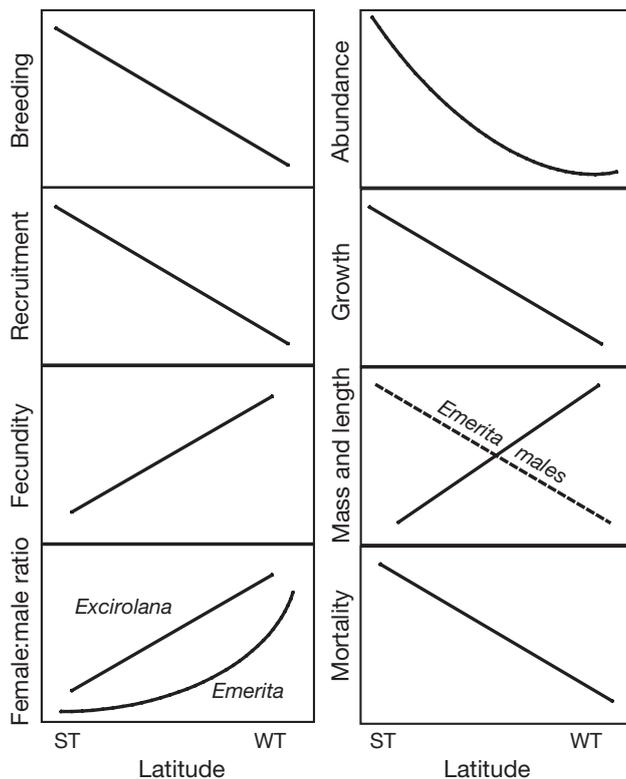

Fig. 5. *Emerita brasiliensis* and *Excirolana braziliensis.* Latitudinal patterns in life history traits on South American sandy beaches. Breeding and recruitment refer, respectively, to the frequency of occurrence of ovigerous females and of juveniles throughout a year. In *E. brasiliensis*, most of these patterns are only valid for females. ST = subtropical, WT = warm temperate

Species ranges, developmental modes and dispersal

Macroscale variations in coastal physiognomy ultimately interact with large scale environmental variables (e.g. temperature) to create asymmetries in the distribution of species. Defeo & Cardoso (2004) suggested that the mole crab *Emerita brasiliensis* had a skewed, unimodal distribution pattern within its range, i.e. abundance did not vary smoothly from the central region to range boundaries (see Sagarin & Gaines 2002). This has been attributed to the disappearance of dissipative sandy beaches, which constitute the suitable habitat for *Emerita brasiliensis*, in tropical regions, giving way to reflective and pocket beaches, mangrove stands, estuaries and coral reefs (Soares 2003, Defeo & de Alava 2005).

Episodic environmental events may alter spatial and temporal patterns of abundance, whereas climatic variations over years to decades can result in interannual changes of distribution and abundance (Lima et al. 2000). Distribution limits of beach species can expand and contract over time, displaying considerable fluctuations in abundance coupled with episodic settlement events and/or mass mortalities (Coe 1953). Arntz et al. (1987) showed dramatic fluctuations in the sandy beach bivalves *Donax peruvianus* and *Mesodesma donacium*, and the mole crab *Emerita analoga* in Peru. After the dominant *M. donacium* experienced mass mortalities due to an increase in sea water temperature during an El Niño Southern Oscillation event, *D. peruvianus* increased its representation within the community from 5 to 60–100% and its density from ca. 20 to 185 ind. m^{-2}, whereas *E. analoga* increased from <1 to 29%, with densities increasing from 0 to 85 ind. m^{-2}. This was accompanied by an expansion of the distributional range to beaches previously unoccupied by these species. On Uruguayan Atlantic beaches, in a guild of suspension feeders of the same genera, *Donax hanleyanus* and *Emerita brasiliensis* dramatically increased in density for 10 yr after the dominant *Mesodesma mactroides* experienced mass mortalities (Defeo 2003). These examples suggest both differential responses to climatic events and also interspecific interactions because of competitive release of resources by dominant community members. In both cases, changes in species composition and abundance occurred after removal of the dominant species, strongly indicating competitive release. Accounting for differences in species life histories and range-limiting factors is therefore necessary in order to better predict macroscale distribution patterns in sandy beach populations.

The mode of species development is crucial to understand the above processes. Sandy beach species have a wide range of development modes, including:

(1) internal fertilization, the absence of pelagic larval stages, parental care and low fecundity, such as peracarids and whelks, and (2) external fertilization, high fecundity and short-lived (h) or long-lived (from a few weeks to months) planktonic larval stages (e.g. clams: McLachlan et al. 1996b). Species belonging to the latter group are usually structured as metapopulations, with variable degrees of connectivity between local populations through larval dispersal (Defeo 1996b).

Contrasting modes of development, usually found in sandy shores, could influence dispersal patterns. Weinberg & Starczak (1989) showed an exceptional degree of genetic differentiation between populations of the ovoviviparous isopod *Excirolana braziliensis* throughout its entire range of distribution in America. This was explained by events of extinction/recolonization, because immigrants of this species with distinct genotypes appeared to not mate randomly and produced hybrids with local members (Lessios & Weinberg 1994). Although it has been suggested that many local groups of broadcast spawners in open sandy coasts are self-sustaining (Efford 1970), a planktonic larval stage suggests dispersal potential (Sorte et al. 2001) and a variable degree of gene flow among sandy beach populations (Tam et al. 1996).

Population structure and habitat harshness: the source–sink hypothesis

Connectivity patterns between sandy beach populations linked by larval dispersal are an unexplored field of research, and the mechanisms influencing larval distribution are poorly understood (McLachlan et al. 1996b). Hydrographic effects on larval dispersal have yet to be elucidated in terms of planktonic stages and the role of near-shore hydrodynamics in settlement processes. This in turn will determine the spatial scales at which the population is to be considered open, i.e. whether it is more related to the arrival rates of larvae than to post-settlement processes, or whether it could be considered as self-sustaining (Defeo 1996b, Camus & Lima 2002).

The combination of geographic diversity and local and stable oceanographic structures provides the basis for larval retention areas (Sinclair 1987). Caddy & Defeo (2003) considered source and sink components in sandy beaches; they assume that 'source populations' are often in areas where there is a high probability of returning water masses or gyres assisting in returning larvae to the local area. If this is true, the age/size structure of the population is probably a good index of the degree of local retention of larvae, and of the probability that their offspring will return to the parental grounds. Thus, source populations should

tend to show a good representation of different age classes, as a result of frequent successful annual recruitments, whereas 'sink' populations would be made up of one or few age groups, occurring irregularly in time. In this context, the population structure of *Emerita brasiliensis* in the upper panel of Fig. 6 could be considered the main source area, because of the presence of all potential year/size classes. Subsequent panels in Fig. 6 represent irregular and sporadic recruitment events of different periodicities. Sink populations have an irregular size structure with sporadic pulses of discrete cohorts, and in some cases biased towards larger size classes because of irregular recruitment pulses causing a discontinuity in the arrival of larvae. Sporadic recruitment pulses and low capacity for self-replenishment in sink populations or at range margins could be caused by several factors, including low fecundity, irregular arrival of larvae due to asymmetric connectivity, or low juvenile survival (Lercari & Defeo 1999, Sorte et al. 2001). In this case (Fig. 6), source populations with multiple size/age groups coincide with dissipative (Defeo et al. 2002) or undisturbed (Lercari & Defeo 1999, 2003) systems, so this approach can also be applied to evaluate the rela-
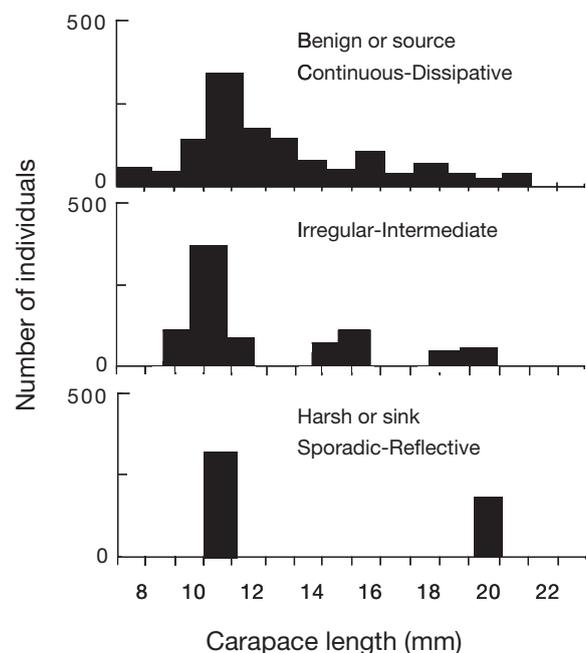

Fig. 6. *Emerita brasiliensis.* The 'source–sink hypothesis', as illustrated by the length frequency distributions of the mole crab from different beach types. Reproductive females on dissipative beaches seed reflective beaches. Sources (upper panel) and sinks (lower 2 panels) can be identified as a result of larval dispersal, retention in the parental spawning area and differential post-settlement mortality rates. The length/age population structure in each case depends on the degree of connectivity between populations (from Defeo unpubl.)

tive importance of morphodynamics or disturbance levels at regional or local spatial scales (Lercari et al. 2002, Defeo & Lercari 2004).

Information on long term variations in abundance or genetic makeup could help to discern source from sink populations. Large fluctuations in abundance are particularly noticeable in species with planktonic larvae (Coe 1953, 1956, Ansell 1983, McLachlan et al. 1996b), when compared to otherwise similar one-phase species with aplanktonic stages. Moreover, most sandy beach species are short-lived (2 to 8 yr), have rapid growth to maturity, high recruitment fluctuations (McLachlan et al. 1996b), and are represented by age-class dominated populations (Defeo et al. 1992b). Thus, short term variations in abundance could mask the elucidation of sources and sinks.

Population responses to the beach environment

The increase in species diversity, total abundance and biomass from reflective to dissipative beaches is now considered a paradigm at the community level. In contrast, there is a paucity of pertinent hypotheses concerning predictions of population patterns (Defeo et al. 2001); few studies have investigated how species respond to the physical environment demographically, i.e. in terms of abundance, growth, mortality, fecundity and other population features. Tests of the SEH (originally formulated at the community level) and the HHH (emphasis on population level) have found 3 patterns:

(1) The SEH and the HHH have predicted variations in abundance, population dynamics and life history traits of truly intertidal species. Some species are capable of maintaining populations across the whole morphodynamic spectrum, whereas species restricted to dissipative systems are more sensitive to harsh habitats (Defeo et al. 1997, McLachlan & Dorvlo 2005). Field and laboratory studies have shown increasing abundance (McLachlan 1990, Defeo et al. 1992a, Dugan & Hubbard 1996, Jaramillo et al. 2000b, Defeo et al. 2002), fecundity, growth, and survival rates (Defeo et al. 2002, Brazeiro 2005) from reflective to dissipative beaches, as well as limited or null capability of burrowing in coarse sands (McLachlan et al. 1995, Nel et al. 1999, 2001, Defeo et al. 2001, de la Huz et al. 2002, Marcomini et al. 2002, Cardoso et al. 2003). Grain size and concurrent changes in swash climate/period may exclude species from coarse-grained beaches (Nel et al. 2001). However, whether exclusion is due to prevention of settlement or to the inability to survive after settlement is uncertain. Higher values for female somatic growth, fecundity, size at maturity and weight at size in dissipative beaches have been related to abundant food availability (Defeo & Scarabino 1990, Defeo 1993, Dugan et al. 1994). Higher intra-annual variability in abundance and narrower reproductive and recruitment seasons have been observed in reflective beach populations (Defeo et al. 2003). This synchronicity may be an adaptation to reduce the effects of harsh reflective beaches and to increase the probability of copulation with the sparse reproductive females (Defeo et al. 2001). Another explanatory hypothesis proposed here is that 'source' dissipative beaches may seed 'sink' reflective beaches. Thus, high fluctuations in larval supply, depending on connectivity between source and sink populations, may occur in reflective beaches. This new hypothesis needs further testing.

(2) In supralittoral forms, clear population responses to beach type have not been observed in cirolanid isopods (Defeo et al. 1997, 2003, Contreras et al. 2003, Defeo & Martínez 2003, Caetano et al. 2005) or amphipods (Gómez & Defeo 1999). They are less influenced by the swash climate and generally have autonomous active movement on upper beach levels (Giménez & Yannicelli 1997). Defeo & Gómez (2005) showed that the supralittoral amphipod *Atlantorchestoidea brasiliensis* exhibited clear population responses to physical variables in a trend opposite to that predicted by the HHH, including an increase in abundance (total, ovigerous females, and juveniles) and individual sizes from dissipative to reflective beaches. Existing hypotheses do not accurately predict population dynamics of supralittoral forms because of a limited appreciation of the role played by life history strategies. The combination of short swashes and steep slopes may, in fact, make microtidal reflective beaches a more stable and safer environment for supralittoral species, because their risk of immersion is substantially lower here than on dissipative beaches. Short (1996) defined modally reflective beaches as the most stable beach type with low backshore mobility. Thus, reflective environments appear to favour supralittoral forms. This has been called the Hypothesis of Habitat Safety for supralittoral forms (Defeo & Gómez 2005), a refinement of the theory developed to explain morphodynamic effects on sandy beach populations. This separates intertidal and supralittoral forms, taking into account both swash and sand effects and differences in life histories (Defeo et al. 2003, McLachlan & Dorvlo 2005).

(3) Inadequate sampling of the appropriate temporal and spatial scales has limited testing of the predictions of the SEH and HHH at the population level. In most studies only 2 beaches have been used for comparison, so that trends in population features cannot be rigorously attributed to beach morphodynamics, but only to location. However, extended studies of mole crabs
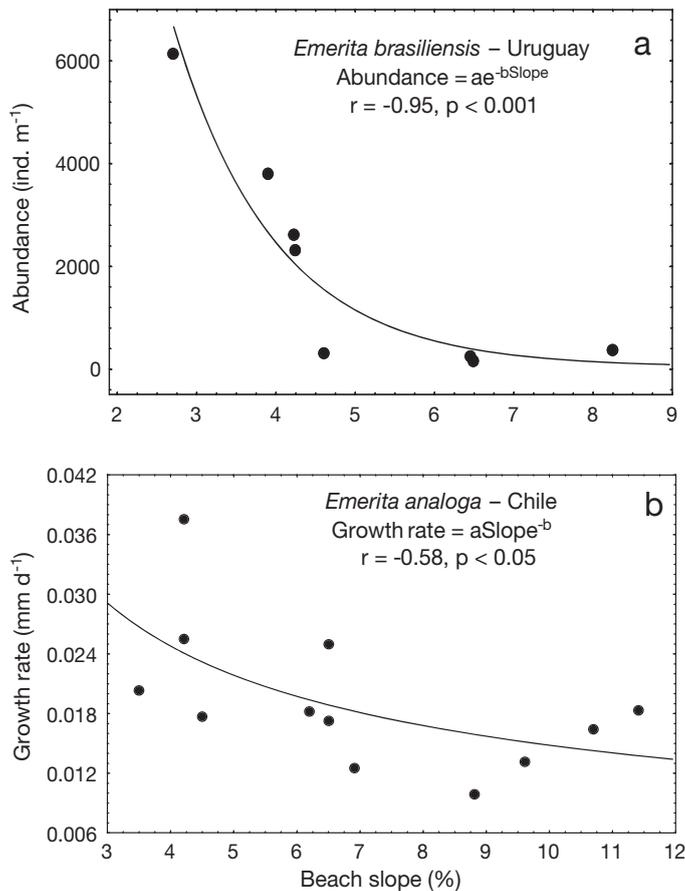
Fig. 7. *Emerita brasiliensis* and *E. analoga*. Population features of 2 intertidal core species of the Americas in support of the HHH. (a) Abundance in Uruguay (from Defeo et al. 2002) and (b) individual growth rates in Chile (after Brazeiro 2005) decrease as beach slope becomes steeper, suggesting harsher conditions towards reflective states

Emerita brasiliensis (Defeo et al. 2002, Fig. 7a) and *E. analoga* (Brazeiro 2005, Fig. 7b) on several beaches covering a wide morphodynamic spectrum support the HHH.

MESOSCALE PATTERNS

The mesoscale concerns variations within a single beach, i.e. an uninterrupted sandy shore, both in the alongshore and across-shore directions.

Alongshore distribution

Marked alongshore variation has been documented at the community and population levels. Species richness may increase with beach length (Brazeiro 1999), with short or 'pocket' beaches supporting fewer spe-cies than longer beaches. Species composition and abundance along the shore also decreases with increasing beach slope and grain size, and with decreasing width and relative tide range (Degraer et al. 2003). Lercari et al. (2002) and Lercari & Defeo (2003) showed that species richness, diversity, evenness, and abundance significantly increased from disturbed sites affected by a freshwater discharge to undisturbed ones.

Sandy beach populations and assemblages may exhibit a well defined alongshore structure with significant across- and alongshore variations (James & Fairweather 1996). Populations tend to be aggregated in elliptical patches from m to km, with the major axis parallel to the shore (Defeo et al. 1986, Defeo 1993, Giménez & Yannicelli 1997), and varying according to the different susceptibility of each species and year group (i.e. recruits vs adults) to environmental factors. Alongshore distribution tends to be unimodal, bell-shaped within the beach, with decreasing abundance from the central region to range boundaries (Defeo et al. 1986, Defeo 1993, Defeo & de Alava 1995, Schoeman 1997, Schoeman & Richardson 2002). Disturbing agents can shift distributions from bell-shaped to asymmetrical.

Gradients in physical factors invoked to explain alongshore patterns (Bally 1981, McLachlan 1983, Schoeman & Richardson 2002) have included exposure from sheltered to exposed beach ends, changing sand particle size, swash climate, morphodynamics, salinity, features associated with river mouths, and also passive sorting by the swash, localized food concentrations or behavioural sorting (Wade 1967, Ansell 1983, Mc-Lachlan & Hesp 1984, Defeo et al. 1986, Donn 1987, Lastra & McLachlan 1996, McLachlan 1996, Dugan & McLachlan 1999). Alongshore variation may also result from a combination of biotic (intra and interspecific interactions) and abiotic factors (Wade 1967, Mouëza & Chessel 1976, Defeo et al. 1986, Defeo 1993, Defeo & de Alava 1995, Giménez & Yannicelli 2000, Schoeman & Richardson 2002). Additional sources of variability include human activity such as artisanal harvesting of target species (Schoeman 1996, Sims-Castley 1997, Schoeman et al. 2000) and their interspecific competitors for food and space (Defeo & de Alava 1995), man-made structures, beach nourishment, and bulldozing (Nelson 1989, Lercari & Defeo 1999, 2003, Peterson et al. 2000, Brown & McLachlan 2002, Degraer et al. 2003). Dillery & Knapp (1969) showed active along-shore movements of *Emerita* of 15 m d^{-1}, extrapolated to 5 km yr^{-1}. However, alongshore movements are less noticeable in bivalves (Dugan & McLachlan 1999). Alongshore patchiness in supralittoral species has been associated with sediment water content and dune vegetation cover (Giménez & Yannicelli 2000).
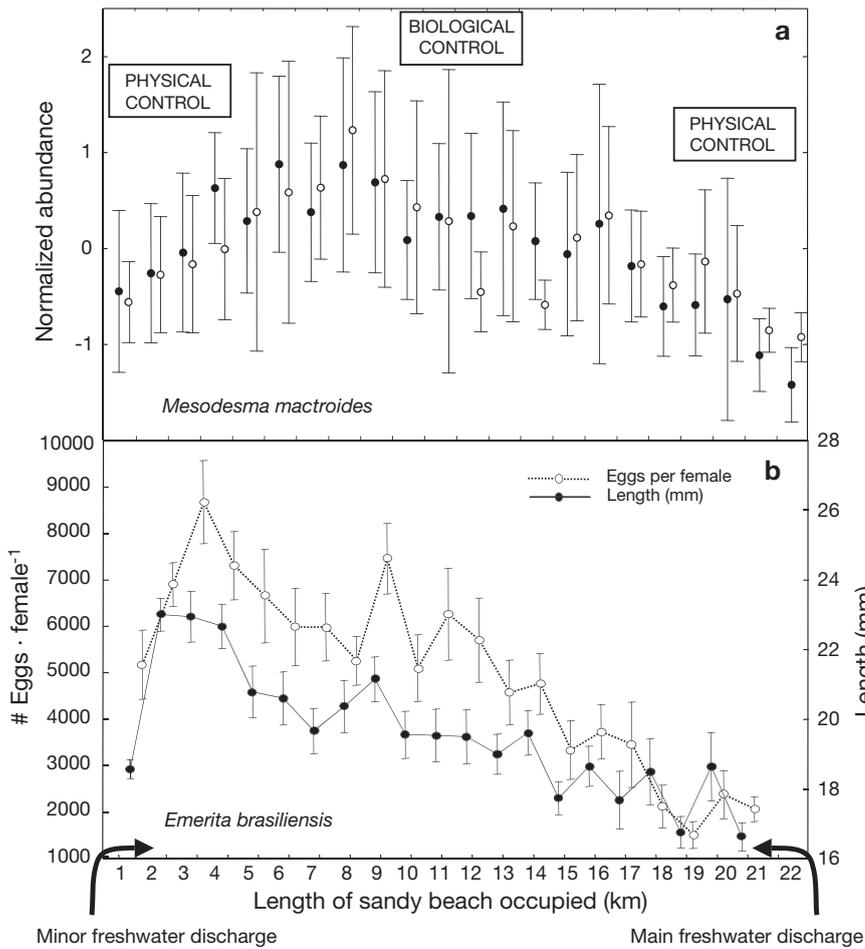
Fig. 8. *Mesodesma mactroides* and *Emerita brasiliensis.* (a) Alongshore variability of yellow clam (○) recruits and (●) adults, over favourable and unfavourable loci. Recruits occupied unfavourable habitats only during periods of good recruitment. (b) Effect of habitat unsuitability, measured as the distance from a freshwater discharge, in individual size and fecundity of female mole crabs. Note the local effect produced by a minor freshwater discharge at Km 1

flows), suggesting active dispersal and microhabitat selection (McLachlan & Hesp 1984, Donn et al. 1986, James 1999).

Habitat suitability may explain variations in the contraction/expansion of the alongshore distribution of a species on a beach. The yellow clam *Mesodesma mactroides* displayed a sequential pattern of alongshore replenishment along a 22 km sandy beach, from the central zones of regular recruitment to the marginal portions disturbed by freshwater discharges, and by concurrent changes in other variables (Defeo 1993). When central sites were fully occupied, marginal sites were occupied by later settlers. Alongshore patterns can be explained by the salinity gradient, higher recruit densities in marginal habitats (only in years of good recruitment), and differential growth and mortality between sites (Fig. 8a). In the same beach, mole crabs *Emerita brasiliensis* displayed reduced individual size and fecundity towards the unsuitable habitat (Fig. 8b), and recruits were found in reduced numbers near the freshwater discharge, a result of high pre-settlement and early post-settlement mortality rates (Lercari & Defeo 1999).

In summary, the considerable alongshore variation in sandy beach populations takes the form of patchiness on several scales, generated by a combination of abiotic and biotic factors. Synthesizing disparate information and following recent theoretical developments (Caddy & Defeo 2003), we propose a mesoscale hypothesis of environmental favourability for sandy beach populations (Fig. 9). In benign environments, such as dissipative beaches or sites undisturbed by human activity, high abundances promote intraspecific interactions (e.g. density-dependent growth and mortality rates); but in marginal habitats, where harsh and fluctuating conditions lead to lower densities and limited biological interactions, the population is physically controlled and environmentally-dependent growth and mortality prevail over density-dependent mechanisms (Fig. 8a). Peripheral populations within the geographic range of a species (macroscale), or those situated in a marginal portion of a habitat affected by a disturbance source (mesoscale) tend to be physically controlled, whereas

On a finer scale, intertidal organisms may experience sorting by alongshore swash circulation resulting in aggregations. Concentration in cusps (spaced undulations of the beach face) has been documented in several sedentary filter feeders (Cubit 1969, Dillery & Knapp 1969, Perry 1980, McLachlan & Hesp 1984, Giménez & Yannicelli 2000). Sorting by cusp swash circulation tended to concentrate less motile forms in the bays, where patches were composed of more small individuals compared to those on promontories (Donn et al. 1986, James 1999). Small organisms living close to the sand surface are subject to greater rates of dislodgement and movement by swash action from promontories to bays than large organisms (James 1999). Alternatively, highly motile species may show uniform distribution throughout cusp systems or even concentrate on promontories (opposite to current
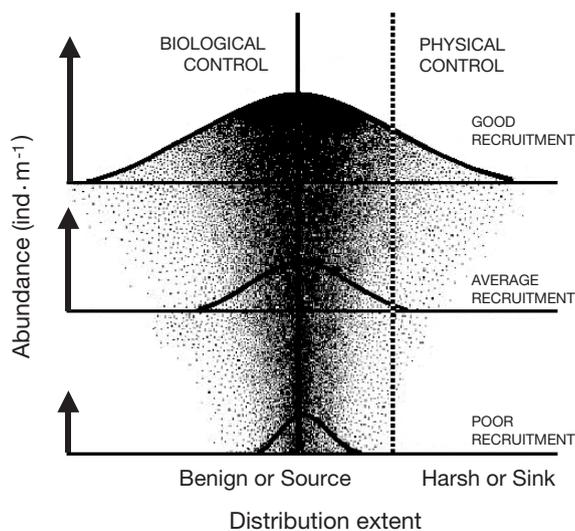
Fig. 9. The Habitat Favourability Hypothesis in sandy beach populations reflecting variations in the contraction or expansion of the distribution of a species on a mesoscale (alongshore or across-shore) or macroscale (range). In benign habitats (dissipative beaches or undisturbed systems) populations are mainly controlled by density-dependent mechanisms, whereas populations in reflective or in grossly disturbed beaches are physically controlled. In a metapopulation context, the solid line shows the expected abundance within source populations (e.g. dissipative beaches), whereas the dashed line shows that sink populations in reflective beaches may be absent in poor recruitment years (after Caddy & Defeo 2003)

populations situated at the centre of a range or in an undisturbed area are more likely to be influenced by biological factors (cf. Figs 6, 8, 9). This model could also explain the effects of morphodynamics on intertidal species; populations inhabiting reflective beaches should be mostly affected by the harshness of the environment, whereas biological factors may become more important in dissipative beaches (Fig. 4).

Zonation

Zonation schemes

Descriptions of zonation of sandy beach macrofauna can be grouped into 4 categories (McLachlan & Jaramillo 1995): (1) no clear zonation; (2) 2 zones, air breathers above the drift line and water breathers (marine forms) below; (3) 3 zones based originally on Dahl's (1952) analysis of crustaceans (see below); and (4) 4 physical zones based originally on Salvat's (1964) description of sediment moisture content. Following Dahl (1952), 3 zones can be distinguished and defined as: (1) the supralittoral zone of air breathers, present on all shores at and above the drift line and typically inhabited by talitrid amphipods, oniscid isopods or ocypodid crabs; cirolanid isopods of the genus *Excirolana* may occur around the drift line; (2) the littoral zone, present on all except the harshest reflective beaches, extends from the drift line down the midshore to just above the water table outcrop; true intertidal species, such as cirolanid isopods, haustorid amphipods and spionid polychaetes, are typical; and (3) the sublittoral zone (or fringe) which extends from the surf zone up onto the swash zone a little way above the water table outcrop; a wide variety of species may be encountered, such as donacid bivalves, hippid crabs, mysids, amphipods and polychaetes.

Quantitative analyses give partial support for 3 zones, but the number of recognizable zones depends on beach type, reflective beaches having fewer zones than dissipative beaches (Defeo et al. 1992a, Jaramillo et al. 1993, McLachlan & Jaramillo 1995, Borzone et al. 1996, Brazeiro & Defeo 1996, Nel 2001, Veloso et al. 2003, Aerts et al. 2004). In flatter, dissipative beaches, lower zones may frequently be fused and divided, whereas on reflective beaches this occurs in the mid and upper zones. At the extremes of beach morphodynamics, only the supralittoral zone may be found on very harsh reflective beaches and up to 4 zones are recognized on wide dissipative beaches. Macrofaunal zones are dynamic and not sharply defined, corresponding loosely to the moisture gradient across the shore and being defined by the distribution of characteristic species. Aperiodic variation related to short term increases in sea level generated by storm surges and barometric tides will cause the fauna to follow the high water level; alternatively, seasonal variation occurs when species occupy higher levels during spring and summer than in autumn and winter (Defeo et al. 1986, de Alava & Defeo 1991, Giménez & Yannicelli 1997, Jaramillo et al. 2000a). As faunal zones are dynamic, temporal studies are needed for a full picture of zonation patterns, requiring intensive sampling to provide unbiased estimates.

Spatial structure and patch dynamics

At the population level, zonation patterns and patchiness respond to an environment that is spatially and temporally structured by sharp gradients (Bally 1983a,b, McLachlan 1983, Defeo et al. 1986, de Alava & Defeo 1991, Jaramillo et al. 1994, Schoeman et al. 2003). Aggregations persist in time, but in contrast to sessile species, the across-shore position of patches and their structure varies according to the susceptibility of each species or population component (i.e. recruits and adults) to variations in beach topography,

morphodynamics, sediment moisture, temperature (Gi-ménez & Yannicelli 2000, Colombini et al. 2002, Defeo & Rueda 2002, Cardoso & Veloso 2003), and food avail-ability, especially in supralittoral species which follow changes in drift line wrack levels (Marsden 1991, Colombini & Chelazzi 2003).

Population variations in across-shore distribution may arise from physical and biological factors acting on different spatio-temporal scales. Daily variations in zonation are related to changes in tidal levels gener-ated by onshore winds, storm surges, and barometric tides (Brazeiro & Defeo 1996). Considerable changes have also been observed between spring and neap tides (McLachlan 1983, McLachlan & Jaramillo 1995). A high orientation capability, particularly in talitrid amphipods, permits zonal recovery in cases of abrupt displacement due to stressful conditions (Scapini et al. 1996). Shifts in zonation between the resting (diurnal) and active (nocturnal) phase have also been shown in talitrid amphipods, with surface activity across-shore varying between adults and juveniles (Scapini et al. 1992, Kennedy et al. 2000, Cardoso 2002, Fallaci et al. 2003). The main microclimatic factor modulating activ-ity in these and other species is sand temperature (Scapini et al. 1997).

Passive transport and sorting by the swash deter-mines differential zonation patterns and patchiness between population components. Smaller individual sizes tend to remain in the swash zone close to the sub-stratum surface and are more dependent on passive transport by waves, whereas large adults regulate their position on the beach by greater mobility and behavioural adaptations, including rapid burrowing (Trueman 1970, McLachlan & Young 1982, Defeo et al. 1986, Veloso & Cardoso 1999). Patchy distribution may also be related to made of locomotion, particularly in supralittoral species (Scapini et al. 1995, Brown 1996, Giménez & Yannicelli 1997). Species-specific behav-ioural responses to swash climate, manifested in swim-ming ability, burying, and orientation are also relevant (Yannicelli et al. 2002). These zonation patterns may vary between seasons and do not always coincide with visible boundaries on the beach face, namely the swash zone, the water table outcrop or the drift line (Brazeiro & Defeo 1996, Colombini et al. 2002).

Segregation by size, documented for amphipods, isopods, mole crabs and clams, suggests a differential capability of each population component to select a desirable microhabitat, as well as a possible evolution-ary process to partition space and avoid intraspecific interactions for food or space (Defeo et al. 1986, de Alava 1993, Defeo 1993, Jaramillo et al. 1994, Mc-Lachlan & Jaramillo 1995, Cardoso & Veloso 2003). Beach levels with optimal environmental conditions (in theory at the centre of the across-shore distributional

range) tend to be occupied at high densities by domi-nant intraspecific competitors for space or food (adults), whereas small individuals (recruits) may be displaced towards suboptimal microhabitats on one or both extremes of the distribution range (de Alava & Defeo 1991, Kennedy et al. 2000). Between-sex dif-ferences in individual size can determine differential zonation patterns, as in *Emerita* species (Trueman 1970, Veloso & Cardoso 1999).

Interspecific interactions could account for variations in zonation patterns, thus determining noticeable dif-ferences between allopatric and sympatric conditions. Defeo et al. (1997) reported maximum densities of *Excirolana armata* similar in allopatry and sympatry, but allopatric populations of *E. braziliensis* were more abundant lower on the shore than at sympatric loca-tions, where distribution was restricted to upper beach levels. McLachlan (1998) and Dugan et al. (2004) pro-vided further evidence of the role of competitive inter-actions in experiments where changes in burrowing performance of one species were monitored at differ-ent densities of other species, even though these effects could be minimal at field densities (McLachlan 1998). Yu et al. (2002) found that feeding habits in 4 sublittoral amphipods could explain variations in zona-tion; when dietary composition overlapped, spatial segregation reduced competition for food.

Predation can also explain temporal variations in zonation patterns on sandy beaches. Predators perform synchronized migrations that follow daily or seasonal changes in zonation of prey (Ansell et al. 1999). Selec-tive predation by fish and aerial predators, depending on beach levels, could also affect zonation patterns differentially, depending on individual sizes and prey availability (Takahashi et al. 1999, Manning & Lind-quist 2003, Yu et al. 2003). Active microhabitat selec-tion could occur in order to avoid predators or search for food concentrations (Takahashi & Kawaguchi 1998).

Modelling the spatial structure of sandy beach popu-lations has received increasing attention (Defeo 1993, James & Fairweather 1996, Giménez & Yannicelli 2000, Defeo & Rueda 2002, Schoeman et al. 2003). Recent analysis using geostatistical techniques showed spatially highly autocorrelated and persistent annual zonation patterns of intertidal isopods and clams (Defeo & Rueda 2002); across-shore-structured processes varied monthly in extent as a function of temporal variations in environmental conditions. The species tended to show bell-shape unimodal distribu-tions, but a bimodal distribution pattern could arise as a result of intraspecific segregation by size during recruitment (de Alava & Defeo 1991, Defeo & Rueda 2002). Schoeman et al. (2003) showed that across-shore patches may develop in response to some pro-cess acting at spatial scales close to 3 m.

Following the Habitat Favourability Hypothesis (Fig. 9), it is hypothesized that the centre of the across- and alongshore range of a species, under optimal conditions of sand moisture, penetrability, and temperature, may be occupied by larger and dominant intraspecific competitors for space or food, whereas small individuals (recruits) may be displaced towards suboptimal conditions on one or both extremes of the distribution range. The same holds true in the case of interspecific competition.

MICROSCALE PATTERNS

The microscale or 'quadrat scale' (Defeo 1996a) concerns variations from mm to m and covers interactions in high-density patches and encompasses the area of influence of an individual (Hall 1983). Small-scale environmental gradients, together with intra- and interspecific interactions, affect populations at this fine spatial scale (Defeo 1996a, 1998). Small-scale data collected to investigate spatial distribution patterns in sandy beach populations are considered Type 1 (sensu Orensanz et al. 1998), i.e. counts of individuals within quadrats. Type 2 (distances between individuals and their nearest neighbours) and Type 3 (maps of all individuals in a 3-dimensional plot) studies have not been conducted yet, despite their importance for describing spatial patterns.

Microscale spatial patterns in the Manila clam *Tapes philippinarum* on a sheltered beach (Hall 1983) showed that recruitment depended partly on segregating and congregating forces between larvae attempting settlement and the adult population. The former may result from negative interactions between adults and larvae, which generate a more regular spacing between individuals as a result of competition for space and food or from filtering of larvae by adults during the feeding process. Defeo (1993) documented a more patchy distribution among recruits than among adult clams *Mesodesma mactroides*, suggesting that individuals tend to space themselves as a function of size. Space limitation increases with density of established adults; high adult density increases the probability that a resident adult population filters out settling larvae, preventing colonization by new recruits (Hall 1983). As in suspension feeders, each animal would establish a territory by its filtering activity, and a 'bottleneck' occurs at high adult den-

sity or biomass; for yellow clams this was close to 100 adults m^{-2} (Defeo 1996b). Filtering out larvae holds bivalve population density below carrying capacity (cf. Peterson 1979).

Scatter diagrams of adult and recruit density per quadrat have been used to assess potential intra- and interspecific interactions (Caddy & Defeo 2003). At this small scale of spatial resolution, Defeo (1996a) showed that the highest densities of recruits of the yellow clam *Mesodesma mactroides* were never coincident with the highest densities of older clams. Maximum recruit density per quadrat occurred during a period of active fishing, whereas adult densities were highest immediately after a fishing exclusion experiment. However, at adult densities >400 ind. m^{-2}, recruits were almost absent (Fig. 10). The upper boundary of the scatterplot, the Constraint Envelope Pattern (CEP sensu Marquet et al. 1995), represents optimal combinations of adult and recruitment density, whereas values within this 'envelope', well below the upper ceiling, represent suboptimal conditions. Fine scale segregation is consistent with the overcompensatory stock-recruitment relationship in the yellow clam, with inhibition of recruitment at highest adult densities under exclusion of fishing activities (Defeo 1998). Active filtering of larvae during feeding activity was a potential explanatory mechanism.

Dugan et al. (2004) demonstrated negative relationships between the mole crab *Emerita analoga* and the surf clam *Mesodesma donacium* at small spatial scales. Spatial overlap in the intertidal distributions of these species varied with abundance in time and space. Highest density zones of each species were distinctly separated at low tide and spatial overlap decreased significantly with increasing density.
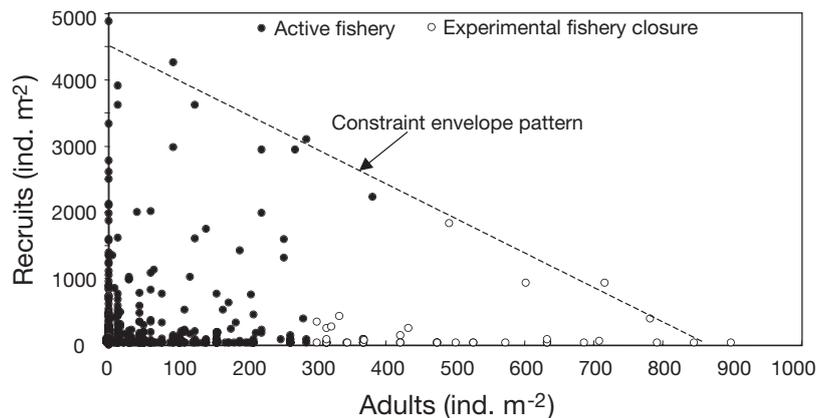
Fig. 10. *Mesodesma mactroides*. Scatter diagram of yellow clam recruit density plotted against adult density in each quadrat during recruitment periods; recruitment densities peaked under low adult densities and high extraction levels between 1983 and 1987 (●) but were low in 1989–1990 (○) as a result of experimental fishery closure. The broken line defines the constraint envelope (Marquet et al. 1995) between stock and recruitment (data from Defeo 1996a)

BIOLOGICAL FACTORS

Competition

Detection of intra- and interspecific competition in sandy beaches has proven difficult (Branch 1984, Defeo 1996b) because of (1) inherent difficulties in experimentally manipulating the generally small and mobile infauna, (2) the 3-dimensional structure of the habitat which enables horizontal and vertical space partitioning (Peterson 1991), and (3) the absence of information about the scale-dependence of processes structuring populations. However, results from analyses conducted at a variety of spatial scales suggest that intraspecific (Defeo et al. 1992b; Defeo 1996a, Marsden 2002, Schoeman & Richardson 2002) and interspecific (Defeo & de Alava 1995, Defeo et al. 1997, McLachlan 1998, Dugan et al. 2004) competition may significantly influence sandy beach fauna. The earliest evidence was provided by Croker & Hatfield (1980), who found horizontal and vertical space partitioning between 3 sympatric haustoriid amphipods along with differential survival in coexistence experiments in the laboratory (see also Croker 1967). This section reviews findings on the role of competition since Croker & Hatfield (1980).

Zonation patterns (see above), abundance and survivorship in the sympatric isopods *Excirolana armata* and *E. braziliensis* are affected by interspecific interactions; a noticeable reduction in body size of both species occurs in sympatric populations (Defeo et al. 1997). *E. braziliensis* is most abundant in fine sands, and has a greater niche breadth through most of its range than that observed in Uruguay, where it mainly inhabits coarse sands and upper beach levels on reflective beaches, being displaced by *E. armata*.

Human exclusion experiments are useful tools to detect the role of intra and interspecific competition, because humans can strongly impact the dynamics and demography of sandy beach macrofauna (Defeo & de Alava 1995, Peterson et al. 2000). A long-term study (1983 to 1990), with a human exclusion experiment based on a fishery closure for 32 mo showed density-dependent growth, mortality, and recruitment of the targeted yellow clam *Mesodesma mactroides*, suggesting that intraspecific competition affects its dynamics (Castilla & Defeo 2001). Particularly, there was strong overcompensation in the stock-recruitment relationship, i.e. inhibition of recruitment at high adult densities (Defeo 1993, 1996b). Stochasticity in reproductive rates and asymmetric intercohort interactions (density-dependent recruitment and survival rates) operating together have been identified as key processes generating large variability in yellow clam recruitment (Brazeiro & Defeo 1999, Lima et al. 2000). Fishing pres-

sure on *M. mactroides* explained temporal variations in recruitment in non-targeted species: recruitment density of the sympatric non-targeted bivalve *Donax hanleyanus* was inversely related to the density of juveniles and adults of the sympatric yellow clam *Mesodesma mactroides* (de Alava 1993, Defeo 1998), defining an 'interspecific stock-recruitment relationship' (sensu Pauly 1980).

McLachlan (1998) found that intra- and interspecific interactions could occur during burrowing at high densities (400 to 600 ind. m^{-2}) of the sympatric *Donax serra* and *Donax sordidus*. Asymmetric competition was postulated: the larger *D. serra*, occupying more space at experimental densities, had significant effects on the smaller *D. sordidus*, but not viceversa. However, the densities required to produce these effects exceeded those normally recorded in the field. In a similar study, Dugan et al. (2004) investigated the hippid crab *Emerita analoga* and the clam *Mesodesma donacium* finding burrowing times of large crabs significantly longer in all densities of clams than in controls, and large crabs displacing small clams from the sand while burrowing. Cardoso & Veloso (2003) showed a negative relationship between densities of *Donax hanleyanus* and *Emerita brasiliensis* over time during a 2 yr study, suggesting competition.

We propose that these biotic interactions are particularly meaningful in dissipative beaches with high species richness, high densities, and relatively stable substrate; whereas populations at reflective beaches could be mainly regulated by individual responses to the environment (Defeo et al. 2003, McLachlan & Dorvlo 2005; see Fig. 4). Since sandy beach populations are highly spatially structured, compensatory and overcompensatory mechanisms are expected to occur at small spatial scales in dissipative beaches with high macrofauna densities.

Predation, mutualism and parasitism

There is little information on effects of these processes on population dynamics or community structure. Concerning predation, studies on ecosystem energetics have quantified the main trophic structures and energy flows, which vary between beach types: reflective beaches function as interfaces processing organic material inputs from the sea, whereas dissipative beaches may have surf diatom accumulations driving resident food chains in open but functional beach and surf zone ecosystems (Brown & McLachlan 1990). High primary and secondary production allow higher predation rates at dissipative beaches (Brown & McLachlan 1990, Colombini & Chelazzi 1996). Removal of macrofauna production is due to 3 main

groups of predators: (1) birds, arachnids and insects from land, (2) fishes from the sea, and (3) resident invertebrates, notably crabs. These forms of predation crop populations and result in significant energy flow, but their effects on population dynamics or community structure are still not known.

Positive interspecific interactions within physically stressful habitats have been sparsely documented. Manning & Lindquist (2003) demonstrated a positive interaction where the clam *Donax variabilis* facilitated epibiotic occupation by providing a stable substrate for attachment of the hydroid *Lovenella gracilis*; the hydroid defended the clam against fishes by means of its nematocysts, but facilitated predation by crabs, because projection of the hydroid above the surface of the sand allowed the crabs to more readily detect clams. Depending on relative predation pressure, the occupation of *D. variabilis* by *L. gracilis* was characterized as beneficial or detrimental to the host.

Parasitism can be a potentially important process influencing demographic patterns and the small-scale spatial distribution of sandy beach macrofauna. Poulin & Rate (2001) and Poulin & Latham (2002) demonstrated that parasites affected the burrowing depth of *Talorchestia quoyana* in New Zealand beaches. Amphipods that harboured larger parasites burrowed deeper than expected based on their body size. Massive natural mortality events decimated yellow clam populations along thousands of km of sandy beaches in Brazil, Uruguay and in Argentina (Fiori & Cazzaniga 1999). Parasites could play a role in explaining these mortality events (Cremonte & Figueras 2004, Fiori et al. 2004), thus providing an alternative explanation to the widely held notion that mass mortalities in beach macrofauna are due to toxins from harmful algal blooms (McLachlan et al. 1996b).

The third dimension, vertical distribution in the sand, is an additional way to partition space in order to ameliorate the strength of biological interactions. This 3-dimensional structure of the sandy beach habitat is a general feature of soft-bottom environments (Peterson & Andre 1980, Wilson 1991, Peterson 1991), but in the case of sandy beach environments, 3-dimensional studies have not been conducted yet.

CONCLUSIONS

Sandy beach research has advanced considerably over the past 2 decades. This review, focusing on community and population ecology, has covered a significant body of knowledge and demonstrated an emerging field of research taking form around central paradigms and theories under test. Beach morphodynamic models have become widely accepted and applied at the community level, with consistent large-scale patterns of increasingly species rich communities towards dissipative beaches and lower latitudes. Population studies on a variety of scales have examined both the dynamics of commercially exploited populations and the regulation and adaptations of populations in general. We propose here that in benign dissipative beaches or undisturbed sites, intra- (density-dependent growth and mortality rates) and interspecific (segregation by species or individual sizes) interactions can be more intense than in reflective beaches or disturbed sites, where the populations are physically controlled (environmentally dependent growth and mortality). We believe the key areas for the future will be investigating the importance of physical and biological factors on finer scales, through population studies and experimental work on ecophysiology and behaviour. Only by deciphering cause and effect relationships at the individual and population levels will we truly begin to understand the processes that underlie the large-scale community patterns that have become clear.

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