Depth-associated patterns in the development of Amphipoda (Crustacea) assemblages on artificial substrata in the São Sebastião Channel, Southeastern Brazil

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Abstract

The vertical distribution of an amphipod assemblage in coastal waters was analyzed through monthly observation for a period of seven months (August, 2002 to March, 2003) on unglazed ceramic panels (30 x 30 cm) immersed at 1 m, 15 m and 30 m depth from fixed structures placed in an oil terminal. Classification analysis of panels, based on composition and abundance of settled amphipod species showed three distinct groups of panels separated basically by depth and immersion duration. The first group defined at 60% similarity comprises mainly shallow and mid water depth panels in an early stage of succession (1 to 3 mo immersion) with the clear dominance of *Jassa slatteryi.* The second group defined at 65% similarity comprises a later stage of succession (3 to 7 mo immersion) including shallow and mid water panels where *J. slatteryi* is replaced by *Ericthonius brasiliensis, Elasmopus pectinicrus* and *Podocerus brasiliensis.* The third group is composed by all the bottom panels where the assemblages were clearly dominated by *Photis longicaudata* from the experiment start. Classification analysis with the inverse matrix of data yielded two species loosely grouped at 45% similarity and one single species. Group I encompassed *Ampithoe ramondi, E. pectinicrus, P. brasiliensis, Stenothoe valida* and *E. brasiliensis* all later settlers. Group II comprised *J. slatteryi, P. longicaudata* and *Paracaprella pusilla,* early settlers. There was a clear switch from an assemblage dominated by early opportunistic colonizers to one characterized by later colonizers that largely replaced the early ones.

Key words: amphipod colonization, depth gradient, resident and transient species.

Introduction

A wide range of environmental and biotic factors influence recruitment rates and colonization trajectories of artificial substrate. Environmental factors include water depth (Rule and Smith, 2007), degree of disturbance (Lenz *et al.,* 2004) and the surface characteristics of the substrata (Lin and Shao, 2002). Biotic factors contemplate the species' ability to compete for the available space on a substratum (Russ, 1980), interactions between earlier species and later colonizers (Connell and Slatyer, 1977), time of immersion (Migotto *et al.,* 2001) and larval supply (Gaine and Bertness, 1992) so that the nature of the trajectories of

assemblages following the introduction of a bare substrate varies with the identity, life-history and abundance of organisms that initiate and facilitate early stages, besides the installation timing.

Despite the likely importance of depth in structuring epifaunal assemblages, it has received very little experimental attention (Rule and Smith, 2007). Benthic amphipods are different from many primary space competitors with regard to recruitment since they brood their young and consequently recruitment occurs largely within the communities (Franz, 1989) and, as has been shown to demonstrated active selection of substratum (Roberts and Poore, 2005). As amphipods are very sensitive to environmental variations and

occur diversely and abundantly in benthic communities they may play important roles as indicators for pollution and other natural and anthropogenic disturbance (Vázquez-Luis *et al.,* 2008; Vázquez-Luis *et al.,* 2009).

In the present study we aim to determine the effect of depth on the structure of amphipod assemblage through the monthly observation of immersed artificial panels placed on the Brazilian southeastern coast as a base for future monitoring programs.

Material and Methods

The São Sebastião Channel is a passage 25 km long with two entrances of about 6 km wide, lying between the continental municipality of São Sebastião and São Sebastião Island, State of São Paulo, southeastern Brazil (Fig. 1). The present study is part of a monitoring program designed to evaluate oil pollution at the São Sebastião Channel due to the presence of an important oil terminal. The experimental design included sites located along the whole São Sebastião Channel but the panels placed outside the terminal structure were consistently stolen.

The experiment embraced a continuous 7 month period, beginning in August of 2002 and ending in March, 2003. Three unglazed ceramic panels (30 x 30 cm) were suspended with lines

Figure 1. Study site in São Sebastião Channel, Southeastern Brazil.

from three fixed structures situated in the pier, 300 m apart. Each line was composed by a surface buoy, a panel placed at the sub surface (about 1 m below the sea level), mid water (ca. 15 m depth), and deep water (ca. 30 m depth and at least, 1 m above the sea floor, considering low tides). The structures act as a triplicate depth treatment. Monthly the panels were inspected using a nylon grid divided in 3 cm squares totalizing 100 subsamples; 10 squares totaling 90 cm^2 were removed from one of the sides and the panel was placed back in the water. The position of the sampled area was noted. All the material collected was then fixed in containers with a 4% solution of formaldehyde and transferred in the laboratory to neutralized alcohol at 70%.

Fauna collected in each panel composed mainly of sessile invertebrates was viewed under the microscope and 10% of the total volume of each sample was removed and prepared for analysis. All amphipod species were then identified at the lowest possible taxonomic level and counted under a dissecting microscope. For quantitative analysis, counts of species with at least a mean number of two individuals per sample as the minimum total for inclusion were log (x+1) transformed to reduce the heterogeneity of the variances. Only 9 of a total of 15 species were abundant enough to undergo further analysis. Their numbers suffered a square root transformation to minimize dispersion. The structure of the biological communities installed in each panel was evaluated by the total number of individuals (N), species richness (S), diversity (Shannon's H') and evenness (Pielou's J). Monthly samples groups and species were determined using the Bray-Curtis index of similarity and the average group sorting strategy. Non-parametric multidimensional scaling (MDS) was used as an ordination metod for exploring differences in amphipod assemblage composition (Vázquez-Luis *et al.,* 2009).

Results

A diverse assemblage of amphipods occupied the artificial panels comprising 3399 individuals (1600 on shallow water, 708 mid water, e 1091 bottom water) representing 15 species. The species were: *Amphilocus neapolitanus* Della Valle, 1893; *Ampithoe ramondi* Audouim,1826; *Caprella scaura* Templeton, 1836; *Caprella equilibra*
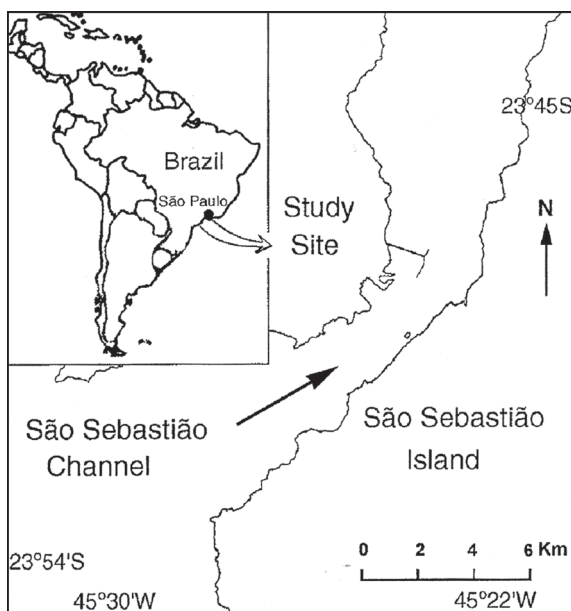
Say, 1818; *Corophium* sp.; *Dullichiellla anisochir* (Krøyer, 1845); *Ericthonius brasiliensis* (Dana, 1853); *Elasmopus pectinicrus* (Bate, 1862); *Jassa slatteryi* Conlan, 1990; *Lembos* sp.; *Leucothoe spinicarpa* (Abildgaard, 1789); *Paracaprella pusilla* Mayer,1890; *Photis longicaudata* (Bate and Westwood, 1836); *Podocerus brasiliensis* (Dana, 1853); *Stenothoe valida* Dana, 1853.

Shallow water assemblages start with opportunistic species that quickly covers the panel surface, being dominant *J. slatteryi, P. pusilla, P. longicaudata, E. brasiliensis* an *S. valida.* In November, three months after immersion the later colonizer *P. brasiliensis* appeared, followed in December by *E. pectinicrus* and *A. ramondi.* In January a last arrival settled *S. valida.* From then on there is a numerical equilibrium among all those settlers (Fig. 2).

Mid water assemblages start with opportunistic species that quickly covers the panel surface, being dominant *P. pusilla, J. slatteryi, P. longicaudata* and *P. brasiliensis. P. longicaudata* presents numerical stability through the entire period while *P. pusilla* and *J. slatteryi* alternatively disappear and reappear throughout the period. In January the later settlers arrive, *A. ramondi, E. pectinicrus* and *E. brasiliensis* (Fig. 3).

Bottom water panels were first colonized by *P. longicaudata, C. scaura, J. slatteryi, P. pusilla* and *Corophium* sp. and maintained the same structure except in December when almost all the species disappeared to return soon afterwards in January (Fig. 4).

For all depth panels after the initial phase of colonization (Fig. 5), the assemblage diversity increases, but approximately after the third month of immersion this diversity falls, as many of the opportunist species are excluded by later colonizers. After six months of immersion, the diversity and evenness of the amphipod assemblages gradually increase with the colonization of the later settlers. The species richness increases with time, from 8 in September to 13 in October and 14 in March. Diversity and evenness are higher at mid panels. Individual abundance was higher at the shallow panels except in October when a *P. longicaudata* peak density was verified at the bottom panels.

The composition of amphipod assemblage differed substantially with depth and immersion duration. Classification analysis of panels, based on composition and abundance of amphipod species, was run on the nine selected species from a total of 15 species considering the mean density of each species for each month and depth. The resulting dendrogram (Fig. 6a) shows three distinct groups of panels separated basically by depth and immersion duration. The first group defined at 60% similarity comprised mainly of shallow and mid water depth panels in early stages of succession, one to three months of immersion, from
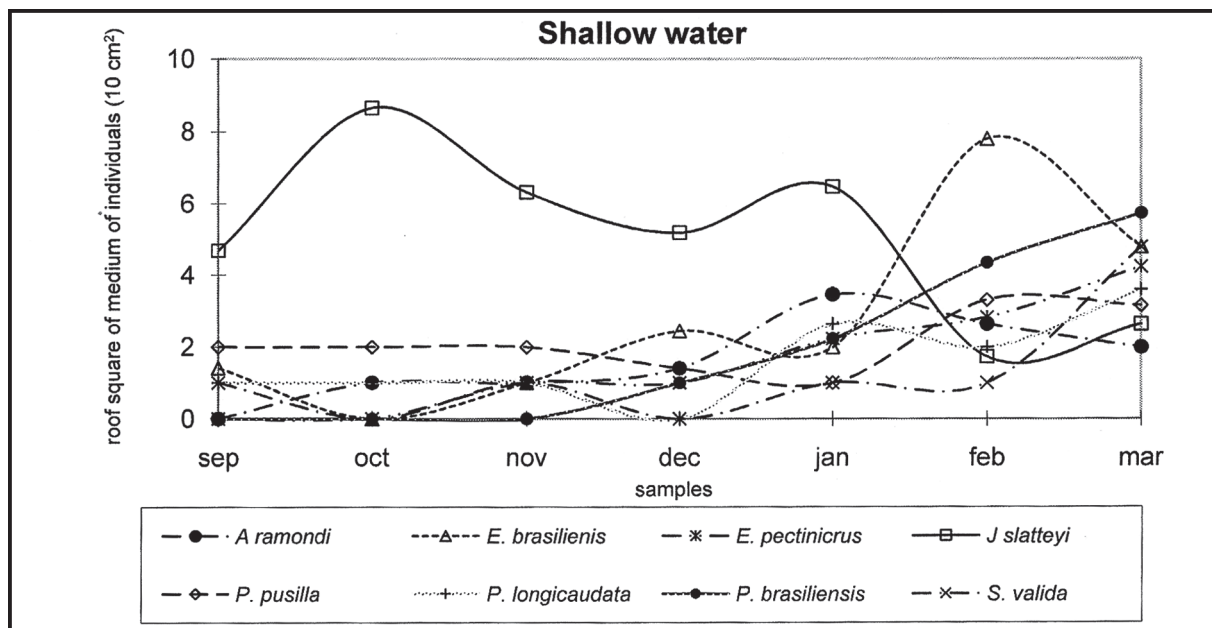

Figure 2. Temporal variation of amphipod species of shallow water panels with densities values root square transformed.

September to December, with the clear numerical dominance of *J. slatteryi.* The second group defined at 65% similarity comprises later succession stages of shallow and mid water panels where *J. slatteryi* is no longer numerically dominant being substituted by *E. brasiliensis, E. pectinicrus* and *P. brasiliensis.* The third group is composed by all bottom panels where the assemblages are clearly dominated from the beginning of the experiment by *P. longicaudata.* The two dimensional MDS plot shows the segregation of the three groups formed by the classification analysis (Fig. 6b)

Classification analysis of the inverse data matrix yielded two species groups at 45% similarity and one single species at 15% similarity (Fig. 7). Group I encompassed *A. ramondi, E. pectinicrus, P. brasiliensis, S. valida* and *E. brasiliensis,* all later settlers. Group II comprised *J. slatteryi, P. longicaudata* and *P. pusilla,* earlier settlers. *C. scaura* was not grouped since it showed an irruptive occurrence.

Discussion

In this study, the amphipods early colonizers of artificial panels were the tube dwellers *P. longicaudata* and *J. slatteryi.* Both are suspension feeders and form dense fouling aggregations (Moore and Cameron, 1999). These amphipods spread fast on free spaces, displaying, however, a lack of competitive ability in invading settling panels already occupied. At first, space, rather than food, controls their distribution, and their ability to quickly increase aggregative size is an advantage. Settlement is quick and after two months the densities of these first settlers have increased markedly and an opportunistic diversity peak is achieved.

Opportunistic species have a classic life history involving rapid colonization and population increase. Classic opportunistic species are thought to be poor competitors for food and space and lack defense against predators and are thus often displaced by later colonists. *P. longicaudata* and *J. slatteryi* are considered examples of the fugitive-dominant mechanism, because they are quick to recruit cleared space, but depend for their existence on a continuing supply of available space (Sebens, 1986). The rapid increase in abundance is typically followed by a subsequent sharp decline which, at least partially, may be explained by over exploration of food resource and displacement by predators (Russ, 1982; Conlan, 1994; Jeong *et al.,* 2007).

In the first stage of occupation opportunistic species may be important in facilitating conditions for subsequent colonization by organism with slower growth pattern (Norkko *et al.,* 2006). After the third month the density of the opportunistic species, *J. slatteryi* and *P. longicaudata,* is inversely related to the density of later colonizers, the tube dwellers *A. ramondi, E. brasiliensis* and *P. brasiliensis* and the free-living species, *E. pectinicrus* and *S. valida,* suggesting that the first group is outcompeted by the later. Between the establishment of the opportunistic group and the later arrivals there was a fall in peak diversity.

Differential colonization of amphipods at different depths is an alternative explanation for the opportunistic pattern observed. For the shallow water assemblage it can therefore be concluded that amphipods assemblage seems to reach its climax after approximately the 6 month period of immersion, because of the high values of diversity and evenness and the absence of a clear dominance. First stage of colonization is dominated by *J. slatteryi* and then by a well balanced assemblage comprising *P. brasiliensis, S. valida, E. pectinicrus, P. longicaudata* and *J. slatteryi.*

For the mid water depth assemblage it can be evidenced a standard of occupation and nesting, with the diversity increasing initially with the first stage of colonization dominated by *P. longicaudata, J. slatteryii* and *P. pusilla* and keeping high and constant from the 4 month immersion period on with the establishment of one assemblage dominated by *P. longicaudata* with *J. slatteryi* and *P. pusilla* alternatively replacing each other. The irregular fluctuations in population densities evidence the population instability of the opportunistic species. This behavior involving a low persistence reflects in the abrupt variation of the two dominant populations throughout the time (Franz, 1989).

For the bottom water panels, the disturbances caused by winds and storms in this area (Tessler, 1988; Valério-Berardo *et al.,* 2000) revolving the bottom sediment, may promote more instability, which may contribute to the lowest values of diversity at this depth.

The colonization curves of panels immersed in the shallow and mid water level off after 6 and 4 months of immersion respectively. This has often been interpreted as a gradual increase in the number of species up to a plateau of equilibrium (*e.g.* Simberloff and Wilson, 1969; Osman, 1978; Schoener, 1979). The equilibrium

number of species is defined as the number at which colonization and decolonization rates are equal and at a low level (MacArthur and Wilson, 1967). It occurred when the species number reached its highest level. Thus, following this interpretation, the equilibrium number of species for São Sebastião panels would be of 13 species per panel side.

Costello and Myers (1996) studying the colonization and turnover of the amphipod species on experimental plastic mesh pads for 12 mo. in the marine subtidal region found through the species colonization curve, ratio of colonization to decolonization rates, and stability of turnover, that the amphipod fauna was in equilibrium after 4 mo. After six mo. of immersion, the diversity and
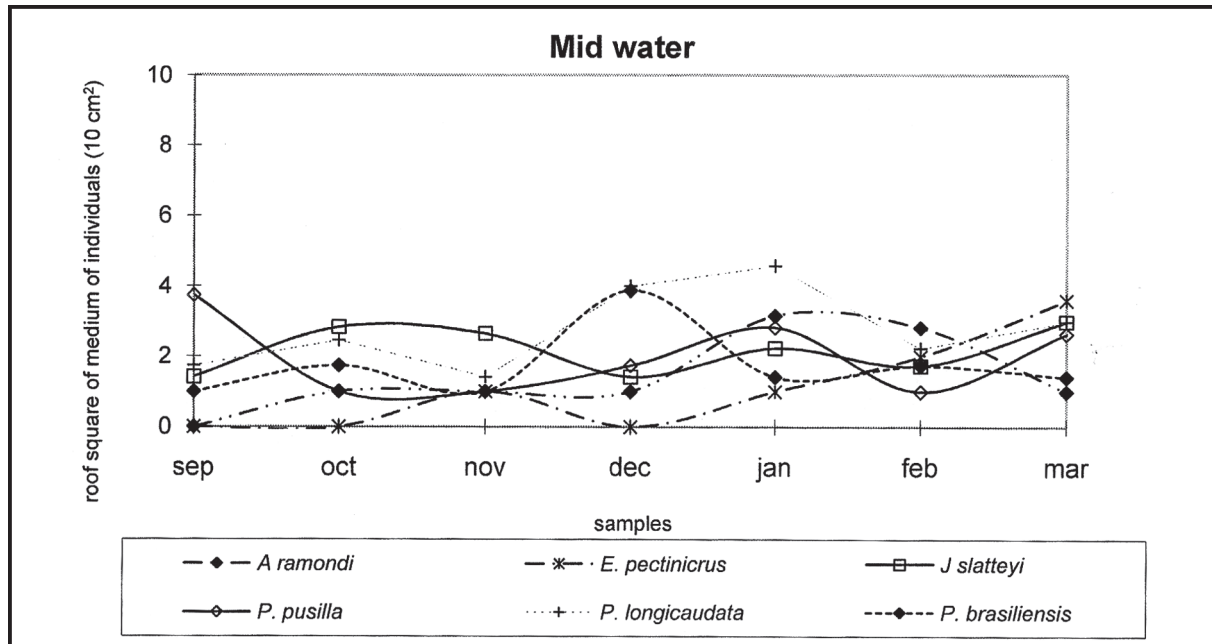

Figure 3. Temporal variation of amphipod species of mid water panels with densities values root square transformed.
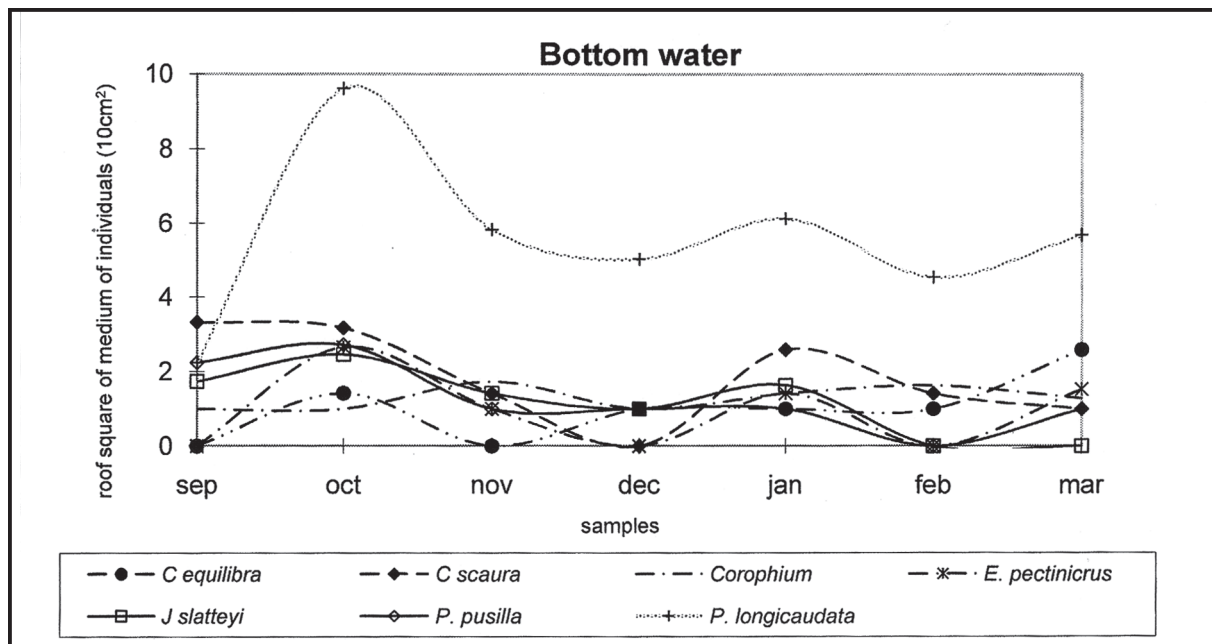

Figure 4. Temporal variation of amphipod species of bottom water panels with densities values root square transformed.
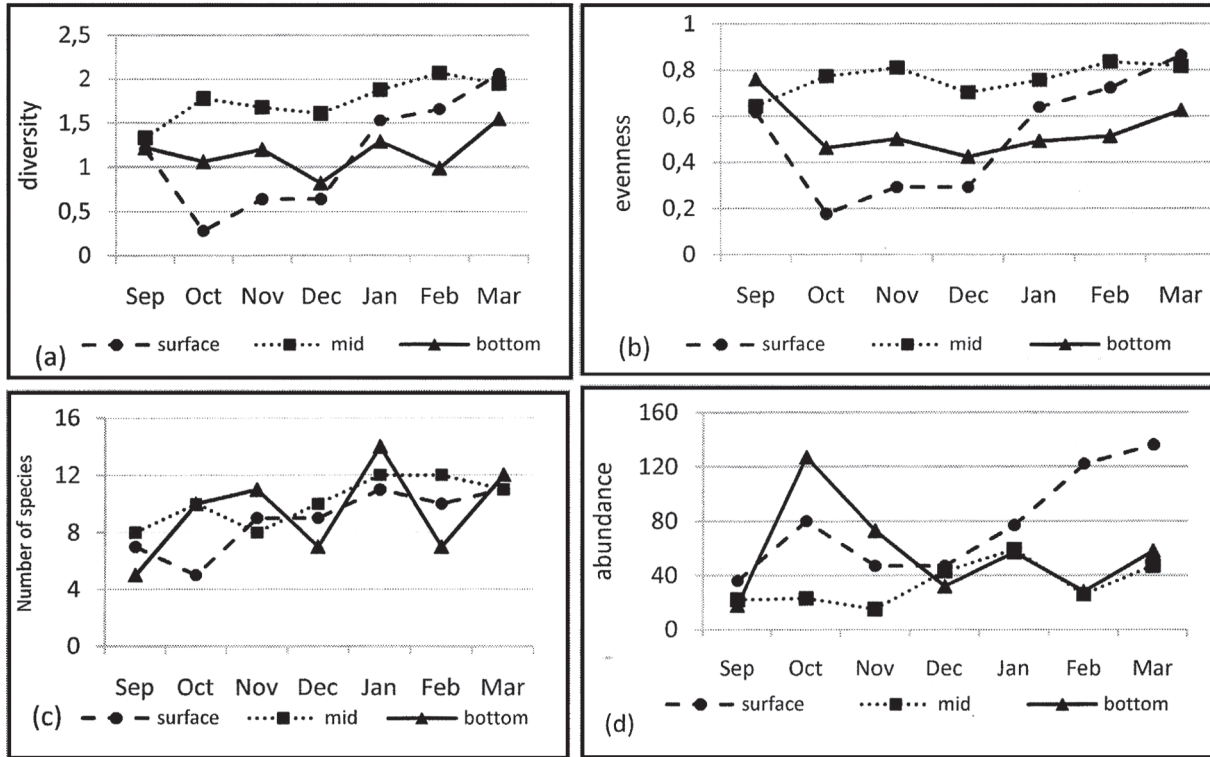
Figure 5. Temporal variation of species diversity (a), evenness (b), richness (c) and abundance (d) of the amphipod assemblages from shallow, mid and bottom water.

evenness of the amphipod assemblages have gradually increased in the majority of the panels, due to the increase in numbers of later colonizer species. As a rule the species richness of the assemblages of amphipods increases with time, from 8 in September to 13 in October and 14 in March. During natural disturbances amphipods that are more mobile have the advantage over more sedentary species in locating food sources.

The panels amphipod fauna in equilibrium is composed by residents (almost always present) and transients (rare in numbers of individuals and frequency of occurrence), with an intermediate group of temporary residents (Costello and Myers, 1996). In spite of the treatment applied to raw data having probably excluded just transient, most species collected were transients. Transients represented 33-44% of the total number of the species observed in each of the three depth-series, so we can conclude that a significant part of the species richness was dependent on the dispersal of amphipods from different nearby habitats. Considering their rarity, it is unlikely that these transient species played any functional role in the observed community. However, they may become residents, should environmental conditions change in the

future. These results suggest that high numbers of rare species may reflect not only a habitats intrinsic richness, but also the distance to different habitats where transients originate.

Depth-associated patterns in the development of benthic assemblages on artificial substrata
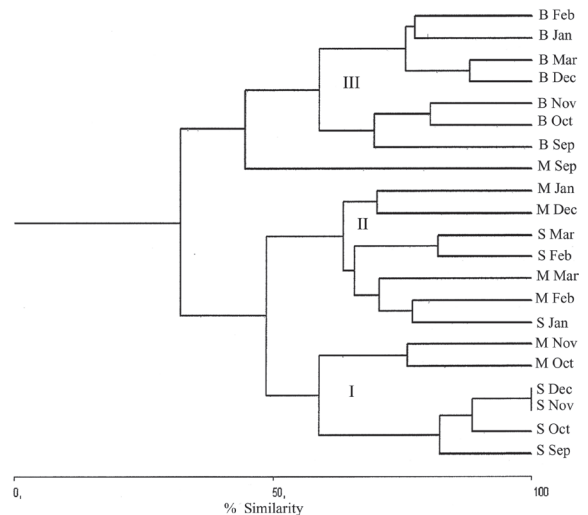

Figure 6a. Similarity dendrogram of total faunal density by month at shallow water panels (S), mid water panels (M) and bottom water panels (B).
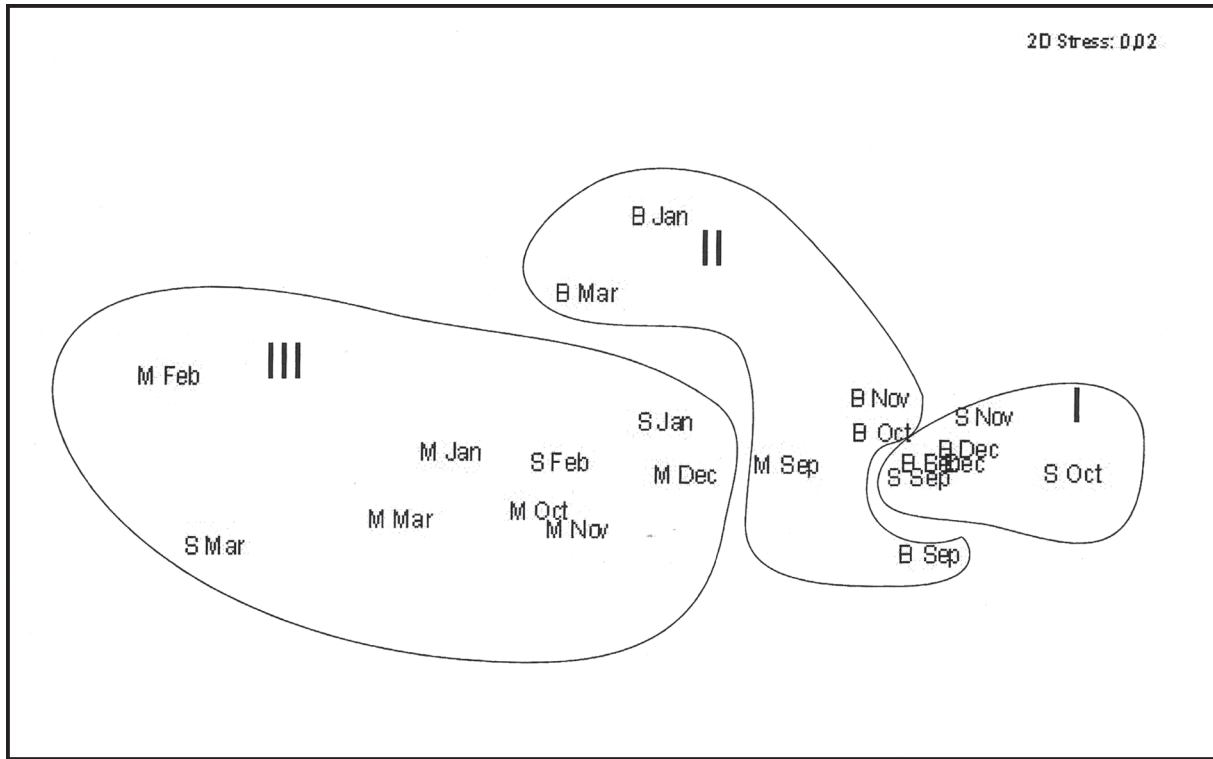
2D Stress: 0,02

B Jan

II

B Mar

III

M Feb

B Nov
B Oct

S Nov

I

S Jan

B Dec

M Jan   S Feb   M Dec   M Sep   S Dec
                                                  S Sep   S Oct

M Oct
M Nov

M Mar

S Mar

B Sep

Figure 6b. MDS plot of total faunal density by month at shallow panels (S), mid water panels (M) and bottom panels (B).

C. scaura

P. longicaudata

II

P. pusilla

J. slatteryi

E. brasiliensis

I

S. valida

P. brasiliensis

E. pectnicrus

A. ramondi

0   50   100
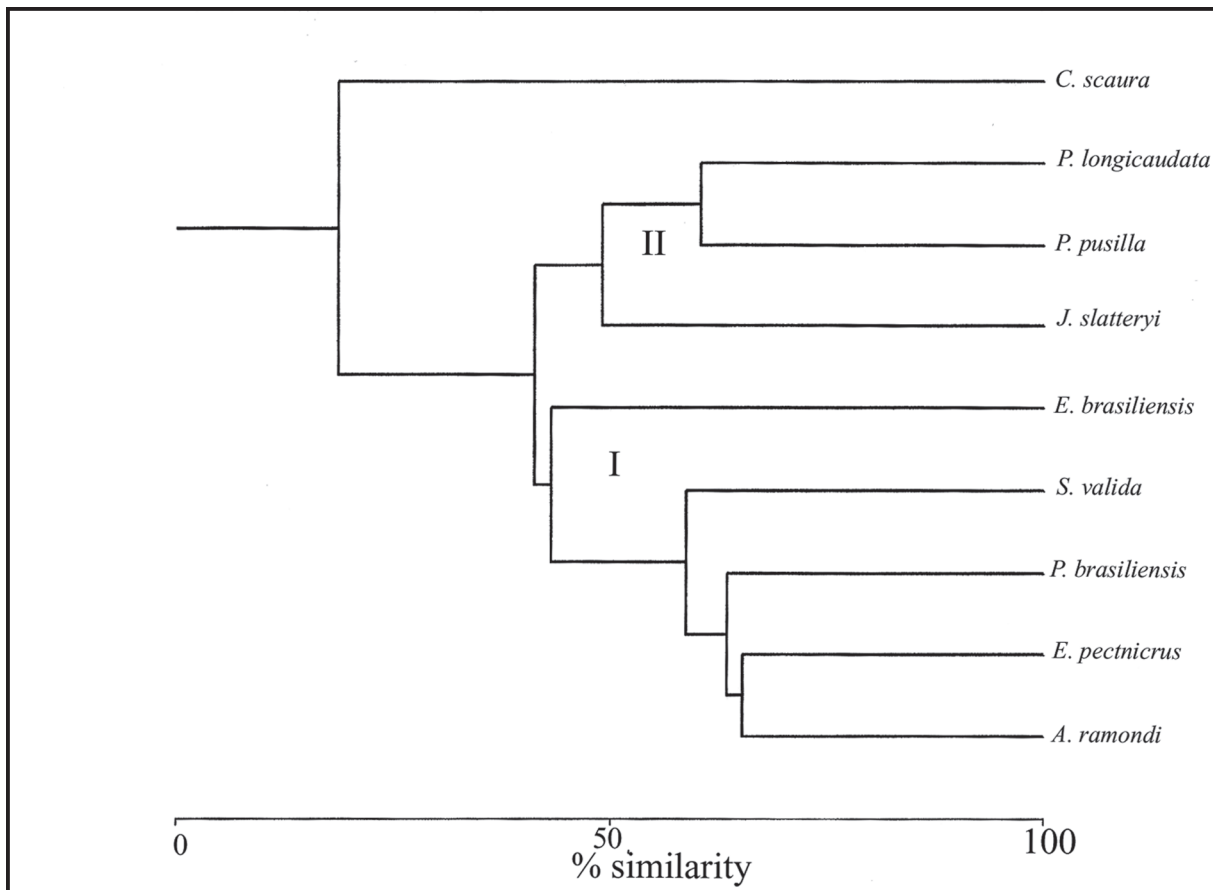   % similarity

Figure 7. Similarity dendrogram of densities of the 9 selected species.

is related to changes in the structure of benthic habitats across a number of physical gradients related to depth and result in corresponding changes in the structure of the associated epifaunal assemblages (Rule and Smith, 2007; Satheesh and Wesley, 2008). Multivariate analyses revealed significant differences in assemblage structure for comparisons of different depths during each sampling period. The results highlight the importance of depth as a structuring factor for epifaunal assemblages. The patterns observed in the current study may be due to the preferential settlement of species within a specific depth range and competitive ability.

References

Conlan, K.E. 1994. Amphipod crustaceans and environmental disturbance: a review. *Journal of Natural History,* 28: 519-554.

Connell, J.H. and Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist,* 111: 1119-1144.

Costello, M.J. and Myers, A.A. 1996. Turnover of transient species as a contributor to the richness of a stable amphipod (Crustacea) fauna in a sea inlet. *Journal of Experimental Marine Biology and Ecology,* 202: 49-62.

Franz, D.R. 1989. Populations density and demography of a fouling community amphipod. *Journal of Experimental Marine Biology and Ecology,* 124: 117-136.

Gaines, S.D. and Bertness, M.D. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature,* 360: 579-580.

Jeong, S.J.; Yu, O.H. and Suh, H.L. 2007. Life history and reproduction of *Jassa slatteryi* (Amphipoda, Ischyroceridae) on a seagrass bed (*Zostera marina* L.) in Southern Korea. *Journal of Crustacean Biology,* 27: 65-70.

Lenz, M.; Molis, M. and Wahl, M. 2004. Testing the intermediate disturbance hypothesis: response of fouling communities to various levels of emersion intensity. *Marine Ecology Progress Series,* 278: 53-65.

Lin, H.J and Shao, K.T. 2002. The development of subtidal fouling assemblages on artificial structures in Keelung Harbor, Northern Taiwan. *Zoological Studies,* 41: 170-182.

MacArthur, R. and Wilson, E.O. 1967. Theory of Island Biogeography. Princeton University Press's Notable Centenary Titles, 224 pp.

Migotto A.E.; Marques, A.C. and Flynn, M.N. 2001. Seasonal recruitment of hydroids (Cnidaria) on experimental panels in the São Sebastião channel, southeastern Brazil. *Bulletin of Marine Science,* 68: 287-298.

Moore, P.G. and Cameron, K.S. 1999. A note on a hitherto unreported association between *Photis longicaudata* (Crustacea: Amphipoda) and *Cerianthus lloydii* (Anthozoa: Hexacorallia). *Journal of the Marine Biology Association of the United Kingdom,* 79: 369-370.

Norkko, A.; Rosenberg, R.; Trhush, S.F. and Whitlatch, R.B. 2006. Scale and intensity dependent disturbance determines the magnitude of opportunistic response. *Journal of Experimental Marine Biology and Ecology,* 330: 195-207.

Osman, R.W. 1978. The influence of seasonality and stability on the species equilibrium. *Ecology,* 59: 383-399.

Roberts, D.A. and Poore, A.G.B. 2005. Habitat configuration affects colonisation of epifauna in marine alga bed. *Biological Conservation,* 127:18-26.

Rule, M.J. and Smith, S.D.A. 2007. Depth-associated patterns in the development of benthic assemblages on artificial substrata deployed on shallow, subtropical reefs. *Journal of Experimental Marine Biology and Ecology,* 345: 38-51.

Russ, G.R. 1980. Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community. *Journal of Experimental Marine Biology and Ecology,* 42: 55-69.

Satheesh, S. and Wesley, S.G. 2008. Seasonal variability in the recruitment of macrofouling community in Kudankulam waters, east coast of India. Estuarine, Coastal and Shelf Science, 79: 518-524.Schoener. A. 1979. Experimental zoogeography: colonization of marine mini-islands. *American Naturalist,* 108: 715-737.

Sebens, K.P. 1986. Spatial relationships among encrusting marine organisms in the New England subtidal zone. *Ecological Monographs,* 56: 73-96.

Simberloff, D.S. and Wilson, E.O. 1969. Experimental zoogeography of islands: the colonization of empty islands. *Ecology,* 50: 278-295.

Tessler, M.G. 1988. Dinâmica sedimentar quartenária no litoral paulista. Ph. D. Thesis, Universidade de São Paulo, Instituto de Geociências, São Paulo, Brazil.

Valério-Berardo, M.T.; Flynn, M.N. and Wakabara, Y. 2000. Structure and dynamics of a shelf amphipod taxocoenosis in Southeastern Brazil. *Bulletin of Marine Science,* 66: 59-72.

Vázquez-Luis, M.; Guerra-García, J.M.; Sanchez-Jerez, P. and Bayle-Sempere, J.T. 2009. Caprellid assemblages (Crustacea: Amphipoda) in shallow waters invaded by *Caulerpa racemosa var. cylindracea* from southeastern Spain. Helgoland Marine Research, 63: 107-117

Vázquez-Luis, M.; Sanchez-Jerez, P. and Bayle-Sempere, J.T. 2008. Changes in amphipod (Crustacea) assemblages associated with shallow-water algal habitats invaded by *Caulerpa racemosa var. cylindracea* in the western Mediterranean Sea. *Marine Environmental Research,* 65: 416-426.