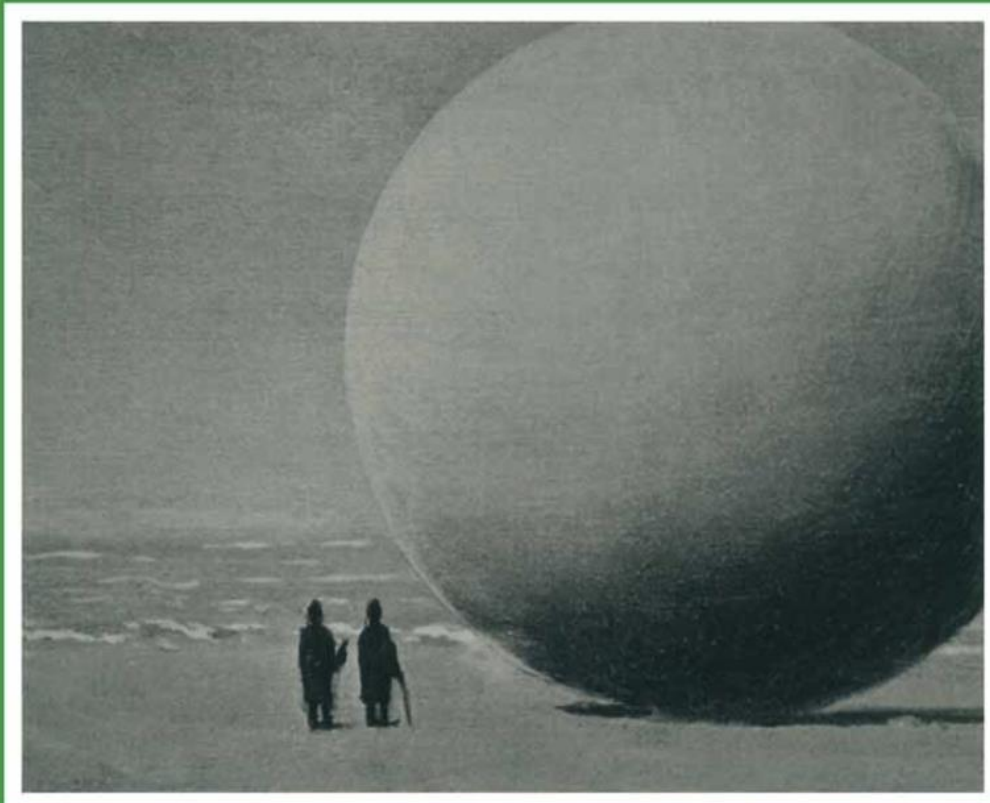


Ecological Studies 151

---

K. Reise (Ed.)

# Ecological Comparisons of Sedimentary Shores



Springer

# 3 Suspension Feeders on Sandy Beaches

E. JARAMILLO and M. LASTRA

## 3.1 Introduction

Sandy beaches are the most common coastal habitat on temperate and tropical coasts; comprising about 75 % of the world's coastal zone (Bascom 1980). Exposed sandy beaches support a diverse and abundant macroinfauna (Brown and McLachlan 1990). In terms of species richness, sandy beach macroinfauna is dominated by crustaceans, bivalves and polychaetes. In terms of abundance, peracarid crustaceans are usually the dominant organisms. However, large suspension feeders, such as anomuran decapods (*Emerita* spp.) and bivalves (*Mesodesma* and *Donax* spp.), are usually the top contributors to biomass (e.g. Hutchings et al. 1983; Donn 1990; Dugan et al. 1994; Jaramillo et al. 2001).

Basically, sandy beaches can be described in terms of wave and sediment characteristics, also called beach morphodynamics. A dimensionless index, Dean's parameter (also called parameter  $\Omega$ ), reflects the interaction between wave height, wave period and sediment fall velocity of sand particles from the sediments at the breaker zone (Short and Wright 1983; Short 1996); i.e.  $\Omega = H_b/T \times \text{sand fall velocity}$ , where  $H_b$  is the height in centimeters of waves at the breaker zone,  $T$  is the wave period in seconds, while sand fall velocity ( $\text{cm s}^{-1}$ ) is derived from the mean grain size of sands from the breaker zone and empirical data given by Gibbs et al. (1971). Using this parameter, three major types of beaches can be described: reflective, intermediate and dissipative.

Reflective beaches are characterized by a virtual absence of surf zone, coarse sand, small waves (usually lower than 1 m) and steep profiles. At the other end of the spectrum, dissipative beaches have a wide surf zone (i.e., waves dissipate most of their energy before reaching the beach face), fine sands, large waves (usually higher than 2 m) and flat profiles. Intermediate beaches lie between both extremes, with bar-trough systems, rip currents and variable seasonal conditions (Short and Wright 1983; Short 1996). The swash

climate of exposed sandy beaches varies with the morphodynamic states. For example, reflective beaches have swashes with short periods, dissipative ones have longer swash periods, and intermediate beaches show swash periods intermediate between that of reflective and dissipative beaches (McArdle and McLachlan 1991). The following Dean's values have been mentioned (e.g. Short and Wright 1983) for the beach types:  $\leq 1.0$ =reflective beaches,  $1.0-6.0$ =intermediate beaches, and  $>6.0$ =dissipative beaches.

Dean's parameter is a useful tool to categorize sandy beaches on microtidal coasts. However, when tide ranges are greater than 2–3 m, the role of tides in beach morphodynamics increases (Masselink and Short 1993). To account for this, McLachlan et al. (1993) created the beach state index (BSI) where  $BSI = \log [(H_b \times MTR/T \times \text{sand fall velocity} \times ET) + 1]$ . MTR is the maximum tide range and ET is the maximum theoretical equilibrium tide for which the earth covered in water is 0.8 m (McLachlan et al. 1993). Based upon a comparative study of about 70 beaches, McLachlan et al. (1993) suggested the following scale for BSI:  $<0.5$ =reflective beaches,  $0.5-1.0$ =low to medium energy intermediate beaches,  $1.0-1.5$ =high energy intermediate–dissipative beaches,  $1.5-2.0$ =fully dissipative beaches, and  $>2.0$ =ultra-dissipative macrotidal beaches.

Beach morphodynamics have been considered a key factor in the community structure of the sandy beach macroinfauna around different zoogeographic regions of the world. A comparative study of sandy beach macroinfauna communities from all around the coast of South Africa, Australia and the coast of Oregon showed a linear increase in species richness and an exponential increase in abundance and biomass of the macroinfauna from reflective to dissipative conditions (Fig. 3.1, McLachlan 1990). Since the BSI allows for comparisons of sandy beaches located at different zoogeographical regions which have very large differences in tidal range, McLachlan et al. (1993, 1996, 1998) subsequently studied the sandy beach macroinfauna in South Africa, Oregon, Australia, south central Chile, and Oman showing that the patterns already found also hold globally. However, recent seasonal studies carried out along the coast line of Chile (from about 19 to 42° S, circa 2500 km) show that these sorts of relationships are indeed quite variable. Thus, the higher abundance and biomass values are found at intermediate beaches with Dean's values close to 3 (Fig. 3.2a). These values of abundance and biomass are usually higher than the values predicted by the worldwide model given by McLachlan et al. (1996) in which the BSI is used (Fig. 3.2b).

In the first part of this study we compare the community structure of the sandy beach macroinfauna vs. beach morphodynamic types on different coasts. We will explore the role of the most distinctive suspension feeder along Chilean sandy beaches – the anomuran crab *Emerita analoga* – in terms of the observed trend for this coast by comparing unpublished information of sandy beach surveys carried out along the Chilean coast and Spain (Galicia)

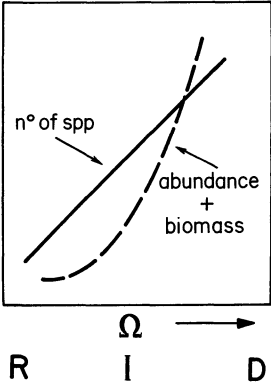


Fig. 3.1. General trends of species richness, abundance and biomass of the sandy beach macroinfauna vs. morphodynamic beach type. R, I, D reflective, intermediate and dissipative beaches (see text)

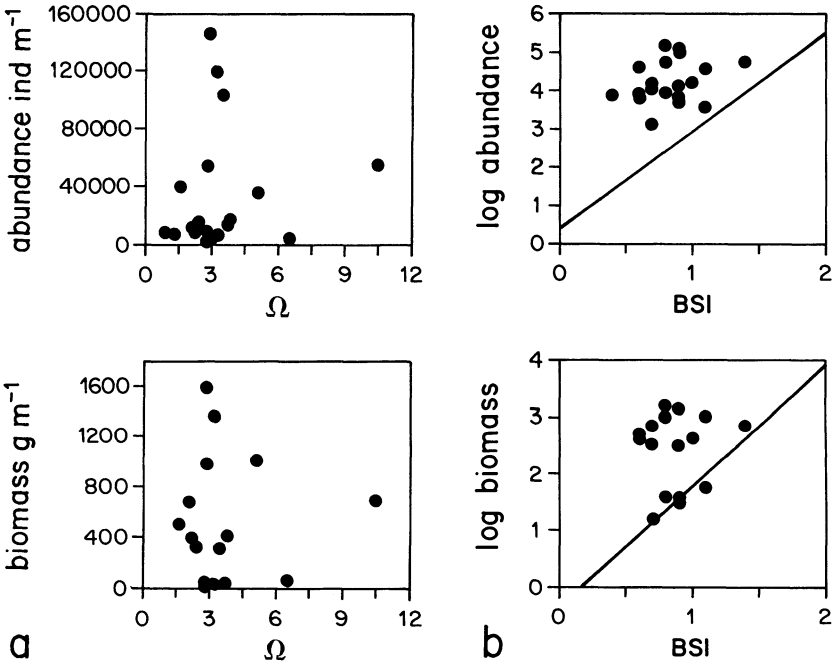


Fig. 3.2. Sandy beach macroinfauna from the Chilean coast. Abundance and biomass of the total macroinfauna vs. beach types defined by Dean's parameter ( $\Omega$ ) (a) and beach state index (BSI) (b). The regression lines are from McLachlan et al. (1996);  $y=0.39+2.55x$  for abundance and  $y=-0.34+2.12x$  for biomass

with published data from Australia (McLachlan et al. 1996) and Oman (McLachlan et al. 1998). In the second part we also examine unpublished and published information to examine whether morphodynamic beach types affect the population biology and behavior of large suspension feeders such as *Emerita* and *Donax*. Finally, we analyze across- and along-shore zonation of these suspension feeders to examine the possible role of biological interactions in shaping spatial distributions on exposed sandy beaches.

### 3.2 Beach Morphodynamic Types vs. Community Structure of the Macroinfauna

*E. analoga* is the most common suspension feeder inhabiting sandy beaches along the Chilean coast. It primarily occupies the lower shore levels (swash-resurgence zone), although stranded animals are sometimes also found at the mid-shore levels or retention zone. Along this coast, the abundance of this species is usually higher than 50 %, while biomass values may well represent more than 80 % of the whole macroinfauna (Fig. 3.3). The dominance of this species results in significant correlations for total abundance and biomass vs. abundance and biomass of *E. analoga* on these beaches ( $\log \text{total abundance} = -3.27 + 1.61 \times \log \text{abundance of } E. \text{ analoga}$ ,  $r=0.85$ ,  $n=19$ ,  $p<0.01$  and  $\log \text{total biomass} = -1.04 + 1.31 \times \log \text{biomass of } E. \text{ analoga}$ ,  $r=0.95$ ,  $n=16$ ,  $p<0.01$ ). Dugan et al. (2000) have reported *E. analoga* as the most abundant species on 22 out of 36 beaches surveyed along the coast of California (5 to 98 % of the total macrofaunal abundance). Similarly, biomass of this crab accounted for 22–99 % of the total biomass on those beaches (Dugan et al. 2000).

The total abundance of the macroinfauna on Chilean beaches is higher than the worldwide model presented by McLachlan et al. (1996) (Fig. 3.4); in other words, similar abundances were found on Chilean beaches with lower BSI values than those studied at other latitudes such as Australia, Spain and Oman. Biomass vs. BSI shows a similar pattern to that of the abundance, and, in some cases, macroinfaunal biomasses on Chilean beaches were higher than those found on Omani beaches, being both similar in BSI (Fig. 3.4). We conclude from this that for the sandy beaches of Chile and also those in California (see Dugan and Hubbard 1996), factors other than beach morphodynamics influence patterns of macroinfaunal community structure in exposed sandy beaches. Those factors would apply primarily to large suspension feeders such as *E. analoga*; e.g. upwelling waters along the coast of Chile and California. Interestingly, sandy beaches located on coasts with upwelling waters (e.g., sandy beaches of Galicia, Spain; de la Huz 1999) but with low abundances and biomass of large suspension feeders (or even absent)

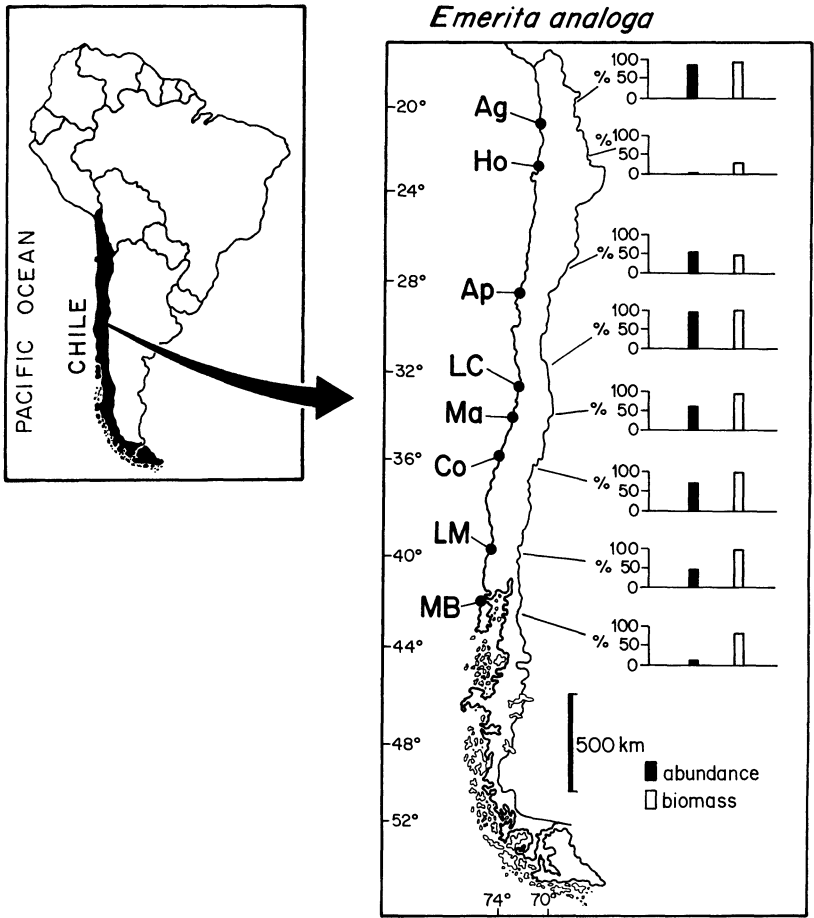
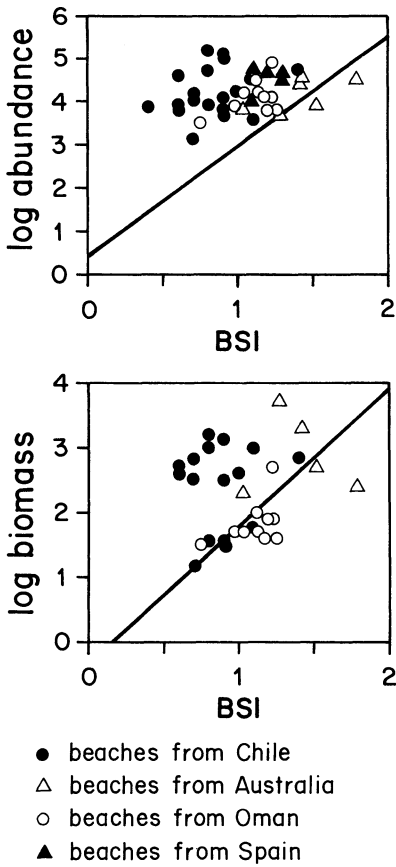


Fig. 3.3. Relative values for *Emerita analoga* (abundance and biomass) at exposed sandy beaches located along the Chilean coast. The names of the study beaches are: Ag Aguila; Ho Hornitos; Ap Apollillado; LC Las Cruces; Ma Matanzas; Co Cobquecura; LM La Misión; MB Mar Brava

agree quite well with the McLachlan model of increasing abundance and biomass from low to high BSI values. At this point it is worthwhile mentioning that earlier studies on the Chilean coast (Jaramillo and McLachlan 1993) were similar to the results of McLachlan et al. (1996), in the sense that abundance and biomass of the macroinfauna increased from reflective to dissipative beaches. However, those studies included three reflective beaches located close to an estuarine outlet where *E. analoga* was absent or in very low abundance. As shown experimentally by Jaramillo (1987), water salinities lower than 20 ppt result in significant mortality of this species. This would



**Fig. 3.4.** Values of abundance and biomass of the total macroinfauna at Chilean, Australian, Omani and Spanish beaches. The Chilean data are taken from Jaramillo (2001), that of Australia from McLachlan et al. (1996), and those of Oman from McLachlan et al. (1998). The data from Spain are unpublished data of M. Lastra. The regression lines originate from the equations given by McLachlan et al. (1996)

explain the low macroinfaunal abundances found by Jaramillo and McLachlan (1993) and the linear increase in total macroinfauna along a range of morphodynamic beach types in that area of the Chilean coast. Indeed, it would be interesting to evaluate if the abundance and biomass of the total macroinfauna inhabiting exposed sandy beaches of the North and South American coasts that have species of *Emerita* agree or not with the worldwide model presented by McLachlan et al. (1996). Apart from *E. analoga*, five species of *Emerita* have been collected along this coast: *E. rathbunae* along the tropical coast of the Pacific Ocean, *E. talpoida* from the Atlantic coast of the USA and the Gulf of Mexico, *E. benedicti* primarily found inside that gulf, *E. portoricensis* from the West Indies in the Caribbean, and *E. brasiliensis* from the Atlantic coast of South America (Tam et al. 1996).

### 3.3 Beach Morphodynamic Types and Abundances and Population Biology of *E. analoga*

Seasonal variability in population abundances of *E. analoga* at two regions of the Chilean coast is shown in Fig. 3.5. In northern Chile, the abundances were higher at an intermediate beach (average Dean's parameter=2.9) as compared with a site with quite reflective characteristics (average Dean's parameter=1.4). On the other hand, two beaches examined in south central Chile, a dissipative site (average Dean's parameter=6.6) and an intermediate beach (average Dean's parameter=4.7), supported similar population abundances of *E. analoga*. This suggests that beach types affect population abundances of this suspension feeder just when beach types are close to or at the reflective condition. This assertion is supported by the fact that, at those sites sampled in south central Chile, growth parameters of *E. analoga* are quite similar (E. Jaramillo, unpubl. data).

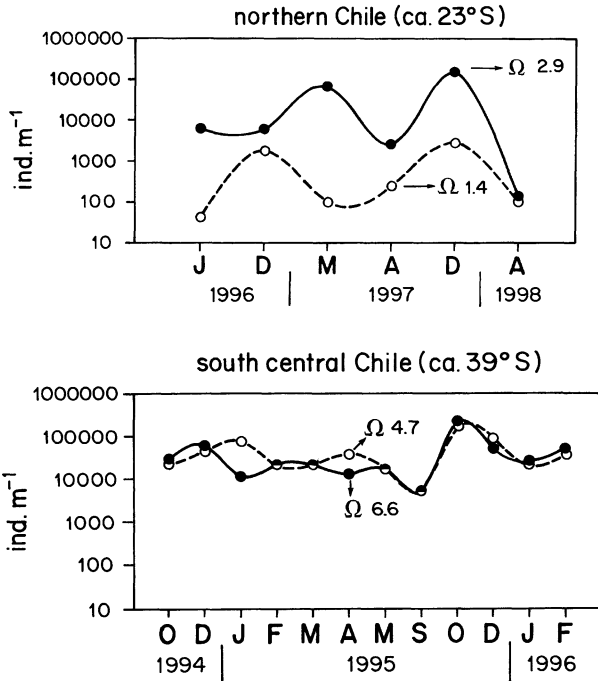


Fig. 3.5. Seasonal variability in population abundances of *Emerita analoga* in two areas of the Chilean coast. The values of Dean's parameter ( $\Omega$ ) are means of the whole study period at each beach. The sampling months at the beaches of northern Chile were July (J) and December (D) 1996, March (M), August (A) and December (D) 1997, and August (A) 1998

### 3.4 Tidal Movements and Burrowing Behavior

It has long been known that large suspension feeders of sandy beaches (e.g. *Emerita*, *Donax*) move up and down the shore with tidal variation (Branch and Branch 1993). However, not much is known about the effects of different beach types upon that sort of movement. Jaramillo et al. (2000) compared tidal variability of *E. analoga* between a dissipative and a reflective beach of southern Chile (ca. 42° S) and found that the movement of this species was greater at the dissipative site. Along a tidal cycle that included two lows and one high tide (ca. 12 h) the population mode of *Emerita* moved up and down following the limits of the swash zone as it moved up and down the beach. In contrast, in the reflective site, most of the animals remained below the lowest swash level through the tidal cycle suggesting that the width of the swash zone may affect the extent of tidal movement in this suspension feeder. In other words, this supports the swash exclusion hypothesis (McLachlan et al. 1993) in the sense that crabs remained below the effluent line on that reflective beach.

Exposed sandy beaches are coastal habitats dominated by sediment instability and strong hydrodynamic forces. One of the main adaptative mechanisms to cope with these factors is burrowing behavior; i.e., in exposed beaches organisms must burrow fast enough to avoid drifting in strong waves and currents. Burrowing rates of sandy beach organisms are usually affected by body size of organisms (see, e.g., McLachlan et al. 1995). Jaramillo et al. (2000) measured burrowing rates of *E. analoga* on both a dissipative and a reflective beach in southern Chile and found that crabs burrowed at similar rates in sediments from both beaches, which suggests that this crab is a sediment generalist (cf. Alexander et al. 1993). Laboratory experiments using *Donax trunculus* from Spain (M. Lastra, unpubl. data) showed ontogenic changes in clams burrowing in different sediment sizes. Those results show that individuals measuring 5–25 mm in shell length burrow faster in medium and fine sands, while bigger animals burrow faster in fine and very fine sands. These results suggest that small (juvenile) clams are able to cope with more reflective morphodynamic conditions (e.g., coarser sands) than adults. To determine whether this trend represents a plastic response of the individuals that inhabit changing sedimentary environments, further studies are needed.

### 3.5 Across- and Along-Shore Zonation

The patchy distribution of sandy beach organisms has been mainly studied in bivalves (e.g. Sastre 1985; Defeo et al. 1986; Jaramillo et al. 1994; Lastra and

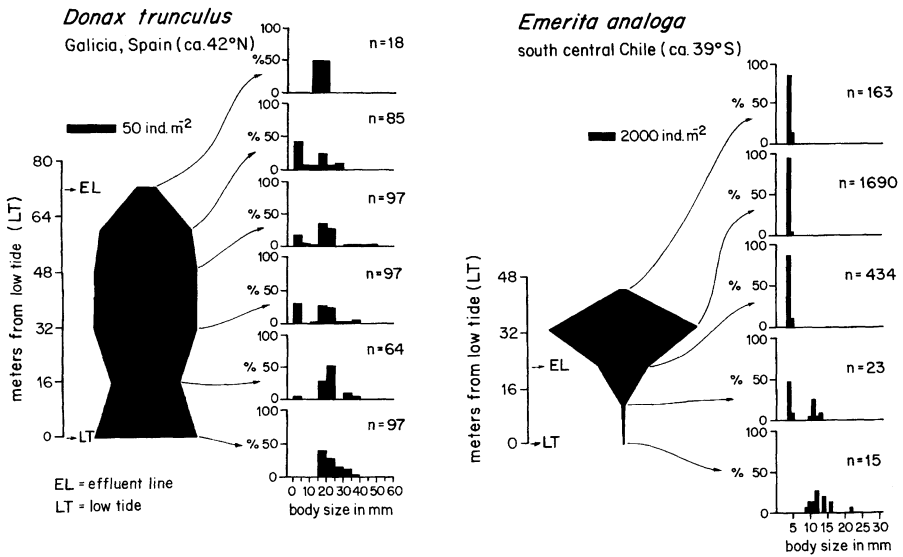


Fig. 3.6. Across-shore distribution of *Donax trunculus* and *Emerita analoga* at an exposed beach in Galicia, Spain, and south central Chile

McLachlan 1996) and anomuran crustaceans such as *Emerita* (Efford 1965; Cubit 1969; Perry 1980); the across-shore distribution of the bivalve *Donax trunculus* and that of *Emerita analoga* in Spain and Chile, respectively. Both of them show space partitioning across the intertidal. This is most obvious with *E. analoga*; i.e., smaller (younger) crabs mostly inhabit the upper levels of the distribution (i.e., at the top of the swash zone). During the times when juvenile *E. analoga* are more abundant on the sandy beaches of south central Chile – spring to early autumn – their highest abundances are usually found in areas where the abundance of larger crabs is lower (Hinrichsen and Rivera 1994). Thus, results presented in Fig. 3.6 suggest that the spatial segregation of juveniles and adults of *E. analoga* on sandy beaches of south central Chile may be due to some sort of biological interactions. Dugan and Hubbard (1996) reached similar conclusions for Californian populations of this species; i.e., measures of crab size increased while population abundance decreased among 12 populations on 50 km of coast.

Physical and biological factors have been proposed as causes of spatial partitioning in the across- and along-shore distribution of large sandy beach suspension feeders, among them sediment size (Maze and Laborda 1988) and intraspecific competition (Guillou and Le Moal 1978; Ansell and Lagardere 1980). Although there is not much experimental evidence for the role of these factors, some published results suggest that biological interactions may well be involved. Field experiments carried out by McLachlan (1998) on a sandy

beach in South Africa showed that the burrowing rates of *Donax serra* and *D. sordidus* were affected at high densities of the former species, a result which suggests that in high density beds of these clams interactions would occur. Similarly, in a field experiment carried out by Defeo (1996) on a sandy beach in Uruguay, density-dependent processes were considered important for *Mesodesma mactroides* and *Donax hanleyanus*. More experiments are clearly needed to elucidate these aspects.

### 3.6 Conclusions

This review has explored the role of large suspension feeders such as *E. analoga* in the observed trends of sandy beach community structure in coastal areas like Chile and California, where these animals are the most abundant organisms. In these areas, the relationship between abundance and biomass of the total macroinfauna does not match the worldwide model in which morphodynamic beach type is considered to be the key factor in shaping macroinfaunal community structure. Although few studies have been carried out, it seems that beach morphodynamic type affects the behavioral aspects of these organisms, such as tidal migration and burrowing behavior. The patchy distribution and often size-structured aggregations of large suspension feeders, such as *E. analoga*, *Donax* and *Mesodesma*, also suggest that biological interactions (an almost unexplored field) may indeed be important in shaping these patterns on exposed sandy beaches.

*Acknowledgements.* We thank Karsten Reise for the invitation to present this study at the Workshop Ecological Comparisons of Sandy and Muddy Shores at Sylt, Germany. E.J. and M.L. acknowledge the assistance of Heraldo Contreras, Marcia González, Cristián Duarte (Instituto de Zoología, Universidad Austral de Chile), María del Rosario de la Huz and María Esther Pita Siebert (Departamento de Ecología y Biología Animal, Universidad de Vigo) while preparing this manuscript. E.J. also appreciates the financial support of CONICYT (Chile), Proyecto FONDAP Oceanografía & Biología Marina, for research funds used in Chile, Oman and Spain, and to the Alfred Wegener Institute for Polar and Marine Biology (AWI, Bremerhaven, Germany) and Universidad Austral de Chile (DID) for financial aid to attend the workshop. M.L. acknowledges financial support from Xunta de Galicia and Universidad de Vigo for research funds used on the coast of Spain, and to AWI which provided the funds to attend the workshop. We also thank Anton McLachlan and Jenifer Dugan for reviewing a former manuscript.

## References

- Alexander RR, Stanton RJ, Dodd JR (1993) Influence of sediment grain size on the burrowing of bivalves – correlation with distribution and stratigraphic persistence of selected neogene clams. *Palaios* 8:289–303
- Ansell AD, Lagardere F (1980) Observations on the biology of *Donax trunculus* and *D. vittatus* at Ile d'Óleron (French Atlantic coast). *Marine Biology* 57:287–300
- Bascom W (1980) Waves and beaches. Anchor Press/Darbleday, New York, 366 pp
- Branch M, Branch G (1993) The living shores of Southern Africa. Strik Publishers, Cape Town, South Africa, 272 pp
- Brown AC, McLachlan A (1990) Ecology of sandy shores. Elsevier Science Publishers BV, Amsterdam, The Netherlands, 328 pp
- Cubit J (1969) Behaviour and physical factors causing migration and aggregation of the sand crab *Emerita analoga* (Stimpson). *Ecology* 50:118–123
- Defeo O (1996) Experimental management of an exploited sandy beach bivalve population. *Rev Chil Hist Nat* 69:605–614
- Defeo O, Layerle C, Masello A (1986) Spatial and temporal structure of the yellow clam *Mesodesma mactroides* (Deshayes 1854) in Uruguay. *Medio Ambiente (Chile)* 8:48–57
- De la Huz MR (1999) Estudio de playas expuestas de Galicia: morfología y macrofauna. Tesis Licenciatura, Universidad de Vigo, Vigo, España, 82 pp
- Donn TE (1987) Longshore distribution of *Donax serra* in two log-spiral bays in the eastern Cape, South Africa. *Mar Ecol Prog Ser* 35:217–222
- Donn TE (1990) Morphometrics of *Donax serra* Roding (Bivalvia: Donacidae) populations with contrasting zonation patterns. *J Coastal Res* 6893–901
- Dugan JE, Hubbard DM (1996) Local variation in populations of the sand crab *Emerita analoga* on sandy beaches in southern California. *Rev Chil Hist Nat* 69:579–588
- Dugan JE, Hubbard DM, Wenner AM (1994) Geographic variation in life history of the sand crab, *Emerita analoga* (Stimpson) on the California coast: relationships to environmental variables. *J Exp Mar Biol Ecol* 181:255–278
- Dugan JE, Hubbard DM, Martin DL, Engle JM, Richards DM, Davis GE, Lafferty KD, Ambrose RF (2000) Macrofauna communities of exposed sandy beaches on the southern California mainland and Channel Islands. Proceedings of the 5th California Islands Symposium. OCS Study, MMS 99-0038:339–346
- Efford IE (1965) Aggregation in the sand crab *Emerita analoga* (Stimpson). *J Anim Ecol* 34:63–75
- Gibbs RJ, Mathews MD, Link DA (1971) The relationship between sphere size and settling velocity. *J Sediment Petrol* 41:7–18
- Guillou J, Le Moal Y (1978) Variabilité spatio-temporal des populations de *Donax* en la bahie de Douarnenez. *Haliotis* 9:77–88
- Hinrichsen CA, Rivera VJ (1994) Variabilidad espacio – temporal de la macroinfauna intermareal en una playa arenosa del centro sur de Chile y su relación con la variabilidad abiótica del sustrato. Tesis Biología Marina, Universidad Austral de Chile, Valdivia, Chile, 32 pp
- Hutchings L, Nelson G, Horstman DA, Tarr R (1983) Interaction between coastal plankton and sand mussels along the Cape coast, South Africa. In: McLachlan A, Erasmus T (eds) Sandy beaches as ecosystems. Junk Publishers, The Hague, pp 481–500
- Jaramillo E (1987) Community ecology of Chilean sandy beaches. PhD dissertation, University of New Hampshire, Durham, NH, USA, 216 pp
- Jaramillo E (2000) The sand beach ecosystem of Chile. In: Seeliger U, Kjerfve B (eds) Coastal marine ecosystems of Latin America. Ecological Studies 144. Springer-Verlag, Berlin Heidelberg New York, pp 219–227

- Jaramillo E, McLachlan A (1993) Community and population responses of the macrofauna to physical factors over a range of exposed sandy beaches in south central Chile. *Estuar Cost Shelf Sci* 37:615–624
- Jaramillo E, Pino M, Filún L, González M (1994) Longshore distribution of *Mesodesma donacium* (Bivalvia: Mesodesmatidae) on a sandy beach of the south of Chile. *Veliger* 37:192–200
- Jaramillo E, Dugan E, Contreras H (2000) Abundance, population structure, tidal movement and burrowing rate of *Emerita analoga* (Stimpson, 1857) (Anomura, Hippidae) at a dissipative and a reflective sandy beach in south central Chile. *Mar Ecol, PSZNI* 21:113–127
- Lastra M, McLachlan A (1996) Spatial and temporal variations in recruitment of *Donax serra* Roding (Bivalvia: Donacidae) on an exposed sandy beach of South Africa. *Rev Chil Hist Nat* 69:631–639
- Masselink G, Short AD (1993) The effect of tide range on beach morphodynamics and morphology: a conceptual beach model. *J Coastal Res* 9:785–800
- Maze R, Laborda AJ (1988) Aspectos de la dinámica de población de *Donax trunculus* (Linnaeus, 1758) (Bivalvia: Donacidae) en la Ria del Barquero (Lugo, España). *Invest Pesqueras* 52:299–312
- McArdle S, McLachlan A (1991) Dynamics of the swash zone and effluent line on sandy beaches. *Mar Ecol Prog Ser* 76:91–99
- McLachlan A (1990) Dissipative beaches and macrofauna communities on exposed intertidal sands. *J Coastal Res* 6:57–71
- McLachlan A (1998) Interactions between two species of *Donax* on a high energy beach: an experimental approach. *J Molluscan Stud* 64:492–495
- McLachlan A, Jaramillo E, Donn TE, Wessels F (1993) Sandy beach macrofauna communities and their control by the physical environment: a geographical comparison. *J Coastal Res (Special Issue)* 15:27–38
- McLachlan A, Jaramillo E, Defeo O, Dugan J, de Ruyck A, Coetzee P (1995) Adaptations of bivalves to different beach types. *J Exp Mar Biol Ecol* 187:147–160
- McLachlan A, De Ruyck A, Hacking N (1996) Community structure on sandy beaches: patterns of richness and zonation in relation to tide range and latitude. *Rev Chil Hist Nat* 69:451–467
- McLachlan A, Fisher M, Al-Habsi HN, Al-Shukairi SS, Al-Habsi A (1998) Ecology of sandy beaches in Oman. *J Coastal Conserv* 4:181–190
- Perry DM (1980) Factors influencing aggregation patterns in the sand crab *Emerita analoga* (Crustacea: Hippidae). *Oecologia* 45:379–384
- Sastre MP (1985) Aggregated patterns of dispersion in *Donax denticulatus*. *Bull Mar Sci* 36:220–224
- Short A (1996) The role of wave height, period, slope, tide range and embaymentisation in beach classifications: a review. *Rev Chil Hist Nat* 69:589–604
- Short AD, Wright L (1983) Physical variability of sandy beaches. In: McLachlan A, Erasmus T (eds) *Sandy beaches as ecosystems*. Junk Publishers, The Hague, pp 133–144
- Tam YK, Kornfield I, Ojeda FP (1996) Divergence and zoogeography of mole crabs, *Emerita* spp. (Decapoda: Hippidae) in the Americas. *Mar Biol* 125:489–497