Succession and seasonal variation in the development of subtidal macrobenthic soft-bottom communities off northern Chile

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ABSTRACT

Community succession is an important process in modulating the structure of benthic soft-bottom communities. A field experiment was conducted aiming (1) to describe the successional development in a subtidal soft-bottom community over a two-year period, (2) to estimate the time necessary for the developing community to resemble the surrounding natural community, and (3) to evaluate the effect of seasonal onset on the colonization over a one-year period of development. Containers filled with fine sediment without any previous biological conditioning were installed in subtidal soft bottoms off Playa Colorado, Bahía Antofagasta, Chile (Humboldt Current System). The experiment was initiated in June 2006. For 24 months three replicate containers together with 4 reference samples from the surrounding natural community were sampled every three months. Succession was detected but did not show a sequential replacement from early to late colonizers, thus did not follow distinguishable seral stages. These results support the tolerance succession model, which states that species dominating later successional stages colonize at the same time as species mainly associated with initial successional stages. Resemblance to the reference community was first recorded after eighteen months. In order to test for seasonal effects of colonization, three containers were installed in each of the four seasons, and the community was allowed to develop for a one-year period. Seasonality had no evident effect, as all establishing communities converged to a similar structure after one year, regardless of the season, when the containers had been installed. This study highlights the strong resilience of northern Chilean sublittoral soft-bottom communities to environmental variations during the cold conditions of the El Niño Southern Oscillation.

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1. Introduction

Although information on recolonization and successional processes in soft-bottom communities is vast, it is not possible to fit a general predictable model to most of the sedimentary habitats. In muddy areas, rich in organic matter, succession can be predicted from a starting point to a deterministic endpoint passing through a few seral stages (Pearson and Rosenberg, 1978; Rosenberg, 2001; Lenihan and Micheli, 2001). However, succession may be much more variable in inter- and subtidal sandy habitats, involving several successional pathways and different endpoints. Thus, recolonization and succession in these highly dynamic systems is complex and hence requires system-specific evaluations (Zajac et al., 1998; Zajac and Whitlatch, 2003; Moseman et al., 2004). According to predictions related to “early–late interactions” (Connell and Slatyer, 1977), in soft sediments succession appears to follow the facilitation and inhibition models (Arntz and Rumohr, 1982, 1986; Zajac et al., 1998; Thistle, 1981; Lenihan and Micheli, 2001). For example, when bare habitat appears after a disturbance, generally pioneer colonizers with opportunistic life history traits arrive first (e.g. spionid polychaetes). These species are well adapted to colonize comparatively quickly and also prepare the habitat for subsequent colonizers (Santos and Simon, 1980a; Arntz and Rumohr, 1982; Zajac and Whitlatch, 1982a; Guerra-García and García-Gómez, 2006; Lu and Wu, 2000, 2007). The initial successional stage of abundant opportunists is usually followed by severe mortality and partial or total replacement by later species. The sharp abundance decline of opportunistic species is generally assumed to be the result of biotic interactions (e.g. predation, inter- and intraspecific competition for space and food), or accumulation of toxic substances (Rosenberg, 2001; Norkko et al., 2006). The resulting “mature” (sensu Margalef, 1968) community is mainly composed of species from the undisturbed surrounding community, including larger and longer-lived species (Pearson and Rosenberg, 1978; Lenihan and Micheli, 2001; Lu and Wu, 2000; MacAllen et al., 2009). Nevertheless, evidence from different soft-bottom systems (e.g. Santos and Bloom, 1980, 1983) suggests that recovery through succession is not

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necessarily a consecutive replacement of colonizers over time (e.g. Zajac and Whitlatch, 2001, 2003). Instead, succession often occurs via slight and stochastic changes in community structure following the “tolerance model” (Connell and Slatyer, 1977). According to this model, species interactions are weak and all members of the community can potentially colonize at any given moment in time.

Another important factor in modulating the development of benthic communities is the supply of colonizers (e.g. larvae) and its spatial and temporal variation. Experimental studies on soft-bottom habitats have shown that early succession in temperate regions strongly depends on the season, in which the new substratum became available (Arntz and Rumohr, 1982; Zajac and Whitlatch, 1982b; Díaz-Castañeda et al., 1989; Lu and Wu, 2007). In addition, post-settlement drifting and migration are important dispersal mechanisms for juvenile and small adult soft-bottom inhabitants (Armonies, 1994; Zühlke and Reise, 1994; Cummings Niño et al., 1995). Both, larval supply and post-settlement dispersal may be influenced by seasonality (Norkko et al., 2006); consequently these sources of variability are important in the early stage of succession and may have effects on later successional stages and community persistence (Santos and Simon, 1980b; Arntz, 1981; Olausson, 1988; Marinielli and Woodin, 2002).

The successional development of sublittoral soft-bottom communities off central Peru (Humboldt Current System, HCS) has been related to the variations of temperature and oxygen content during the El Niño Southern Oscillation (ENSO) (Arntz, 1986; Tarazona et al., 1988b,a, 1996; Arntz et al., 2006). During cold and coldest La Niña (LN) conditions, shallow soft bottoms are typically hypoxic and the community is composed of few species. The intrusion of warm and oxygen-rich waters during El Niño (EN) triggers the development of a much more diverse community, suggesting progression towards an advanced successional stage (Tarazona et al., 1988b,a, 1996; Arntz et al., 2006). Off northern and central Chile the increase of wave action and freshwater runoff during EN accompanied by huge terrestrial sediment loads are frequent sources of disturbances (Thiel et al., 2007; Thatje et al., 2008). These events leave extensive defaunated habitat areas, but community recovery through succession has not yet been examined thoroughly. During LN conditions, however, large-scale disturbances are rare and small-scale biotic disturbances are apparently of more relevance. Predation by crabs and fish opens space for colonization (e.g. VanBlaricom, 1982; Sousa, 2001; Jesse and Stotz, 2002; Leon and Stotz, 2004), but at present there is no local information on the macrobenthic recovery available. The published information about the dynamics of shallow macrobenthic communities off northern Chile describes only changes in community composition and structure during and shortly after EN events (Carrasco and Moreno, 2006; Laudien et al., 2007; Moreno et al., 2008; see review in Thiel et al., 2007), but other important ecological aspects (e.g. general community succession, colonization processes) and succession during LN have not yet been described. The present study was conducted on subtidal soft bottoms off northern Chile in order to understand the community succession and patterns of recovery.

The objectives of this study were (1) to describe the successional development of the subtidal soft-bottom macrobenthic community over two years, (2) to estimate the recovery time of the developing community, i.e. the time required to converge to the same community structure of the surrounding undisturbed habitat, and (3) to examine whether communities initiated during different seasons differ in their community structure after one year of succession.

2. Materials and methods

2.1. Study site

The study was conducted in the sublittoral zone off “Playa Colorado” (23°30’S; 70°31’W) located at the interior northern part of Antofagasta Bay, northern Chile. The bay is situated in the southern part of Peninsula Mejillones, which is characterized by several upwelling areas, where cold water with high nutrient and low oxygen contents rise to the sea surface. Upwelling events occur year round, although less intense during austral winter. The sea surface temperature ranges from 14 to 22 °C. From the surface to 40 m depth, oxygen concentrations are relatively low (<2 mL O2 L−1, Escribano and Hidalgo, 2001) and below this depth the Oxygen Minimum Zone (<0.5 mL O2 L−1) extends to deeper waters (~200 m, Escribano et al., 2002, 2004). With the intensification of upwelling during the summer month’s oxygen depleted waters can ascend to shallow waters close to the coast in the study area (P. Davila unpublished data; Escribano et al., 2000; Escribano and Hidalgo, 2001).

2.2. Experimental set-up

Forty-one labeled round containers (conical terracotta flowerpots; 40 cm upper diameter, 30 cm lower diameter and 48 cm in height) were installed at 14 m water depth by SCUBA divers in June 2006. Thirty-six replicate containers were designated for the two experiments of this study (see below) and 5 extra containers were placed to account for eventual losses. To allow for vertical exchange processes, the bottoms of the containers were replaced by reinforced plastic mesh (1 mm) before installation. Containers were buried approximately 43 cm into the sediment and filled with a sand:bentonite (80:20) mixture, resembling the granulometric structure of the soft sediments in the bays adjoining Peninsula Mejillones (Rojo and Laudien, 2005), including the study site. We used Calcium-Bentonite (IBECO® AGROMONT S&B Industrial Minerals GmbH, Oberhausen, Germany), which is calcium-phyllosilicate clay, mainly consisting of montmorillonite used herein as a substitute of the fine sediment fraction. This inorganic mixture provides homogeneous sediment conditions without any biological conditioning (i.e. organic carbon, bacterial or larval occurrence), thus reducing patchiness between replicates. The use of artificial substrata has been proven effective in previous colonization studies (e.g. Arntz and Rumohr, 1982, 1986; Veit-Köhler et al., 2008), because it avoids potential environmental impacts due to extraction of large in situ quantities of natural sediment difficult to clean from any biogenic matter without modifying its granulometry.

The distance between containers was ≥1.5 m and thus adequate to guarantee interspersion (Quinn and Keough, 2002). Containers were deployed in two parallel lines and filled at the same day to avoid variability due to different onsets of the colonization process. Bags containing the experimental sediment were carefully located on the bottom and then placed at the side of each container. Thereafter three divers worked together in opening the bags and filling the containers, trying to avoid disturbance of the surrounding sediments as much as possible. During the course of the experiment, the fouling attached to the exposed 5 cm rim of the containers was removed monthly. Every three months three containers were randomly assigned to be sampled.

2.3. Description of successional development and convergence to the natural community

Over a two-year period samples were collected every three months (Fig. 1) using an air-lift device extracting a 10 cm deep sediment layer inside a round core (15 cm diameter) pushed centrally into each of the respective experimental containers. Every container was sampled just one time. The material retained in the mesh bag (0.5 mm) of the air-lift device was further sieved on a 0.5 mm mesh in the laboratory. The material was further sieved on a 0.5 mm mesh in the laboratory. The material was preserved in a methanol solution stained with Bengal rose. In situ sampling was performed every four months. The distance between containers was ≥1.5 m and thus adequate to guarantee interspersion (Quinn and Keough, 2002). Containers were deployed in two parallel lines and filled at the same day to avoid variability due to different onsets of the colonization process. Bags containing the experimental sediment were carefully located on the bottom and then placed at the side of each container. Thereafter three divers worked together in opening the bags and filling the containers, trying to avoid disturbance of the surrounding sediments as much as possible. During the course of the experiment, the fouling attached to the exposed 5 cm rim of the containers was removed monthly. Every three months three containers were randomly assigned to be sampled.
at different temporal (i.e. succession) and spatial gradients (e.g. Warwick, 1988). Biomass (wet mass) of the different taxa was obtained after putting the organisms shortly on blotting paper and recorded with a 0.01 g precision. Furthermore, taxa were classified into feeding groups according to the literature (Gutiérrez et al., 2000; Laudien et al., 2007; Moreno et al., 2008). To evaluate if developing communities resembled the natural macrobenthic composition, four haphazard samples from the surrounding area were taken at each sampling day using the same technique employed for the containers.

2.4. Influence of the seasonal onset of the succession

To evaluate if there is an effect of the seasonal onset on the structure of the developing community, three additional containers were installed every three months; i.e. in June 2006, October 2006, January 2007 and March 2007. After 12 months of exposure, the respective communities were sampled and thereafter compared (Fig. 1). As colonizer supply can seasonally vary, it was hypothesized that communities starting succession at different seasons would differ in structure after one year of exposure.

2.5. Data analysis

Differences in taxonomic richness, total abundance and total biomass (wet mass) were examined using two-way analysis of variance (ANOVA) with origin (two levels, developing and reference community) and time intervals (eight levels: 3, 6, 9 ... 24 months) as fixed factors plus the interaction factor. Prior to the analyses the assumptions of data normality were explored using the Anderson–Darling test. Abundance and biomass data were log-transformed to achieve data normality, while values of taxonomic richness were processed without transformation. When the ANOVA detected significant differences the a posteriori Tukey HSD test was conducted to detect the treatments accounting for differences. These analyses were carried out using the MINITAB statistical software (Release 14) for MS Windows. In addition, non-metric Multi Dimensional Scaling (nmMDS) ordination plots, conducted from a Bray–Curtis similarity matrix after square-root transformation of the data, were used to visualize dissimilarities between communities after each time interval and in the seasonality experiment. Differences in community structure within time intervals during succession and seasons were analyzed with one-way analysis of similarity (ANOSIM). To evaluate if succession followed a sequential pattern, the ‘seriation with replication routine’ from the RELATE analysis was applied to community stages of different time intervals. To test the convergence to the natural surrounding structure, communities from each time interval were compared with their respective reference samples also using ANOSIM. When ANOSIM detected differences, pairwise comparisons were used to identify which treatments differed. However, with three replicates for each interval it was only possible to reach a significance level of \( p = 0.1 \). Therefore, the interpretation of pairwise comparisons was based on \( R \)-values (rather than \( p \)) as suggested by Clarke and Gorley (2006). These authors stated that the level of significance largely depends on the number of replicates and is thus always influenced by the sample size, whereas \( R \) is largely not a function of the number of replicates (i.e. possible permutations), but an absolute measure of differences between two (or more) groups in the high-dimensional space of the data (R. Clarke, personal communication). To visualize and facilitate the interpretation of pairwise comparisons an nmMDS plot (based on a dissimilarity matrix calculated from Euclidian distances between \( R \)-values) was generated. The nmMDS ordination plots, ANOSIM and RELATE were performed using the PRIMER v6 software package (Clarke and Gorley, 2006).

3. Results

3.1. Successional community development

During the course of succession, a total of 48 taxa were recorded from the experimental containers (Table 1) and the surrounding area (Table 2). For most sampling dates, the most abundant taxa included the cephalochordate *Branchiostoma elongatum*, the bivalves *Tagelus dombeii*, *Linucula pisum*, *Mysella* sp., polychaetes from the families

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**Fig. 1.** Sampling design. Three replicate sediment samples taken after 3, 6, 9 ... 24 months. Time intervals for the seasonal variability in the experiment are indicated by abbreviations; Au (Autumn), Wi (Winter), Sp (Spring), Su (Summer).
Cirratulidae and Spionidae, the amphipods *Cancilla buxinoides* and *Spionidae*, the amphipods *Pagurus villosus* and *Semele solida* –– 18 226 75 113 207 18 113 207

**Bivalvia**

*Choromytilus chorus* –– 113 5211 5702 2122 990 5037 6579

**Crustacea**

*Amphelisca sp.* 113 –– 226 226 99 –– 198 240

*Branchiostoma elongatum* 132 94 169 –– 18 75 18 94

*Chordata*–

*Eudevenopus* 2122 14 28 42

*Gastropoda*–

*Nemertea*–

*Indeterminate* 56 14 42 14 14 14 14

*Chordata*–

*Branchiostoma elongatum* –– 28 70 56 –– 28 56 70

**Total** 2858 4910 7159 8207 2773 2391 6707 8956

Abundance of the fauna in the reference samples was higher than in the experimental containers except for samples taken 3 and 6 months after the start of the experiment (Fig. 2). Biomass in the experimental containers progressively increased from the beginning of the experiment, reaching maximum values after 9 to 12 months (Fig. 2). Thereafter biomass values decreased towards the end of the experimental time. ANOVA did not detect significant differences in biomass values according to the origin (*F* = 1.18, *p* > 0.05) or time intervals (*F* = 3.49, *p* < 0.05), and the interaction factor was not significant either (*F* = 1.23, *p* > 0.05). Biomass from reference communities showed only minor fluctuations over time and was lower compared to the one of the experimental communities (Fig. 2).

Comparisons of the community structure after 3 to 24 months detected significant differences between treatments (one-way ANOSIM, *R* = 0.51, *p* < 0.05). Clearly, only 15 and 21-month old experimental communities were overlapping, while the rest indicated strong dissimilarities. Temporal changes in community structure did not follow a clear sequential pattern (Fig. 3). For example, the dissimilarity between 3- and 18-month-old community stages did not differ from the dissimilarity detected between 9- and 21-month-old stages. The absence of a consecutive pattern was supported by the RELATE analysis, which did not show any tendency of seriation (*p* = 0.105, *p* > 0.05). The proportions of distinct feeding groups encountered during the succession were relatively equally distributed during the 24 months (Fig. 4).

The comparison of experimental communities from distinct time intervals with their respective references from the surrounding community (Table 2) indicated no significant differences in composition after 18 months (*R* = 0.315, *p* < 0.05, Table 3). Although the

**Table 1**

Total abundance (individuals m⁻²) of macrofaunal taxa in experimental containers exposed over different time intervals (in months).

<table>
<thead>
<tr>
<th>Taxa</th>
<th>3</th>
<th>6</th>
<th>9</th>
<th>12</th>
<th>15</th>
<th>18</th>
<th>21</th>
<th>24</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Polychoerida</strong></td>
<td>–</td>
<td>56</td>
<td>–</td>
<td>18</td>
<td>–</td>
<td>18</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Aristotleidae</strong></td>
<td>116</td>
<td>2300</td>
<td>113</td>
<td>94</td>
<td>18</td>
<td>282</td>
<td>75</td>
<td>–</td>
</tr>
<tr>
<td><strong>Glyceridae</strong></td>
<td>–</td>
<td>18</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Goniadidae</strong></td>
<td>–</td>
<td>37</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Lumbrineridae</strong></td>
<td>–</td>
<td>18</td>
<td>18</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Magelonidae</strong></td>
<td>–</td>
<td>18</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Maldanidae</strong></td>
<td>–</td>
<td>18</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>377</td>
</tr>
<tr>
<td><strong>Nephtyidae</strong></td>
<td>–</td>
<td>18</td>
<td>56</td>
<td>37</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Nereididae</strong></td>
<td>37</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Oribinidae</strong></td>
<td>–</td>
<td>37</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>56</td>
<td>–</td>
</tr>
<tr>
<td><strong>Paraonidae</strong></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>56</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Polyonioidea</strong></td>
<td>–</td>
<td>18</td>
<td>56</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Spionidae</strong></td>
<td>3225</td>
<td>2093</td>
<td>829</td>
<td>94</td>
<td>2018</td>
<td>1112</td>
<td>1791</td>
<td>1075</td>
</tr>
</tbody>
</table>

**Table 2**

Total abundance (individuals m⁻²) of macrofaunal taxa recorded from the reference community at distinct time intervals (in months) resembling the sample intervals of the succession experiment.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>3</th>
<th>6</th>
<th>9</th>
<th>12</th>
<th>15</th>
<th>18</th>
<th>21</th>
<th>24</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Polychoerida</strong></td>
<td>141</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>127</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Cirratulidae</strong></td>
<td>–</td>
<td>14</td>
<td>42</td>
<td>84</td>
<td>–</td>
<td>14</td>
<td>84</td>
<td>84</td>
</tr>
<tr>
<td><strong>Glyceridae</strong></td>
<td>–</td>
<td>28</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Lumbrineridae</strong></td>
<td>28</td>
<td>42</td>
<td>–</td>
<td>28</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Nephtyidae</strong></td>
<td>84</td>
<td>28</td>
<td>28</td>
<td>84</td>
<td>28</td>
<td>42</td>
<td>42</td>
<td>42</td>
</tr>
<tr>
<td><strong>Orbinidae</strong></td>
<td>–</td>
<td>28</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Polynoidae</strong></td>
<td>14</td>
<td>–</td>
<td>–</td>
<td>28</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Spionidae</strong></td>
<td>2051</td>
<td>1315</td>
<td>2621</td>
<td>5702</td>
<td>2122</td>
<td>990</td>
<td>5037</td>
<td>6579</td>
</tr>
</tbody>
</table>

**Cirratulidae** and Spionidae, the amphipods *Amphelisca sp.*, *Eudevenopus sp.*, and ostracods (Table 1). There were no significant differences in taxonomic richness concerning origin (*F* = 2.84, *p* > 0.05), time interval (*F* = 0.96, *p* > 0.05) and the interaction factor (origin × time intervals; *F* = 1.36, *p* > 0.05) (Fig. 2). For abundance values the two-way ANOVA detected significant differences according to the origin (*F* = 19.46, *p* < 0.001) and for different time intervals (*F* = 2.73, *p* < 0.05), and the interaction factor was also significant (*F* = 8.82, *p* < 0.001). Specifically, the 12-month value accounted for the differences (Tukey test *p* < 0.05).
community stages after 6 months development were at the threshold of the significance level, we concluded that those communities were different as the R-value was high (see Table 3).

3.2. Effects of seasonal onset on soft-bottom colonization

Seasonal onset showed no effect in any of the parameters analyzed: there were no detectable effects on taxonomic richness, total abundance, or biomass (ANOVA, p>0.05) (Fig. 5). The nMDS plot (Fig. 6) also showed no clear dissimilar groups between seasons. The ANOSIM (R = 0.16, p>0.05) confirmed the lack of differences in community structure among seasons.

4. Discussion

4.1. Pattern of successional community development

The results of this study indicate that macrobenthic soft-bottom community development did not follow a sequential succession. Community stages reflected a stochastic temporal distribution rather...
than a successive sequence of community changes as observed elsewhere after natural disturbances (Pearson and Rosenberg, 1978; Lenihan and Micheli, 2001) or in colonization experiments (Arntz and Rumohr, 1982, 1986; Berge, 1990). This study provides evidence that succession in northern Chilean sandy subtidal habitats is more variable and does not include distinguishable seral stages, which are more

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**Fig. 1.** (A) Non-metric MDS plot of community structure calculated from Bray-Curtis measures after square-root transformation for the experimental community after distinct time intervals. (B) Non-metric MDS plot calculated from Euclidian distance from pair-wise R-values after ANOSIM from communities after distinct development times.

**Fig. 4.** Feeding groups proportional to the total abundance observed throughout the colonization experiment.
related to recovery patterns observed in sandy intertidal flats (e.g., Zajac and Whitlatch, 2003). Succession in the sense of progression from early to late colonizers might be mostly applied in muddy habitats rich in organic matter (Pearson and Rosenberg, 1978; Rhoads and Germano, 1986). The present study supports Connell and Slatyer’s (1977) “tolerance succession model”, stating that any potential colonizer can establish successfully, regardless of whether earlier colonizers have preceded or not. Often the most appropriate model of succession in sedimentary systems is the “facilitation model”, in which succession starts with the arrival of opportunistic species, successively replaced by mid and late colonizers (e.g., Pearson and Rosenberg, 1978; Arntz and Rumohr, 1982, 1986; Berge, 1990; Rosenberg, 2001; Rosenberg et al., 2002; Kröger et al., 2006). However, the present experiment did not detect a true peak of opportunistic taxa, and neither a dominance of exclusively late species towards the end. Abundant taxa (e.g., spionids,

![Taxonomic richness](image1)

![Abundance](image2)

![Biomass](image3)

Fig. 5. Changes in primary community parameters after distinct seasonal onsets of the colonization process.
very similar taxonomic richness and total abundance) occurred after 4.3. Resemblance to the surrounding community

resources, presumably each specialized on different kinds of food. The present study supports the observation that other trophic groups, but only decreased in abundance (Tarazona et al., 1996). However, deposit feeders were not completely replaced by concentrations and higher temperatures during EN (Tarazona et al., 1996). Santos and Bloom (1983) evaluated the succession after 3 months (Wu and Shin, 1997; Lu and Wu, 2000; Guerra-García et al., 2003; Guerra-García and García-Gómez, 2006), temperate soft-bottom communities require between one and eight years (Rosenberg, 1976; Arntz and Rumohr, 1982; Nilsson and Rosenberg, 2000). This is in line with the present study, which showed that after 18 months the community reached the structure of the undisturbed surrounding community (sensu Santos and Bloom, 1980). While the Antofagasta zone is located at subtropical latitudes the presence of cold upwelled waters produces a resemblance with the environmental conditions in temperate zones. Under colder conditions (i.e. polar regions) convergence of experimental and natural macrofauna communities requires even more time (e.g. Conlan and Kvitek, 2005; Bowden et al., 2006; Teixidó et al., 2007).

Distinct feeding groups encountered during the colonization process occurred at equal proportions throughout the experimental time, which again is in contrast to most observations from developing communities after intense disturbances. Elsewhere, changes from surface deposit feeders to deep subsurface deposit feeders have been reported with increasing developmental time (Rhoads and Germano, 1986; Zajac et al., 1998; Nilsson and Rosenberg, 2000; Van Colen et al., 2008). Changing dominance patterns from deposit feeders to scavengers and suspension feeders have been observed on hypoxic soft bottoms off central Peru after episodes of increased oxygen concentrations and higher temperatures during EN (Tarazona et al., 1996). However, deposit feeders were not completely replaced by other trophic groups, but only decreased in abundance (Tarazona et al., 1988a,b, 1996). The present study supports the observation that trophic complexity does not necessarily coincide with advanced successional development (e.g. Wolff et al., 1977; Arntz and Rumohr, 1982). The distribution of the feeding groups suggests that the community is composed of species capable to efficiently exploit resources, presumably each specialized on different kinds of food (Connell and Slatyer, 1977).

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Experimental studies examining the recolonization of small patches of disturbed sediment have shown that recovery patterns depend on local environmental characteristics. While communities in shallow subtropical areas could recover within a few weeks to four months (Wu and Shin, 1997; Lu and Wu, 2000; Guerra-García et al., 2003; Guerra-García and García-Gómez, 2006), temperate soft-bottom communities require between one and eight years (Rosenberg, 1976; Arntz and Rumohr, 1982; Nilsson and Rosenberg, 2000). This is in line with the present study, which showed that after 18 months the community reached the structure of the undisturbed surrounding community (sensu Santos and Bloom, 1980). While the Antofagasta zone is located at subtropical latitudes the presence of cold upwelled waters produces a resemblance with the environmental conditions in temperate zones. Under colder conditions (i.e. polar regions) convergence of experimental and natural macrofauna communities requires even more time (e.g. Conlan and Kvitek, 2005; Bowden et al., 2006; Teixidó et al., 2007).

Eudevenopus sp., Ostracoda, Nassarius guyi, Mysella sp. and T. dombeii) were present from the beginning of succession and persisted throughout the entire study period.

During EN events, community succession in hypoxic areas off central Peru was not due to replacement of resident species, but rather by the addition of “new” immigrants to the community facilitated by improvement of oxygen concentrations (Tarazona et al., 1988a,b, 1996). Santos and Bloom (1983) evaluated the succession after 3 disturbance (hypoxia) events and concluded that there are no successive patterns in species composition or densities during recolonization. Colonization by opportunistic species may not always occur after a disturbance and the mode of response to disturbed habitat patches frequently depends on habitat conditions, the life history of a species and its mobility patterns (Zajac et al., 1998; Zajac and Whitlatch, 2003). The present study suggests that disturbances can trigger a multifaceted species’ population responses, which were reflected in a variable community structure (Zajac and Whitlatch, 1991) and thus the observed successional pathway.

4.2. Succession and feeding groups

4.3. Resemblance to the surrounding community

Resemblance to the reference community (in this case, equal or very similar taxonomic richness and total abundance) occurred after 18 months of community development, suggesting that colonization follows a deterministic pattern even though it is non-sequential. This is consistent with the prediction that soft-bottom communities commonly return to an almost identical faunal structure after severe disturbances (Santos and Bloom, 1980; Rosenberg, 2001). In terms of biomass, the values within the experimental containers exceeded those of the natural community at months 9, 12 and 15 due to the presence of the comparative large bivalves Argopecten purpuratus and T. dombeii. In the absence of these large species, biomass values from experimental and reference communities were similar. Hence, as in the experiment of Arntz and Rumohr (1982), it is suggested that biomass is not an optimal indicator of recovery after short periods of recovery, and that taxonomic richness and total abundance can be more informative over such time scales.

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4.4. Soft-bottom succession follows the tolerance model

Connell and Slatyer (1977) mentioned that the tolerance model is mostly applicable for animals that resist physical and biotic stress (e.g. hypoxia and predation), and in situations, where most of their natural enemies are excluded by stressful environmental conditions. In this case the community may be limited by resources. Although we did not measure abiotic parameters, this scenario appears to apply to the shallow soft-bottom community of Antofagasta Bay. Similar to other areas of the Humboldt Current System, shallow macrobenthic communities are primarily controlled by oxygen concentration and water temperature (Tarazona et al., 1988a,b, 1996; Gutiérrez et al., 2000; Palmer et al., 2005; Sellanes et al., 2007). The waters of Antofagasta Bay are characterized by a rather low oxygen concentration, especially during the summer months when upwelling is more intense and upwelled waters may bring low oxygen (≤2mLO2L−1) to the shallow bottoms impacting benthic communities (≤1.5mLO2L−1 at 14 m, P. Davila unpublished data; Escribano et al., 2000; Escribano and Hidalgo, 2001). Hypoxic events are likely to occur but their effects are rather subtle because there is no evidence of mass mortalities. An indication for this scenario applicable to the present study is the abundance of spionid polychaetes (e.g. Paraprionospio pinnata), which are also among the main components of the macrozoobenthic community of hypoxic areas (Carrasco, 1997; Palma et al., 2005; Carrasco and Moreno, 2006). Hypoxic events may usually not reach lethal levels for most species of the infaunal community, yet oxygen concentrations might be too low for epibenthic and mobile fish and crab predators. The latter, e.g. flatfish Paralichthys spp. and crabs Cancer spp., feed on a wide prey spectrum (e.g. Leon and Stotz, 2004), but hypoxic conditions affect their predation efficiency (Cisterna et al., 2008). It is likely that communities in Antofagasta Bay are adapted to resist hypoxic events and therefore the assumptions of the model are fulfilled.
4.5. Effect of the season on the onset of successional development

Despite the different seasonal onset, the communities established after one year did not differ in composition. This is in agreement with other studies demonstrating the effects of the seasonal onset on initial community succession, but a convergence towards a similar structure at later stages (Díaz-Castañeda et al., 1989; Rosenberg, 2001; Lu and Wu, 2007). At the same location of the present study, but at greater depth (50–60 m), polychaete assemblages show high persistence without exhibiting a clear seasonal or annual fluctuation in composition, despite the high oceanographic variability including moderate and intense EN events (Carrasco, 1997; Carrasco and Moreno, 2006). In accordance, in the neighboring Mejillones Bay (northern bay of the Peninsula Mejillones) a seven-year time series (including EN 1997–1998) of benthic community data from shallow areas (10 and 20 m) showed little seasonal variations in terms of diversity and evenness of macrobenthic communities (Laudien et al., 2007).

Dispersal of juveniles as well as adults from the surrounding habitat may play an important role during the colonization process, especially at small spatial scales (Zajac et al., 1998). Small patches of sediment can be quickly colonized by drifting, crawling or actively swimming species or lateral immigration (Armonies, 1994; Zühle and Reise, 1994; Cummings et al., 1995; Reise, 2002; Zajac and Whittatch, 2003). Motile taxa such as the amphipods Eudevemonus sp., Harpinia sp., Ampelisca sp., the lancelet B. elongatum, or the hermit crab Pagurus sp. likely immigrated as subadults or adults into the experimental communities of the present study. Lateral immigration of juveniles and adults can sometimes confound larvae settlement events (Van Colen et al., 2008), and both colonization mechanisms are important in small habitat patches. Although the potential effects of the enclosed containers precluding lateral immigration are important (e.g. Smith and Brumsickle, 1989), our results showed that they were of minor importance during the experiments.

In conclusion, macrobenthic development of small azoic sediment patches located in shallow northern Chilean habitats follow a non-sequential but deterministic pattern according to the ‘tolerance model’ (Connell and Slatyer, 1977). Communities starting to develop in different seasons converged to a similar structure after one year, which is in line with the notion of high persistence of benthic communities off northern Chile. These results highlight the recovery capacity of the benthic fauna from shallow subtidal soft bottoms, which is considered an important community feature in response to small-scale disturbance. This provides the basis for further understanding of the recovery dynamics from large-scale disturbances (i.e. EN) in the SE Pacific.

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