MUDFLAT SURFACE MORPHOLOGY AS A STRUCTURING AGENT OF ALGAE AND ASSOCIATED MACROEPIFAUNA COMMUNITIES: A CASE STUDY IN THE RIA FORMOSA

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Abstract

Although mudflats seem relatively planar, closer inspection reveals a succession of meso-topographical features, including consecutive convex and concave meso- and micro-topographical features. The objective of this study was to determine the influence of meso-scale surface sediment morphology on the dynamics of the macroalgae Ulvales (Chlorophyta) and associated macroepifauna in the Ria Formosa tidal lagoon (Southern coast of Portugal). Sampling took place at four sites in the Ria Formosa with monthly periodicity. Two were located on convex sections (mounds) of the mudflat and the other two on concave sections (depressions)., Macroalgae and related macroepifauna were sampled at each station. Biomass was quantified by determination of the ash-free dry weight (AFDW). Data were analysed using the software package “PRIMER” (Plymouth Routines In Multivariate Ecological Research). Results show a clear distinction between convex and concave areas. In

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convex sections, *Enteromorpha* dominated, to the point of being the only algal species present during part of the year. Conversely, biomass and dynamics of *Enteromorpha* and *Ulva* were almost the same in concave sections. The associated macroepifauna was also different in protruding or depression sections of the mudflat. In the convex areas, the macroepifauna population showed less diversity and was dominated by the snail *Hydrobia ulvae*. In concave areas, the species diversity was larger, but dominated in terms of biomass by the amphipod *Melita palmata* and the gastropod *Nassarius pfeifferi*. Results of the study indicate that the benthic communities associated with concave or convex features were different. No relevant differences in texture and sediment physico-chemical characteristics were found between convex and concave sections of the sampling sites. The inference is that the morphological nature of the bottom in tidal mudflats can act as a structuring agent of benthic communities.

Keywords: Ulvales; benthos; epifauna; mudflat surface morphology; Ria Formosa

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1. Introduction

Shorelines of estuaries and coastal regions frequently include large areas of intertidal mudflats. Their geomorphological cross-shore profile is often characterised by an almost continuous succession of convex and/or concave areas, generating an undulating benthic surface (Whitehouse et al., 2000). The incidence, dimensions and frequency of these particular meso topographical features are primarily controlled by tidal range, wave dynamics as well as sediment supply and composition (Whitehouse and Roberts, 1999). A typology for mudflats linking the overall profile shape to these primary forcing factors was described by Dyer (1998) and Dyer et al., (2000), who related mudflat slope to tidal range and exposure in a classification sequence. On the other hand, biotic control of the physical characteristics of habitats has been proposed in the concept of “organisms as ecosystem engineers” introduced by Jones et al. (1994) and Lawton (1994). Within the framework of this concept, biotic habitat engineering (e.g. bioconstructive or bioturbative, stabilization or destabilization, inhibitory or facilitation processes) is the main causal agent for the surface morphology of sediments (Reise, 2002).

This study focused on mudflat areas of the Ria Formosa coastal lagoon, defined by Andrade (1990) as being intertidal sediments with no halophyte vegetation, and sparsely ondulating morphology. Sediment is composed by silts and clay with a sand content always inferior to 10% (w/w). Undulation is herewith identified as a geomorphological feature on a scale of approximately thirty centimeters height and a couple of meters width. Green macroalgae mats (Chlorophyta) inhabit these geomorphological features in the Ria Formosa mudflats (Aníbal, 2004). In addition, a structured macroepifaunal community of species lives on the the sediment surface and in the associated algae mats (Aníbal and Sprung, 1998). Previous studies have suggested that the most relevant ecological relation between green macroalgae and the macroepifaunal community may be of a non-trophic nature, and based instead, on protection offered by the mats against predation (Aníbal, 1998). This hypothesis has also been described elsewhere (Thiel and Reise, 1993; Raffaelli, 2000). However, few studies have focused on the influence of surface morphological features on community structure associated with macroalgal blooms in tidal flats. The objective of this study was to assess the influence of the convex and concave sections of the mudflat on the dynamics of green macroalgae and associated macroepifauna in the Ria Formosa.

2. Study area

The Ria Formosa tidal lagoon is located on the Southern Portuguese coast (36º 58’ to 37º 03’ N and 7º 32’ to 8º 02’ W). It is a system of salt marshes and tidal flats, separated from the Atlantic by a belt of sand dunes that extends for 55 km along the coast (Fig. 1). The entire lagoon occupies an area of approximately 100 km^2, of which 48 km^2 are covered by salt marshes and 32 km^2 is occupied by a network of tidal channels (Teixeira and Alvim, 1978). Tidal amplitude varies from 0.5 m (neap tide) to 3.5 m (spring tide), maintaining an average depth of 2 m inside the lagoon (Águas, 1986).

During Spring tides, 50 km^2 of the lagoon area is exposed to the atmosphere, of which 8 km^2 are covered by *Spartina*, 8.2 km^2 by *Zostera* and *Cymodocea* and 2.5 km^2 by macroalgal mats, comprised mainly of *Ulva* and *Enteromorpha* (Machás and Santos, 1999). An additional 20 km^2 are occupied with aquaculture ponds and salt water beds (CCRA, 1984). The temperature in the water column ranges from 11.9 to 27 ºC (Falcão and Vale, 1990), and salinity oscillates between 35.5 and 36.9 (Falcão et al., 1985), except after heavy rainfall, when surface salinity can be lower. The lagoon does not receive any significant freshwater input. However, a rather intensive exchange of 50-75% of the water mass per tidal cycle makes its entire water mass residence time fluctuate between 12 and 48 hours (Neves et al., 1996).

3. Material and methods

3.1. Field

Sampling took place with monthly periodicity between February 1996 and February 1997 at four intertidal sites in the Ria Formosa (Fig. 1). Two sites were located on convex sections of the mudflat (stations I and IV-Fig. 2) and the other two on adjacent concave areas (stations II and III-Fig. 2). Sampling took place during ebb tide, with approximately twenty centimeters of water above the sediment. This strategy allowed sampling to take place first at the convex station then at the concave site within thirty minutes, while also permitting the collection of those species that only occur when the sediment is covered by water (*e.g.* fish).

At each sampling station, five replicate samples of the macroalgal cover (0.028 m^2 cross-sectional area) and its related macroepifauna were taken, by means of an open-ended cylinder, according to McIntyre et al. (1984). Samples were only taken at sites with macroalgal mats. Replicates were washed through 0.5 mm mesh nets, to eliminate micro and meiofauna, and preserved at –30 ºC. At the following low tide period, the areal algal cover on the sediment surface was determined for each station according to Greig-Smith (1964) and Kershaw (1973).

In order to ensure that no substantial differences, other than those caused by the surface morphology, existed between the concave and convex sections of the mudflat, both stations where re-sampled for grain-size composition, water and organic matter content (Loss on Ignition), and benthic pigment concentrations. Two cores (2.2 cm i.d. and 10 cm length) where taken at the top, the slope and the base of transects established across the convex to concave sections of the mudflat at each site (see

Figure 2). Each pair of cores was sectioned immediately at 1 cm intervals, and the.layers corresponding to the same depth intervals of both cores, where combined to minimize horizontal variability for each representative section.

3.2. Laboratory

After thawing at room temperature, the samples containing the algae and associated macroepifauna were carefully washed to remove sediment residue using 0.5 mm mesh sieves. After being sorted and conserved in 4% formalin, organisms were identified to *taxon* level, and their ash-free dry weight (AFDW) determined according to the procedure described by Winberg (1971). The drying procedure took at least two days at 60 ºC, until constant weight was achieved. Ignition took place for 3 hours at 450 ºC.

Green macroalgae were identified to the genus. Although recent phylogenetic research provided strong evidence that *Ulva* and *Enteromorpha* are not distinct evolutionary entities and should not be recognized as separate genera (Tan et al., 1999; Hayden et al., 2003), the morphological differences between *Ulva* and *Enteromorpha* can provide distinct adaptive strategies to stress factors such as current induced shear stress. These differences might be important as to whether the species settles on exposed, convex areas or in more sheltered concave zones of the mudflat. Consequently, in this case, the two *taxa* will be presented as separate genera. Green algal biomass (g.m^{-2}) was determined for each sample as the ratio between its AFDW value and the sampling area, multiplied by it's relative cover ratio (Aníbal, 1998; Aníbal, 2004). This procedure allowed measured biomass to be compared both between sites and monthly sampling periods. Macroepifauna biomass and abundance was calculated using the same principle and expressed in mg.m^{-2} and ind.m^{-2} respectively.

The sediment characterization was based on grain size composition analysis, water and organic matter content and benthic pigment concentrations. Grain size analysis was performed by dry-sieving of combined sampled layers (0 to 5 cm and 5 to ten centimetres depth), following the Wentworth sediment classification scheme (Gale and Hoare, 1991). Water content was determined by drying the sediment at 60 ºC, until constant weight was achieved. The organic matter content of the sediment was assessed by Loss on Ignition (three hours at 450 ºC). The benthic pigment concentrations (Phaeopigments and Chl. a) were determined using the Lorenzen equations after cold extraction with 90% acetone in water (Lorenzen, 1967; Lorenzen and Jeffrey, 1980).

3.3. Data analysis

Macroalgae and macroepifauna mean monthly biomass values per station were compared using the software package "PRIMER" (Plymouth Routines in Multivariate Ecological Research). To simplify the input of data, stations were renamed according to an alphabetical sequence: I to A, II to B, III to C and IV to D. Conversely, sampling months were numbered from "1" (February 96) to "13" (February 97). The data matrix was built with the different *taxa* in rows, and the respective biomass values per station and month in columns. Similarity was calculated by Bray-Curtis coefficient, using double square-root transformed data (Clarke and Warwick, 1994). Analysis of similarity ("ANOSIM") was used to verify the significative differences among convex and concave sections of the mudflat. Multi dimensional scaling ("MDS") was used to obtain a graphic visualisation of the distance between stations based on their similarities. Similarity percentage ("SIMPER") tests were then applied to identify which of the studied *taxa* were the most responsible for the results given by the other statistical treatments (Clarke and Gorley, 2001).

4. Results

4.1. Monthly variations within the sampling stations

In mudflats, as in most coastal ecosystems, species generally show an aggregated spatial distribution (Krebs, 1998; Barnes and Hughes, 1999). This distribution is characterised by a great variance to mean ratio within samples collected simultaneously at the same place (Sokal and Rohlf, 1995). Although the dispersion of macroalgae biomass values was high within months, there is same obvious inter-month variability. Consequently, further analysis will focus more on the trends expressed by the variation of the mean values, than in the analysis of dispersion.

Algae genera *Enteromorpha* and *Ulva* dominated the sampling sites, and 28 macroepifaunal species were found associated with the macroalgal mats (Tables 1 and 2). At station I, maximum biomass of green algae was evident during Spring (75.1 gm^{-2} in May), decreased throughout Summer and increased again during Fall (Fig. 3). By contrast, maximum macroepifaunal biomass and abundance were observed in June and November while minimum peaks occurred in April 96 and January 97 (Fig. 4). Observed fluctuations of epifaunal biomass were due almost entirely to the population dynamics of the gastropod *Hydrobia ulvae*, with only minor contributions by the other nine identified species (Table 2).

By contrast, at Station II , while both species of green algae contributed equally to total algal biomass throughout the year, during Summer the population almost disappeared (Fig. 3). The monthly macroepifaunal average abundance peaked twice, one in the beginning of Spring and the other in Autumn (Fig. 4). Average abundance was higher in March (1133 ind.m^{-2}) and October (690 ind.m^{-2}). Mean biomass showed a similar trend, with the notable exception of July, when the annual maximum of 12899 mg.m^{-2} was recorded. The macroepifaunal community was composed of sixteen *taxa*, but the main contributor to the variability in abundance was the amphipod *Melita palmata*. Conversely, the gastropod *Nassarius pfeifferi* was the principal cause of the observed fluctuations in biomass, again with the exception of July. Even so, just three individuals of *Carcinus maenas* captured in the five replicates sampled at this station contributed 12750 mg.m^{-2}.

The dynamics of algal species at station III were comparable to those found at station II, albeit displaying higher absolute values of average biomass (Table 1), in particular during Spring, Autumn and Winter (Fig. 3). Summer was once again the season of lower observed biomass values. The capture of decapods in June and February 97 (Fig. 4) caused some dispersion around mean biomass values at station III. Dynamics of the twenty three species sampled throughout the year at this station showed many similarities with station III. The amphipod *Melita palmata* had once more an important role in the community, in particular regarding the inter-month variation in abundance.

At station IV, biomass dynamics of the green algae population was similar to observations at station I (Fig. 3). Maximum average biomass was observed in March (61.7 g.m^{-2}) and February 97 (69.4 g.m^{-2}). Macroepifauna population dynamics at station IV was dominated by two phenomena: high recruitment of the gastropod

Hydrobia ulvae in January (5324 ind.m^{-2}) and February 97 (15270 ind m^{-2}); and the presence of two individuals of the decapod *Pachygrapsus marmoratus* in October (5068.1 mg.m^{-2}). Excluding these two phenomena, average abundance and biomass were similar to those recorded for station I (Fig. 4). The analysis of the sediment at the sampling sites (Fig. 2), showed no relevant differences between concave and convex sections of the mudflat, as regards to the grain size, water and organic matter content and benthic pigment concentrations.

4.2. Multivariate analysis

Aiming to relate the sediment surface shape (convex or concave) with the specific *taxa* composition and corresponding biomass, multivariate analysis was performed on the dataset using the monthly mean biomass values of the sampled *taxa* per station. Analysis of the dataset by the ANOSIN routine showed that fauna and flora composition were different in convex and concave sections of the mudflat (Table 3). The MDS output (Fig. 5) also confirmed that the concave sections (B and C) were graphically closer to each other and perfectly separated from the convex sections (A and D). The Stress value (0.15) indicated a good fit between the graphic plot of the stations and the data matrix originating the representation (Clarke and Warwick, 1994).

Analysis of the data matrix by the SIMilarity PERcentage method (SIMPER), showed that the two genera of Ulvales were responsible for grouping the stations in relation to their sediment surface morphology. The Ulvales percentile contribution was 34.67% to the grouping of convex stations but just 9.81% for the concave stations. In the case of convex sections (stations I and IV), *Hydrobia ulvae* also had an important percentile contribution towards their dissimilarity from the concave sections (38.97%). By contrast, *Nassarius pfeifferi* and *Melita palmata* were the macroepifaunal *taxa* which, contributed more to the grouping of concave stations, with percentages of similarity of 46.21 and 12.00 %, respectively. The five *taxa* mentioned above had a total percentile contribution in excess of 65% of all 30 taxa sampled toward the separation of sampling stations into the two distinct groups associated with sedimentary surface morphology.

5. Discussion

Surface topography is a consequence of hydrodynamic processes that occur when sediment is immersed (Huettel et al., 1998; Whitehouse and Roberts, 1999). The contrasting dynamics of Ulvales and related macroepifauna in convex and concave mudflat sections, may be thus explained as the result of differential colonization processes evidenced by organisms adapted to different environmental stress factors (Aníbal and Sprung, 1999). This hypothesis is supported by the sediment characterization at the sites, where no relevant difference between convex and concave sections was identified. This fact only emphasizes that surface topography is the major forcing function affecting the distribution of *taxa* in these mudflats.

In convex sections, the current during high-tide, and desiccation and photoinhibition during low-tide are maximized (Soe-Htun et al., 1986; Lobban and Harrison, 1994). In these sections, the dominant macroalgae was *Enteromorpha*. This algae is made of many long and narrow thallus (Koeman, 1985), thus offering less resistance to current flow than *Ulva*, which has a fan shape (Vogel, 1994). A few species of small size, such as the snail *Hydrobia ulvae*, constituted the macroepifauna populating convex sections. While in the general mudflat environment detritivores seem to constitute the most representative group of macroepifauna (Valiela, 1995), the high hydrodynamical stress predictable over convex sections of the flat makes their survival difficult. This might be due to two different factors: low deposition of particulate organic matter (Huettel et al., 1996) and export of decaying macroalgae detritus to the adjacent concave sections. However, *Hydrobia ulvae* overcomes the absence of free floating or deposited detritus by browsing for microalgae on the macroalgae thallus (Sprung, 1994). Its reduced size (1 to 4 mm) and shape makes it less vulnerable to current drag and allows it to shelter more easily among the algae. In addition, its shell functions as an anchorage point for the germination of *Enteromorpha* propagules, precluding them from sinking in muddy sediment (Schories et al., 2000).

In concave sections, where shear caused by overlying water current is weaker (Huettel et al., 1996), population dynamics of *Enteromorpha* and *Ulva* were almost identical, with similar biomass values. The greater deposition of organic matter in these areas favours detritivory based on the consumption of decaying macroalgae detritus (Sogard and Able, 1991; Valiela, 1995). Consequently, associated macroepifauna (Fig. 6) is dominated by detritivore species like the amphipod *Melita palmata* and the gastropod *Nassarius pfeifferi* (Sprung, 1994). The larger residence time of organic matter in the concave section also enhances remineralization processes, originating higher concentrations of nutrients than in the convex sections, which can support more abundant primary and secondary production. This point is made very clear by looking at the biomasses of different *taxa* at the sampling stations.

In this kind of study, there is always the question of possible migration of individuals between stations while the sampling process is under way, thus skewing the results. These movements become a source of error in results because the same *taxa* are being contemplated twice (Krebs, 1998). Our results suggest however that migratory movement between adjacent parts of the sediment surface are not occurring. Proof of this hypothesis can be extracted from analysis of the *Hydrobia ulvae* data. Sampling was always initiated at the convex sections, where *Hydrobia ulvae* was present. The adjacent concave stations were sampled as the tide ebbed,. If there was to be any migratory movements or even advective transfer, *Hydrobia ulvae* would be sampled on both station types. The same reasoning is valid for almost all the other *taxa*. Albeit present on both station types, their numbers and biomass did not evidence the same representativity.

Another interesting aspect of this study has to do with the distance separating the sampling sites from the associated tidal channels. Although showing similar dynamics, in relation to algae and macroepifauna, both convex and concave stations are located at different distances from the tidal channels. Therefore, the results seem to suggest that conditions that control dynamics of algae and associated fauna, are more closely related to the local functional role of sediment morphological features, as opposed to the eventual control exerted by flood and ebb periods, resulting from different proximities to the main tidal channel.

In general, the concave sections of the mudflat were more diverse and sheltered higher biomass than the convex areas. This might also be explained by the fact that these sections of the mudflat remain moist even during low-tide, due to less exposure to wind and solar radiation. These characteristics create shadow areas where species that are poorly adapted to a higher current stress can survive more easily (Vogel, 1994).

6. Conclusions

In conclusion, this study strongly suggests that mudflats are not simple plains from the benthic community point of view, but instead that local communities are associated with specific bottom topography.

Convex sections of the mudflat, with higher exposure to hydrodynamic stress are associated with a less diverse population, made of smaller sized organisms that possibly seek shelter and food among the macroalgae. In concave sections of the mudflat on the other hand, more intense deposition and higher residence time of the detritus pool is probably the main controlling factor over the population, thus promoting a food web based on detritivory.

This information is vital for the experimental design of future studies in tidal environments, under penalty of under-estimating intra-species ecological relations, as well as between local organisms and their surrounding environment.

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References

Águas, M., 1986. Simulação da circulação hidrodinâmica na Ria Formosa. In: Anónimo (Ed.), Os sistemas lagunares do Algarve. Universidade do Algarve, Faro, pp. 78-90.

Andrade, C., 1990. O ambiente de barreira da Ria Formosa (Algarve-Portugal). M.Sc. Thesis, University of Lisbon, Portugal, unpublished.

Aníbal, J., 1998. Impacte da macroepifauna sobre as macroalgas Ulvales (Chlorophyta) na Ria Formosa. M.Sc. Thesis, University of Coimbra, Portugal, unpublished.

Aníbal, J., 2004. Processos ecológicos que controlam a dinâmica das macroalgas Ulvales (Chlorophyta) na Ria Formosa. Ph.D. Thesis, University of Algarve, Faro, Portugal, unpublished.

Aníbal, J., Sprung, M., 1998. Dynamics of green algae and its associated fauna in the Ria Formosa: is herbivory important? Proceedings of 1st Interdisciplinary Symposium on Estuarine Processes, Faro, Portugal, pp. 1-2.

Aníbal, J., Sprung, M., 1999. Influence of the mudflat surface shape on the green macroalgae and its associated macroepifauna. Intertidal Mudflats: Properties and Processes, Plymouth, England, p 4.

Barnes, R. S. K., Hughes, R. N., 1999. An introduction to marine ecology. Blackwell Scientific Publications, Oxford, pp. 296.

CCRA, 1984. Programa de ordenamento e desenvolvimento da Ria Formosa. Documento de trabalho da Comissão de Coordenação da Região do Algarve, pp. 126.

Clarke, K. R., Warwick, R. M., 1994. Changes in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, UK, pp. 144.

Clarke, K. R., Gorley, R. N., 2001. PRIMER v5: user manual and tutorial. Plymouth, PRIMER-E Ltd, UK, pp.91.

Dyer, K. R., 1998. The typology of intertidal mudflats. In: Black, K. S., Paterson, D. M., Cramp, A. (Eds.), Sedimentary Processes in the Intertidal Zone. Geological Society, London, Special Publications, Vol. 139, pp 11-24.

Dyer, K. R., Christie, M. C., Wright, E. W., 2000. The classification of intertidal mudflats. Cont. Shelf Res. 20, 1039-1060.

Falcão, M., Pissarra, J., Cavaco, M., 1985. Carcterísticas físicas e químicas da Ria Faro-Olhão: 1984. Relatório Técnico do Instituto Nacional de Investigação das Pescas nº 61, pp. 1-24.

Falcão, M, Vale, C., 1990. Study of the Ria Formosa ecosystem: benthic nutrient remineralization and tidal variability of nutrient in the water. Hydrobiologia 207, 137-146.

Gale, S. J., Hoare, P. G., 1991. Quaternary sediments: petrographic methods for the study of umlithified rocks. Belhaven Press, New York, pp. 323.

Greig-Smith, P., 1964. Quantitative plant ecology. 2nd Ed., Butterworths, London, pp. 242.

Hayden, H. S., Blomster, J., Maggs, C. A., Silva, P. C., Stanhope, M. J., Waaland, J. R., 2003. Linnaeus was right all along: *Ulva* and *Enteromorpha* are not distinct genera. Eur. J. Phycol. 38, 277-294.

Huettel, M., Ziebis, W., Forster, S., 1996. Flow-induced uptake of particulate matter in permeable sediments. Limnol. Oceanogr. 41(2), 309-322.

Huettel, M., Ziebis, W., Forster, S., Luther III, G. W., 1998. Advective transport affecting metal and nutrient distribution and interfacial fluxes in permeable sediments. Geochim. Cosmochim. Acta 62 (4), 613-631.

Jones, C. G., Lawton, J. H., Shachak, M., 1994. Organisms as ecological engineers. Oikos 69, 373-386.

Kershaw, K. A., 1973. Quantitative and dynamic plant ecology. 2nd Ed., American Elsevier, New York, pp. 308.

Koeman, R. P. T., 1985. The taxonomy of *Ulva* Linnaeus, 1753, and *Enteromorpha* Link, 1820, (Chlorophyceae) in the Netherlands. Drukkerij Van Denderen B. V., Groningen, Netherlands, pp. 201.

Krebs, C. J., 1998. Ecological methodology. 2nd Edition, Benjamin Cummings Publishers, USA, pp. 624.

Lawton, J. H., 1994. What do species do in ecosystems? Oikos 71, 367-374.

Lobban, C. S. and Harrison, P. J., 1994. Seaweed ecology and physiology. Cambridge University Press, New York, pp. 366.

Lorenzen, C. J., 1967. Determination of chlorophyll and phaeopigments: spectrometric equations. Limnol. Oceanogr. 12, 343-346.

Lorenzen, C. J., Jeffrey, S. W., Determination of chlorophyll in seawater-report of intercalibration tests. UNESCO Technical Papers in Marine Science,.pp. 35.

Machás, R., Santos, R., 1999. Sources of organic matter in Ria Formosa revealed by stable isotope analysis. Acta Oecologica 20(4), 463-469.

McIntyre, A. D., Elliott, J. M., Ellis, D. V., 1984. Introduction: design of sampling programmes. In: Holme, N. A. & A. D. McIntyre (eds). Methods for the study of marine benthos. Blackwell Scientific Publications, Oxford, pp. 1-26.

Neves, R., Leitão, P. C., Coelho H., 1996. Hydrodynamics characterization of Ria Formosa with MOHID system. 3º Congresso de Água, APRH2, pp. 447-458.

Raffaelli, D., 2000. Interactions between macro-algal mats and invertebrates in the Ythan estuary, Aberdeenshire, Scotland. Helgoland Mar. Res. 54, 71-79.

Reise, K., 2002. Sediment mediated species interactions in coastal waters. J. Sea Res. 48, 127-141.

Riedel, R., 1986. Fauna y flora del Mediterráneo. Ediciones Omega, Barcelona, pp. 857

Ruffo, S., 1982. The Amphipoda of the Mediterranean. Mémoires de l' Institute Océanographique, Monaco , nº 13, pp. 364.

Schories, D., Anibal, J., Chapman, A. S., Herre, E., Isaksson, I., Lillebo, A. I., Pihl, L., Reise, K., Sprung, M., Thiel, M., 2000. Flagging greens: hydrobiid snails as substrata for the development of green algal mats (*Enteromorpha* spp.) on the tidal flats of North Atlantic coasts. Mar. Ecol. Prog. Ser. 199, 127-136.

Soe-Htun, U., Ohni, M., Mizuta, S., 1986. Effects of salinity and temperature on the growth of the green alga, *Enteromorpha prolifera*, in culture. Reprints of Usa Marine Biological Institute 8, 9-13.

Sogard, S. M., Able, K. W., 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapodes. Estuar. Coast. Shelf Sci. 33, 501-519.

Sokal, R. R., Rohlf, F. J., 1995. Biometry: Principles and Practice of Statistics in Biological Research. 3rd Edition, W.H. Freeman and Company, USA, pp. 887.

Sprung, M., 1994. Macrobenthic secondary production in the intertidal zone of the Ria Formosa - a lagoon in southern Portugal. Estuar. Coast. Shelf Sci. 38, 539-558.

Tan, I. H., Blomster, J., Hansen, G., Leskinen, E., Maggs, C. S., Mann, D. G., Sluiman, H. J., Stanhope, M. J., 1999. Molecular phylogenetic evidence for a reversible morphogenetic switch controlling the gross morphology of two common genera of green seaweeds, *Ulva* and *Enteromorpha*. Mol. Biol. Evol. 16(8), 1011-1018.

Teixeira, A., Alvim, A. J., 1978. Reconhecimento dos sapais da Ria de Faro. Pedologia 13, 69-109.

Thiel, M., Reise, K., 1993. Interaction of nemertines and their prey on tidal flats. Neth. J. Sea Res. 31, 163-172.

Valiela, I., 1995. Marine ecological processes. 2^{nd} Ed., Springer-Verlag, New York, pp. 686.

Vogel, S., 1994. Life in moving fluids. 2^{nd} edition, Princeton University Press, pp.467.

Whitehouse, R. J. S., Roberts, W., 1999. Predicting the morphology evoluation of intertidal mudflats. HR Wallingford Report SR538/Environmental Agency R & D Technical Report W191, Wallingford, Oxon, UK.

Whitehouse, R. J. S., Bassoullet, P., Dyer, K. R., Mitchener, H. J., Roberts, W., 2000. The influence of bedforms on flow and sediment transport over intertidal mudflats. Cont. Shelf Res. 20, 1099-1124.

Winberg, G. G., 1971. Methods for the estimation of production of aquatic animals. Academic Press, London, pp. 175.

Figure legends

Fig.1. Geographic location of Ria Formosa showing the location of sampling stations.

Fig. 2. Sediment characterization of the convex, slope and concave sections at the sampling sites. The cold box in the background has 30 L capacity and is included for scaling purposes .

Fig. 3. Monthly variation of green algae biomass (g AFDW.m^{-2}) observed from February 1996 to February 1997.

Fig. 4. Monthly variation of macroepifaunal biomass (g AFDW.m^{-2}) observed from February 1996 to February 1997.

Fig. 5. MDS ordination of stations (A ≡ station I , B ≡ station II, C ≡ station III, and D ≡ station IV) using monthly data spanning an year, from February 96 (1) to February 97 (13).

Fig. 6. Pictographic representation of the main *taxa* associated with different sediment surface morphologies: (1) *Enteromorpha*; (2) *Ulva*; (3) *Hydrobia ulvae*; (4) *Melita palmata*; (5) *Nassarius pfeifferi* (adapted from Riedel, 1986 and Ruffo, 1982).

Table 1: Annual average biomass (g AFDW.m^{-2}) of Ulvales per station

Taxa	Stations			
	I	II	III	IV
Enteromorpha spp. Linnaeus, 1753	34.3	4.9	13.5	32.7
Ulva spp. Link, 1820	0.1	4.8	11.5	1.0

Table 2: Annual average biomass (mg AFDW.m^{-2}) of macroepifauna *taxa* per station.

Group	*Taxa*	Stations			
		I	II	III	IV
Gastropods	*Gibbula umbilicalis* (da Costa, 1778)		82.6	170.7	
	Gibbula varia (Linnaeus, 1767)		563.6	165.0	
	Hydrobia ulvae (Pennant, 1777)	102.5	2.0	3.3	207.3
	Hydrobia ventrosa (Montagu, 1803)	3.4			
	Rissoa membranacea (J. Adams, 1800)	0.5		2.2	
	Cerithium vulgatum (Bruguière, 1792)			312.2	
	Bittium reticulatum (da Costa, 1778)			0.5	
	Amyclina corniculum (Olivi, 1792)			31.1	
	Nassarius pfeifferi (Philippi, 1844)	10.8	655.1	480.0	
	Haminoea navicula (da Costa, 1778)		10.9	500.8	
Crustaceans	*Nebalia* sp. Leach, 1814		0.8	0.2	
	Tanais dulongii (Audouin, 1826)	8.3	4.1	0.6	35.4
	Cyathura carinata (Kroyer,1847)	0.9	10.5	5.4	26.2
	Sphaeroma spp. (Fabricius, 1775)			1.2	
	Idotea chelipes (Pallas, 1766)		3.5	0.6	
	Gammarus sp. Fabricius, 1775		1.9	6.9	0.2
	Melita palmata (Montagu, 1804)		55.0	135.9	0.6
	Elasmopus rapaz A. Costa, 1853				0.1
	Microdeutopus sp. A. Costa, 1853		4.7	0.3	
	Palaemon elegans Rathke, 1837		12.9		
	Palaemonetes varians (Leach, 1814)		17.1		
	Carcinus maenas (Linnaeus, 1758)	1.0	1151.0	1317.7	20.6
	Pachygrapsus marmoratus (Fabricius, 1787)			365.2	427.9
Insects (larvae)	*Chironomidae*	0.3		0.1	2.1
	Tipulidae	9.0	2.7	2.6	21.7
Echinoderms	*Holothuria* sp. Linnaeus, 1767	2.1			
Fishes	*Anguilla anguilla* (Linnaeus, 1758)			25.8	
	Pomatoschistus minutus (Pallas, 1770)			26.8	
Total *taxa*	**28**	10	16	23	10

Table 3: Output of the ANOSIM test

Sample statistics (Global R):	0.855
Nº permutations:	999
Nº permutations ≥ Global R:	0
Significance level of sample statistics:	0.1%

Figures

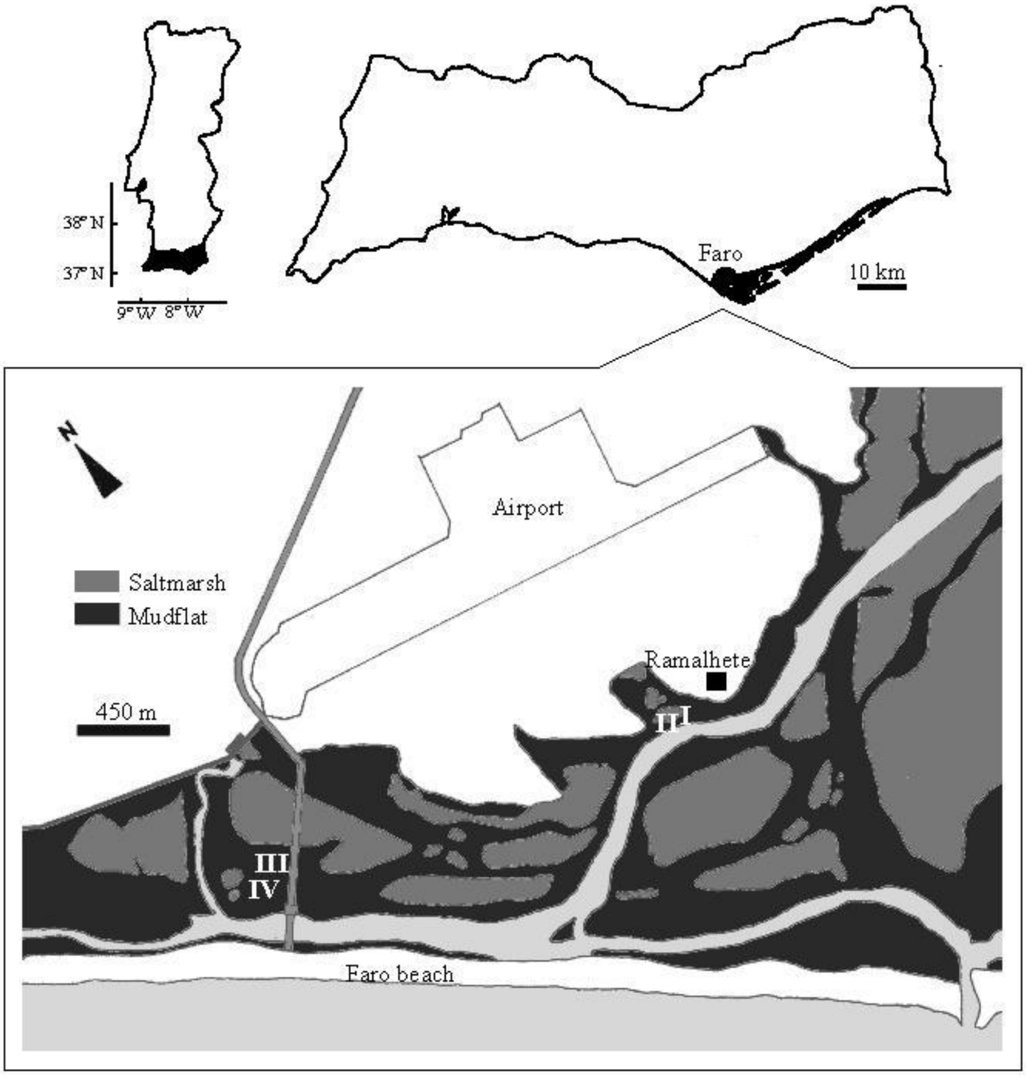

Figure 1. Anibal et al

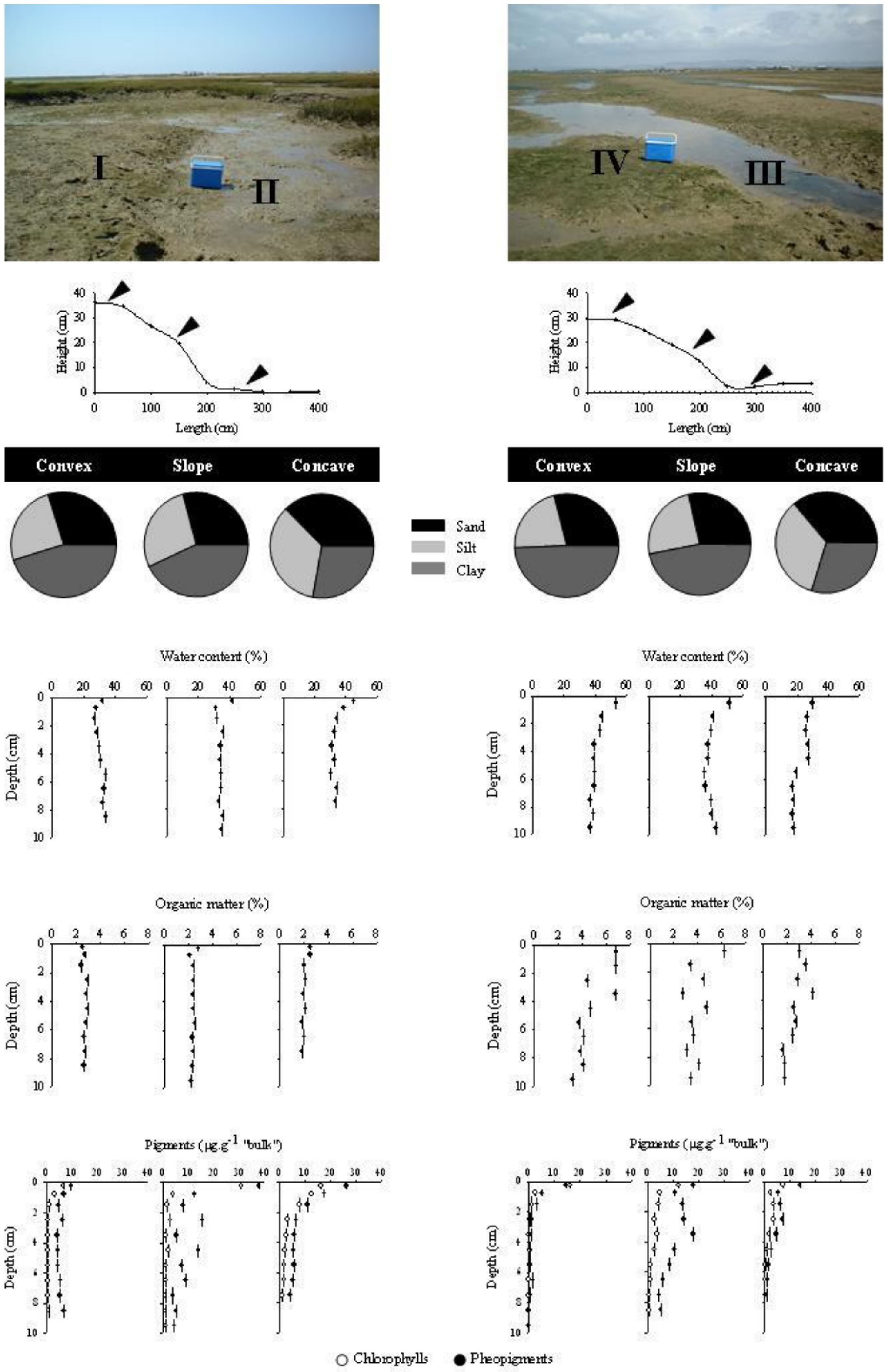

Figure 2. Anibal et al

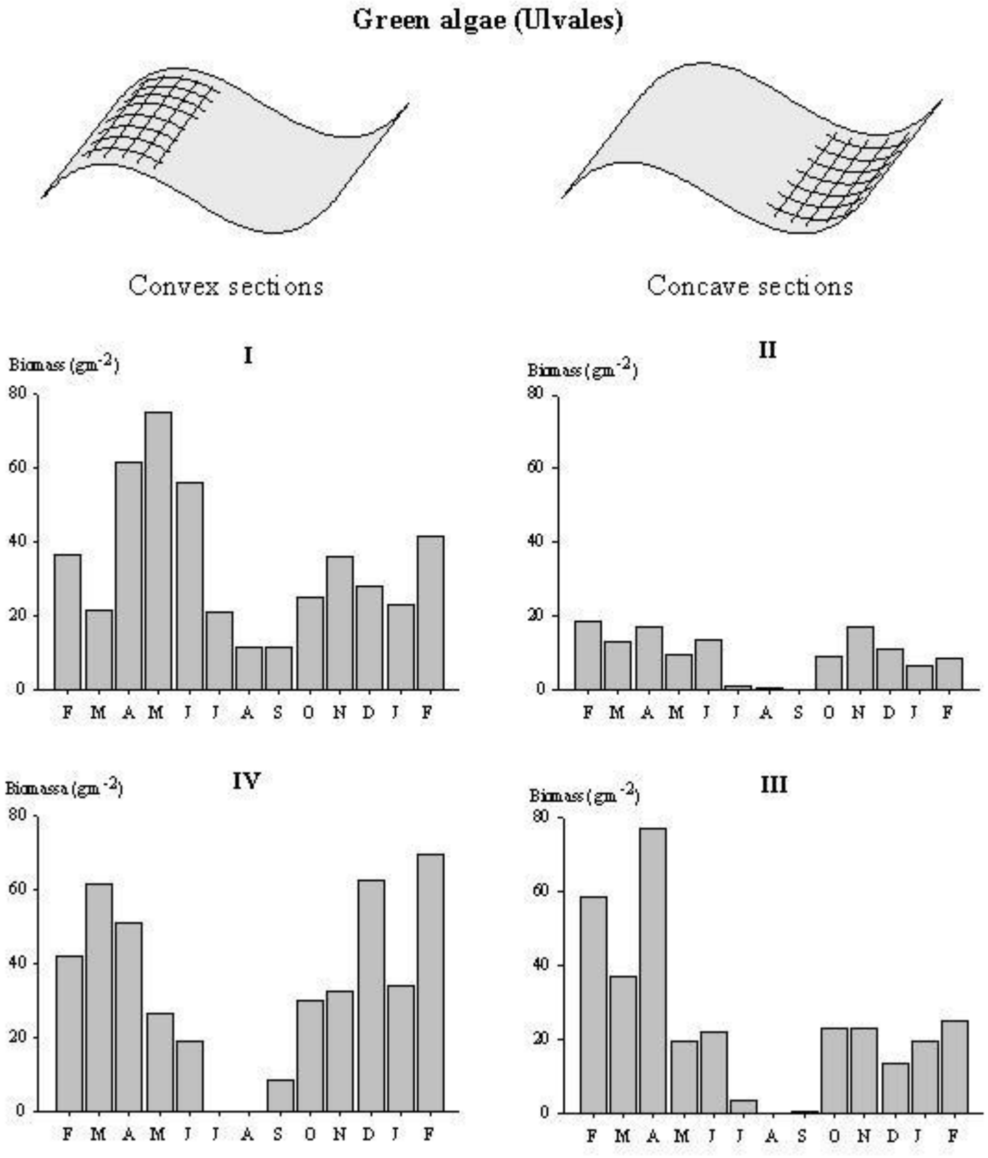

Figure 3. Anibal et al

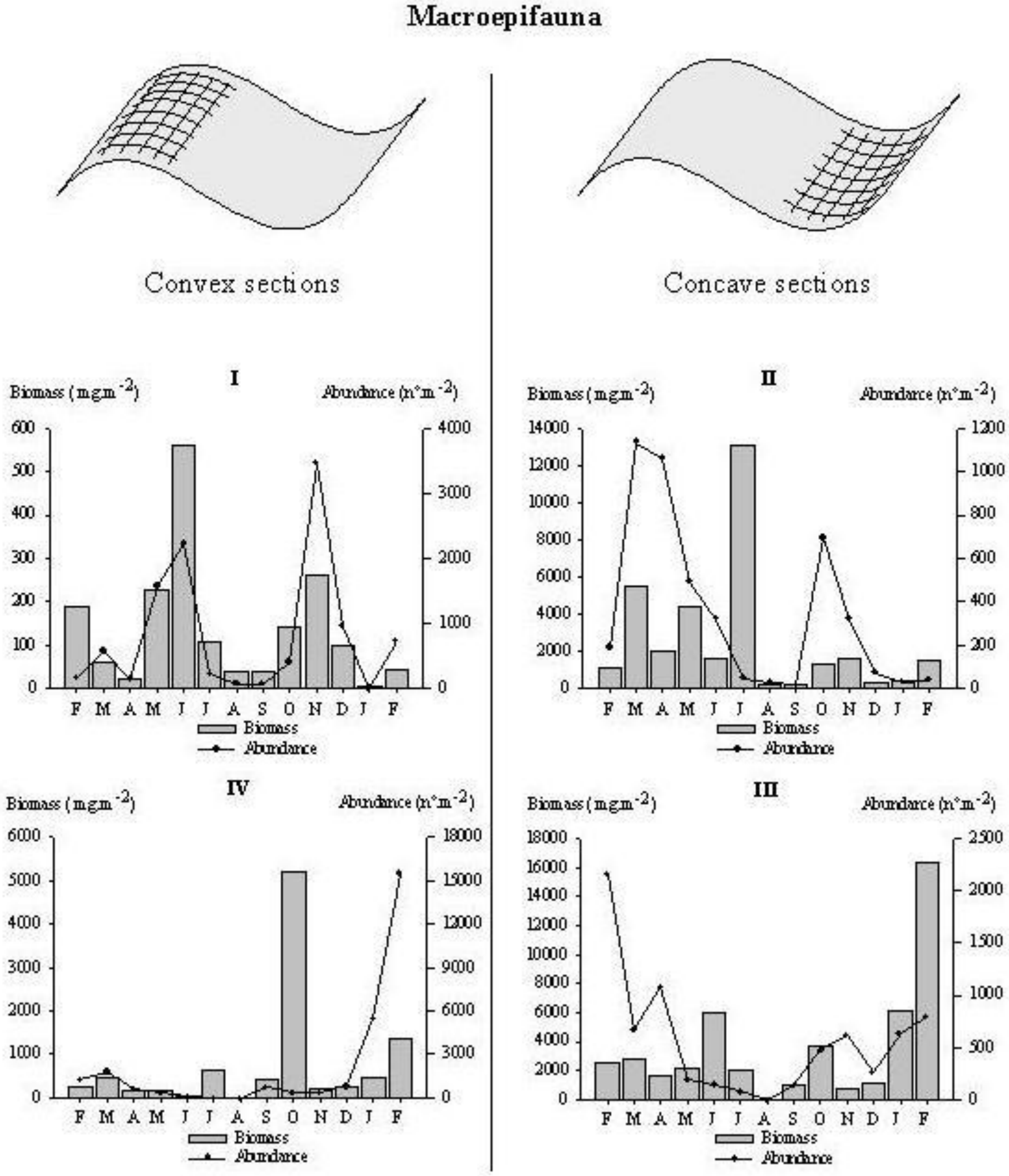

Figure 4. Anibal et al

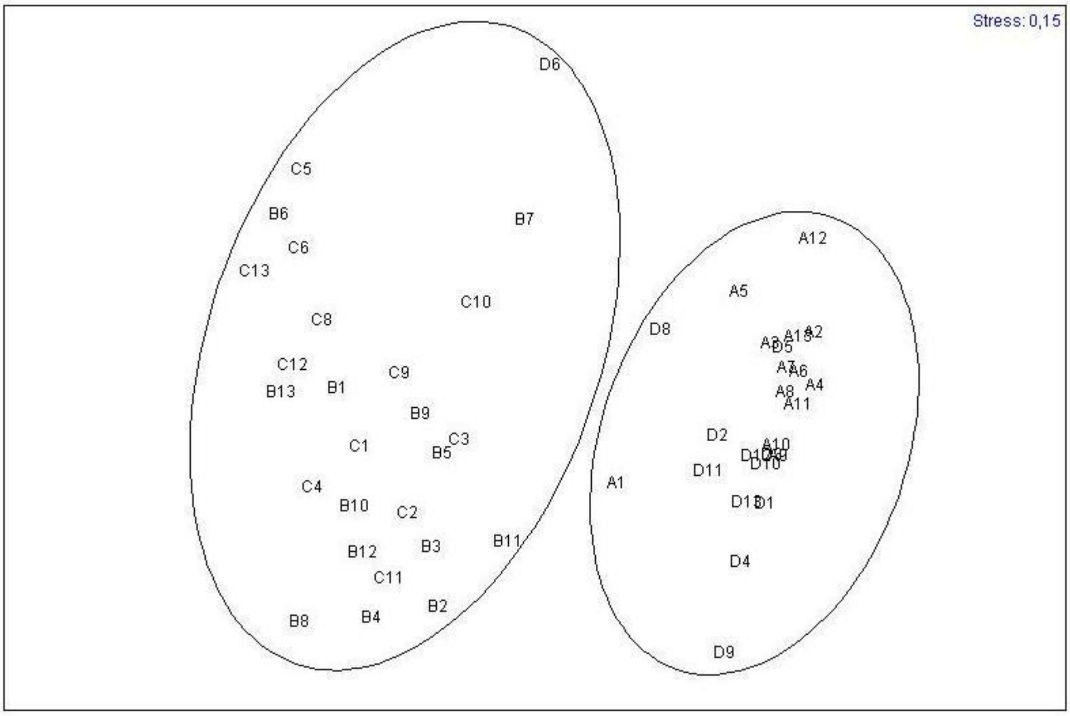

Figure 5. Anibal et al

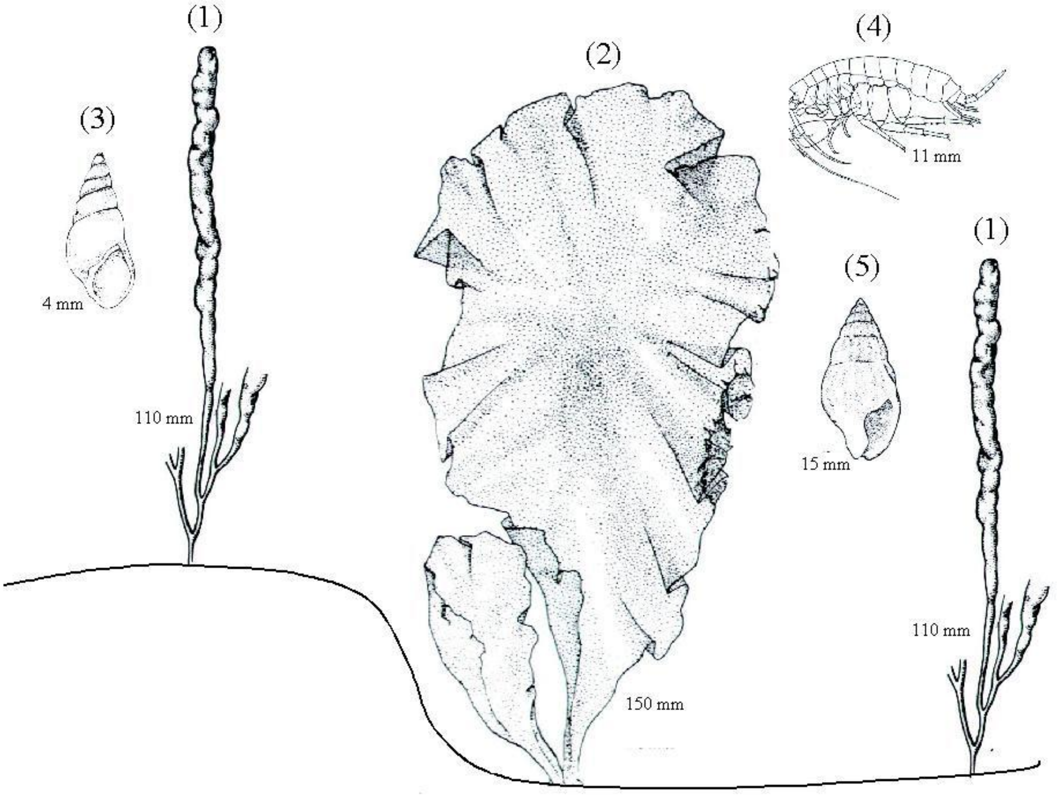

Figure 6. Anibal et al