

**Community succession and seasonal  
onset of colonization in sublittoral hard  
and soft bottoms off northern Chile**

Doctoral thesis

by

**Aldo S. Pacheco V.**

Submitted to Faculty 2 (Biology & Chemistry),

Bremen University

in partial fulfilment of the requirements for the degree of

*Doctor rerum naturalium* (Doctor of Natural Sciences)

April 2009, Bremen



Universität Bremen





**I would like to dedicate this thesis to the memory of the following good souls:**

**Dr. Victor Alamo Vasquez *for introducing me to the fascinating world of marine science***

**Dr. Manuel Valencia Valencia *for your unconditional guidance, your life lessons won't  
be forgotten in my soul***

**Mario Villegas Ortiz *for blessing my life with your friendship and for showing me how to  
enjoy life at the sea***



**Advisory Committee:**

1. Reviewer: Prof. Dr. Wolf Arntz (Alfred Wegener Institute for Polar and Marine Research (AWI) Bremerhaven, Germany)
2. Reviewer: Dr. Marcelo Oliva (Universidad de Antofagasta, Antofagasta, Chile)
3. Examiner: Prof. Dr. Claudio Richter (Alfred Wegener Institute for Polar and Marine Research (AWI) Bremerhaven, Germany)
4. Examiner: Dr. Jürgen Laudien (Alfred Wegener Institute for Polar and Marine Research (AWI) Bremerhaven, Germany)

<b>Contents</b>	<b>Page</b>
<b>Abstract</b>	v
<b>Zusammenfassung</b>	vii
<b>Resumen</b>	viii
<b>List of figures</b>	x
<b>1 Introduction</b>	1
1.1 Succession of benthic communities	1
1.2 Succession in hard-bottom epibenthic communities	2
1.3 Succession in soft-bottom macrobenthic communities	4
1.4 The Humboldt Current System off northern Chile	6
1.5 The importance of understanding benthic succession in the coastal ecosystem off northern Chile	7
1.6 The effects of seasonality on benthic community development	9
1.7 Comparison between hard- and soft-bottom succession	10
1.8 Aims of the study	12
1.8.1 Hypotheses	12
1.8.2 Specific objectives	12
<b>2 Study sites</b>	13
<b>3 Materials and methods</b>	15
3.1 <i>In situ</i> succession experiment in a hard-bottom subtidal habitat	15
3.2 <i>In situ</i> succession experiment in a soft-bottom subtidal habitat	16
3.3 Statistical analysis	18
<b>4 Results</b>	20
4.1 Publications	20
4.1.1 Publication I: Succession and seasonal variation in the development of sublittoral epibenthic hard-bottom communities off northern Chile. Marine Ecology. Submitted.	22
4.1.2 Publication II: Hard-bottom succession of subtidal epibenthic communities colonizing hidden and exposed surfaces off northern Chile. Scientia Marina. In press.	46
4.1.3 Publication III: Succession and seasonal variation in the development of subtidal macrobenthic soft-bottom communities from northern Chile. Journal of Sea Research. Submitted	60
4.1.4 Publication IV: First record of <i>Cymatium keenae</i> Beu, 1970 (Mollusca: Ranellidae) from Antofagasta Bay, northern Chile, in connection with El Niño events. Helgoland Marine Research 62(Suppl 1): S107-S110	83

4.1.5 Publication V: <i>Dendropoma mejillonensis</i> sp. nov. a new species of vermetid (Caenogastropoda) from northern Chile. The Veliger 50(3): 219-224	86
<b>5 General discussion and conclusions</b>	91
5.1 Succession and convergence towards natural communities in hard-bottom habitats	91
5.2 Succession and convergence towards natural communities in soft-bottom habitats	94
5.3 The effects of the seasonality during the onset of successional development	96
5.3.1 Seasonality in hard-bottom communities	96
5.3.2 Seasonality in soft-bottom communities	97
5.4 Succession in subtidal benthic habitats: hard- vs. soft-bottom processes	99
<b>6 Future perspectives of research</b>	102
<b>7 Acknowledgements</b>	105
<b>8 Appendix</b>	108
<b>9 References</b>	110

## **Abstract**

Community ecological succession consists of the sequence of changes in species composition through time that occurs after a site has been disturbed or on the appearance of a pristine substratum, and it is one of the key processes modulating patterns of diversity, structure and evolutionary history of benthic landscapes. I have used field experiments to describe the successional development of both sublittoral hard- and soft-bottom communities off northern Chile. The Humboldt Current System off northern Chile is an excellent natural laboratory to study succession because there are several sources of disturbances operating at different scales including the El Niño Southern Oscillation (ENSO), which drastically influences biodiversity patterns. This thesis specifically aimed (i) to describe the successional development of subtidal hard- and soft-bottom communities over 27 months and a two year period, respectively; (ii) to estimate the time necessary for the developing communities to resemble the surrounding natural community, and (iii) to evaluate the effect of the seasonal starting point of community succession over a one year period of development. Succession in hard-bottom habitats showed a progressive change in community structure and competition for space, which was identified as the most important factor during succession. After 27 months, the developing communities contained the same species as the natural community but did not yet fully resemble their surroundings. Seasonality had an effect on successful species settlement, but the final stages of the developing community were influenced by interspecific competition for space (i.e. hierarchical competition). Succession followed a non-rigid, but deterministic pattern, in which colonial suspension-feeding species were hierarchically dominant over solitary species. This dominance of suspension feeders appears to be favoured by high levels of primary production associated with upwelling. On hidden surfaces of the hard substratum early successional species survive better and can laterally spread over exposed habitats as strong interactions for space among species are alleviated in hidden habitats.

Succession in soft-bottom habitats supported the “tolerance succession model” where components of the later successional stages can colonize at the same time with species generally associated to the early successional stages. Resemblance to natural sediment communities occurred after eighteen months. Seasonality had no evident effect on the resulting community composition and all communities starting in different seasons converged into a similar composition after one year of exposure. These results support the notion that benthic community can return to an almost identical faunal structure with the same dominants after disturbance events. Both, hard- and soft- bottom communities showed a high capability to return and to converge towards natural surrounding communities, which highlights the resistance of the benthic system to small scale disturbances. Furthermore, the finding of new species in both study locations suggest that the components and their potential colonizing role need to be surveyed in detail to

understand the species turnover during succession. My results demonstrate that benthic communities from northern Chile present a high resistance capacity to small scale disturbance during cold conditions with hard bottoms responding slower compared to the relatively quick recovery detected in soft bottoms. The question to be resolved in the future is whether or not this resistance capacity is also valid during strong El Niño events. Enhancing the temporal and spatial scale of this type of experiments is therefore recommended not only for the understanding resistance and succession, but also other ecosystem stability properties such as resilience, persistence and elasticity.

## Zusammenfassung

Die ökologische Sukzession einer Gemeinschaft beruht auf der Abfolge von im Laufe der Zeit stattfindenden Veränderungen der Artenzusammensetzung, nachdem ein Ort gestört wurde oder wenn ein junefräuliches Substrat auftritt, und sie ist eines der Schlüsselmuster für die Bildung von Vielfalt, Struktur und Entstehungsgeschichte benthischer Landschaften. Ich habe Feldexperimente benutzt, um die Sukzessionsentwicklung sublitoraler Hart- und Weichbodengemeinschaften vor Nordchile zu beschreiben. Das Humboldtstrom-System vor Nordchile ist ein ausgezeichnetes natürliches Labor zur Untersuchung der Sukzession, weil es dort mehrere Störungsquellen gibt, die auf unterschiedlichen Skalen inkl. El Niño und Südliche Oszillation (ENSO) wirken und die Biodiversitätsmuster drastisch beeinflussen. Diese Dissertation zielte besonders darauf, (i) die Sukzessionsentwicklung von sublitoralen Hart- und Weichbodengemeinschaften über einen Zeitraum von 27 Monaten beziehungsweise zwei Jahren zu beschreiben; (ii) die Zeit einzuschätzen, welche die sich entwickelnden Gemeinschaften benötigen, um sich der natürlichen Gemeinschaft in der Umgebung anzugleichen, und (iii) die Auswirkung des saisonalen Ausgangspunktes auf die Gemeinschaftssukzession über einen Entwicklungszeitraum von einem Jahr zu beurteilen. Die Sukzession auf Hartboden-Lebensräumen zeigte eine fortlaufende Änderung der Gemeinschaftsstruktur und der Konkurrenz um Raum, die als wichtigster Faktor während der Sukzession bestimmt wurde. Nach 27 Monaten enthielten die sich entwickelnden Gemeinschaften die selben Arten wie die natürliche Gemeinschaft, hatten sich aber noch nicht völlig ihrer Umgebung angeglichen. Saisonalität hatte sich auf die erfolgreiche Ansiedlung von Arten ausgewirkt, aber die endgültigen Stadien der sich entwickelnden Gemeinschaft wurden durch interspezifische Raumkonkurrenz (d.h. hierarchischen Wettbewerb) beeinflusst. Die Sukzession folgte keinem starren, aber einem deterministischen Muster, in dem koloniale Suspensionsfresser-Arten hierarchisch über solitäre Arten herrschten. Diese Überlegenheit der Suspensionsfresser scheint durch auftriebsbedingte hohe Primärproduktion begünstigt zu werden. Frühe Sukzessionsarten überleben besser auf verborgenen Oberflächen des Hartsubstrats und können sich seitwärts über exponierte Lebensräume ausbreiten, weil in verborgenen Lebensräumen die starken Interaktionen um Raum unter den Arten abgeschwächt sind.

Die Sukzession in Weichboden-Lebensräumen unterstützte das "Toleranz-Sukzessionsmodell", nach dem Bestandteile der späteren Sukzessionsstadien gleichzeitig mit Arten kolonisieren können, die gewöhnlich in frühen Sukzessionsstadien auftreten. Die Angleichung an natürliche Sedimentgemeinschaften erfolgte nach achtzehn Monaten. Saisonalität hatte keine offensichtliche Auswirkung auf die sich ergebende Zusammensetzung der Gemeinschaft, und bei Beginn zu unterschiedlichen Jahreszeiten fanden alle Gemeinschaften ein Jahr nach der Aussetzung zu einer gleichartigen Struktur. Diese Ergebnisse unterstützen die Vorstellung, dass benthische Gemeinschaften nach

Störungsereignissen zu einer nahezu identischen Faunastruktur mit den selben Dominanten zurückkehren können. Sowohl Hart- wie auch Weichbodengemeinschaften zeigten eine hohe Fähigkeit, zur Struktur der natürlichen Gemeinschaften in der Umgebung zurückzufinden, was die Widerstandsfähigkeit des benthischen Systems gegenüber kleinskaligen Störungen hervorhebt. Zudem deuteten neue Artenfunde in beiden Untersuchungsgebieten darauf hin, dass die einzelnen Komponenten und deren potentielle Rolle bei der Besiedlung detailliert erforscht werden muss, um den Artenumschlag während der Sukzession zu verstehen. Die Ergebnisse der vorliegenden Untersuchung zeigen, dass benthische Gemeinschaften in Nordchile eine hohe Resistenz gegenüber kleinskaligen Störungen während kalter Bedingungen aufweisen, wobei Hartböden im Vergleich zur in Weichböden beobachteten relativ schnellen Erholung langsamer reagieren. Die in Zukunft zu klärende Frage ist, ob diese Widerstandsfähigkeit auch während starker El Niño-Ereignisse gilt oder nicht. Es empfiehlt sich daher, die zeitliche und räumliche Skala dieser Art von Experimenten auszudehnen, um nicht nur die Resistenz und Sukzessionsentwicklung zu verstehen, sondern auch andere Stabilitäts-Eigenschaften des Ökosystems, wie Persistenz und Elastizität.

## Resumen

La sucesión comunitaria es el proceso del cambio secuencial de la composición de especies a través del tiempo que ocurre después de que un lugar ha sido perturbado o cuando un hábitat prístino aparece. Es uno de los procesos claves en la modulación de los patrones de diversidad, estructura e historia evolutiva del paisaje bentónico. En este estudio he examinado, a través de experimentos de campo, el desarrollo sucesional de organismos submareales de fondos duros y blandos del norte de Chile. El sistema de la Corriente de Humboldt del norte de Chile es un excelente laboratorio natural para estudiar sucesión debido a la presencia de varias perturbaciones operando a diferentes escalas incluyendo las que están asociadas al ciclo ENSO (El Niño Oscilación del Sur) y que conllevan consecuencias drásticas en los patrones de biodiversidad. Los objetivos específicos fueron (i) describir el desarrollo sucesional de comunidades submareales de fondos duros y blandos por un periodo de 27 meses y dos años respectivamente, (ii) estimar el tiempo necesario en que las comunidades en desarrollo reensamblan las comunidades naturales circundantes (iii) evaluar el efecto de la estacionalidad en el punto de partida de la sucesión comunitaria por un periodo de un año de desarrollo. La sucesión en hábitats de fondos duros mostró cambios progresivos en la estructura comunitaria identificándose a la competencia por el espacio como el factor más importante durante el proceso. Después de 27 meses, las comunidades en desarrollo presentaron las mismas especies como la comunidad natural pero aun no reensamblaron totalmente al entorno. La estacionalidad tuvo un efecto en el asentamiento exitoso de las especies pero los estadios finales de la sucesión fueron influenciados por la competencia inter-especifica por el espacio (i.e. competencia jerárquica). La sucesión siguió un patrón determinista pero no rígido, en el cual especies suspensívoros y coloniales dominaron jerárquicamente sobre las especies solitarias. La dominancia de suspensívoros parece ser favorecida por los altos niveles de producción primaria asociados a la surgencia. Adicionalmente, en las superficies ocultas de los sustratos duros, las especies tempranas de la sucesión sobreviven mejor para luego expandirse lateralmente sobre las superficies expuestas debido a que las interacciones por el espacio entre especies se aminoran en los hábitats ocultos.

La sucesión en hábitats de fondos blandos siguió el modelo de "sucesión tolerante" en donde organismos que son componentes usuales de los estadios tardíos de la sucesión colonizan al mismo tiempo junto con especies normalmente asociadas a los estadios tempranos del proceso. Después de diez y ocho meses ocurrió semejanza a las comunidades del sedimento naturales. La estacionalidad no tuvo un efecto evidente en la comunidad resultante y todas las comunidades convergieron en una composición similar después de un año de exposición empezando en las diferentes estaciones del año. Estos resultados apoyan la noción de que las comunidades bénticas pueden retornar a casi una idéntica estructura faunística con los mismos organismos dominantes después de eventos

de disturbio. Ambos tipos de comunidades mostraron una gran capacidad de retornar y converger a la estructura de las comunidades naturales circundantes, lo cual resalta la capacidad de resistencia del sistema bentónico ante perturbaciones de pequeña escala. El descubrimiento de nuevas especies en ambos lugares de estudio sugiere que los componentes y su rol colonizador necesitan ser evaluado para un mejor entendimiento del recambio de las especies durante la sucesión. Este trabajo ha demostrado que las comunidades bénticas del norte de Chile presentan una alta capacidad de resistencia frente a disturbios de pequeña escala durante condiciones frías del sistema, con los fondos duros respondiendo mas lentamente comparado con la rápida recuperación detectada en los fondos blandos. La pregunta que debe resolverse en el futuro es si esta misma capacidad es también válida durante los eventos El Niño fuertes. Por lo tanto se recomienda aumentar la escala temporal y espacial de este tipo de experimentos, no solo para el entendimiento de la resistencia y sucesión sin no también las otras propiedades de estabilidad del ecosistema como la persistencia y elasticidad.

<b>List of Figures</b>	<b>Pag</b>
<b>Fig. 1</b> Conceptual models of community succession in benthic habitats. (a) Deterministic model, in which the initial stage is known (thus predictable) and the processes lead to a particular end point (i.e. “climax community”) (e.g. Pearson and Rosenberg 1978; Rhoads and Germano, 1988; Lenihan and Micheli, 2001). (b) Certainty in the start of the succession but different and unpredictable end points may exist (e.g. multiple stable states; Sutherland and Karlson, 1977; Osman, 1977; Sutherland, 1981). (c) Unpredictable start points (i.e. the magnitude of a disturbance) where the end points are different only from a small range of possibilities, and those are predictable (e.g. divergent succession (Petraitis and Latham, 1991; Petraitis and Dudgeon, 2004, 2005; Underwood and Chapman 2006).	2
<b>Fig. 2</b> Synthesis of the three models of mechanisms producing the sequence of species in succession (adapted from Connell and Slatyer 1977)	5
<b>Fig. 3</b> The multivariate ENSO index from 1959-2007 showing the fluctuations among the cold and coldest LN periods and warm EN events.	7
<b>Fig. 4</b> Study area showing the specific locations of the succession experiments. The main upwelling centres are marked with grey shading	14
<b>Fig. 5</b> Installed polyethylene panel used for the hard-bottom succession experiment at 17 m depth of Anemones Wall (Península Mejillones, northern Chile)	15
<b>Fig. 6</b> View of the photographic device and technique employed to sample natural hard-bottom communities used as controls (Photo by Christian Guerra).	15
<b>Fig. 7</b> Installed container used for the soft-bottom succession experiment (Photo by Christian Guerra).	17
<b>Fig. 8</b> Air-lift sampling system used in the soft-bottom succession experiment (Photo by Jürgen Laudien).	17
<b>Fig. 9</b> Left row, view of the panels with respective epibenthic community from each sampling date. The yellow numbers indicate the number of sampling months. The right row is a view of the surrounding community taken at the respective sampling date.	94
<b>Fig. 10</b> Summary of important processes modulating the successional development of hard-bottom communities	99

### 1 Introduction

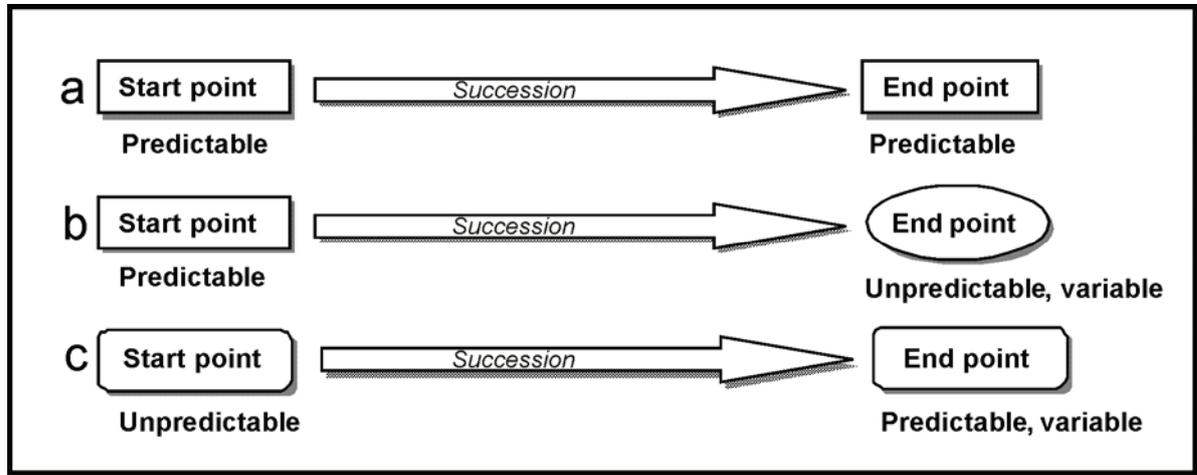
#### 1.1 Succession of benthic communities

Ecological succession consists of the sequence of changes in community structure that occurs after a site has been disturbed or after the appearance of a pristine habitat (Berlow, 1997). Generally, succession is described as sequence of colonization and extinction events after a substratum becomes available for colonization, developing from a starting point towards an end point which resembles the undisturbed natural community. Overall, the sequence is mediated by biological interactions (i.e. inhibition, facilitation and tolerance, Connell and Slatyer, 1977) among early, middle and late colonizing species. Although such a directional sequence may occasionally be observed, ecologists are usually faced with a more complex and dynamic phenomenon because several factors can strongly influence the process (Berlow, 1997). Succession depends on the severity of the disturbance (i.e. total or partial biota removal, Pearson and Rosenberg, 1978; Sousa, 2001; Gutt and Starmans, 2001; Valdivia et al., 2005), the size of the patch to be colonized (e.g. Petraitis and Latham, 1999; Petraitis and Dudgeon, 2004), the seasonal variation in the supply of colonizers (e.g. Morgan, 2001) and the coupling with disturbance events (e.g. Cifuentes et al., 2006; Sugden et al., 2007). Moreover the biological interactions, particularly those that account for the dynamics of space occupancy (i.e. predation, competence, Vance, 1988; Siddon and Witman, 2004) and biological traits (e.g. larval development and type of growth, Sousa, 1980; Dean and Hurd, 1980), modulate succession. When operating simultaneously, the factors can simplify or complicate community response to disturbance. Consequently, successional sequences are complex and have variable sequences, but show some repeated patterns (Underwood and Chapman, 2006).

Several types of successional sequences, resulting in different degrees of predictability from a start point to an end point, have been reported (Fig. 1). To understand succession in the marine benthic realm, a close examination of particular communities within a particular ecosystem is required. The knowledge of the causes of successional patterns can help us to understand the dynamics of community structure and the responses through recovery to

## Introduction

abiotic, biotic and human induced disturbances. The last one is particularly relevant as coastal marine landscapes are increasingly dominated by anthropogenic disturbance regimes.



**Figure 1** Conceptual models of community succession in benthic habitats. (a) Deterministic model, in which the initial stage is known (thus predictable) and the process leads to a particular end point (i.e. “climax community”) (e.g. Pearson and Rosenberg 1978; Rhoads and Germano, 1988; Lenihan and Micheli, 2001). (b) Certainty in the start of the succession, but variable and unpredictable end points can result (e.g. multiple stable states; Sutherland and Karlson, 1977; Osman, 1977; Sutherland, 1981). (c) Unpredictable start points (i.e. the magnitude of a disturbance), where the end points are different only from a small range of possibilities and those are predictable i.e. divergent succession (e.g. Petraitis and Latham, 1991; Petraitis and Dudgeon, 2004, 2005; Underwood and Chapman 2006).

### 1.2 Succession on hard-bottom epibenthic communities

Inter- and subtidal rocky bottoms are initially colonized by a suite of competitively subordinate sessile invertebrates and algae followed by middle colonizers (Publication I and II). The dynamics between early and middle successional stages are highly complex depending on pulses of recruitment, physical disturbances and predation (e.g. Dayton, 1971; Paine, 1974; Berlow and Navarrete, 1997; Vance, 1988; Osman and Whitlatch, 2004). The late successional species usually are competitively superior, capable in monopolizing space in absence of disturbances (e.g. Paine and Suchanek, 1983; Bullard et al., 2004). The sequence also includes changes from small bodied organisms to large species.

## Introduction

---

Moreover, in subtidal benthic habitats early and middle successional species can be either solitary or colonial forms, but later colonizers are likely to be colonial species, which are able to overgrow and cover subordinate species (e.g. Jackson, 1977; Witman and Dayton, 2001; Dayton, 2003; Teixidó et al., 2002, 2007).

The most remarkable feature of community succession on hard bottoms is the presence of several and variable outcomes. Here, succession can lead to multiple end points (i.e. multiple stable states, Sutherland and Karlson, 1977; Osman, 1977; Sutherland, 1981), divergent or convergent end points (i.e. alternative states, Petraitis and Latham, 1991; Petraitis and Dudgeon, 2004, 2005) but also to a deterministic, thus directional end point. However, the multiple stable states theory was formulated on the dynamics of developing fouling communities, which do not necessarily reflect the situation of natural benthos communities. In fouling communities the supply of colonizers in the water column can substantially differ to those arriving on the bottom. The alternative states described in several studies by Petraitis and Dugdeon (2004, 2005) depend on the patch size to be colonized: large patches of clean areas can switch from kelp stands to mussel beds. The present study did not approach the effect of area size on community development but recovery through succession at small spatial scale disturbance was predicted to be deterministic (Publication I).

The duration of the successional sequence is variable and seems to be system specific, but in temperate zones it can last between 2 and 8 years (see discussion in Publication I). Nonetheless, it is difficult to determine whether or not communities eventually reach a stable final state (i.e. mature or climax). In shallow hard-bottom communities of the Humboldt Current System from northern Chile, stability is very difficult to assert because of the strong changes produced by the extremes of the ENSO cycle (see chapter 1.4). To avoid controversy and discussion about stability (see e.g. Scheffer and Carpenter, 2003) this study focused on a comparison between communities in succession (on artificial substrata) with natural surrounding references resembling advanced states of successional development.

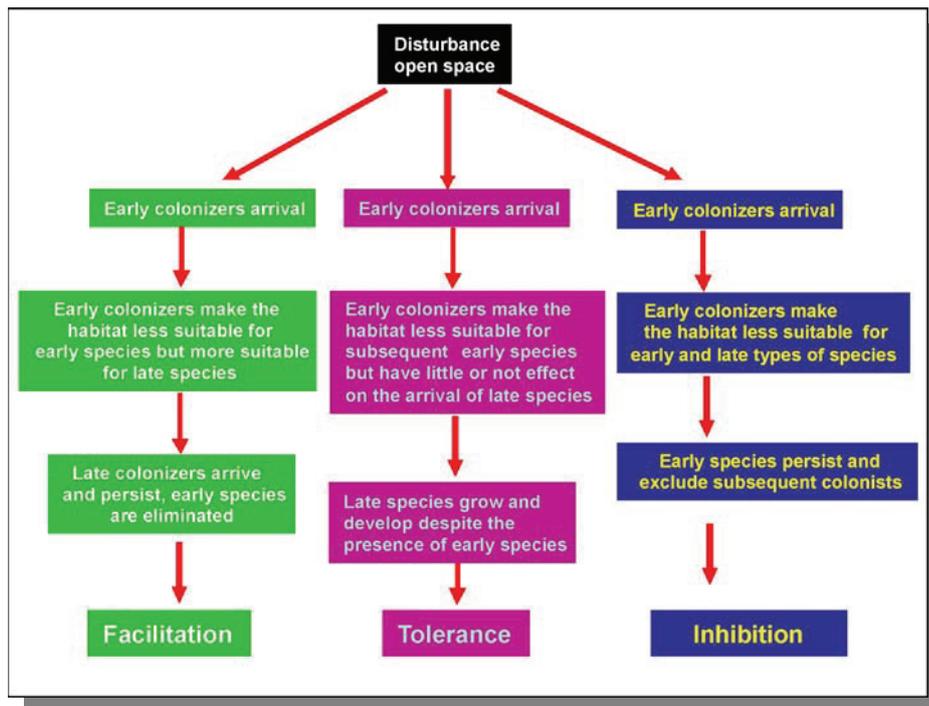
### 1.3 Succession in soft-bottom macrobenthic communities

Successional colonization of soft bottom sediments is generally described to start with the arrival of early colonizers, which are usually species with opportunistic life history traits (e.g. spionid polychaetes, Arntz and Rumohr 1982, 1986; Diaz-Castaneda et al., 1989; Lu and Wu, 2000; Lenihan and Michelli, 2001). These species are adapted to utilize the newly available resources quicker than their competitors (Guerra-García and García-Gomez, 2006, Lu and Wu, 2000, 2007). The dominance of these opportunistic species at the initial successional stage is usually followed by severe mortality by predation or displaced by middle species, which outcompete the pioneers for space and food (Rosenberg, 2001; Norkko et al., 2006). Finally, late colonizers are mainly components from the undisturbed surrounding habitat (Rhoads and Germano, 1988; Lenihan and Micheli, 2001). This sequential pattern is in line with the predictions of the “facilitation and inhibition” models of succession (Connell and Slatyer, 1977, Fig. 2). However, few examples have suggested a pattern close to the “tolerance” model of succession, where colonizers with either early or late characteristics are able to simultaneously colonize a new patch of sediment (Santos and Bloom, 1980, 1983), thus a gradual sequence of composition changes during the successional development is not evident (Publication III, Zajac et al., 1998; Zajac and Whitlatch 2003). Hence, before any attempt of generalization about the process close examination is necessary.

Disturbed sediments can be colonized following two main processes: (i) large areas are more likely to be colonized through larvae settlement (Santos and Simon, 1980; Woodin, 1991) while (ii) small patches can be quickly colonized by juveniles or adults crawling, drifting and swimming from the adjacent area (Armonies, 1994; Cummings et al., 1995; Norkko et al., 2006). However, both processes can also operate simultaneously depending on the pool of larvae available. The process is not only spatial scale dependent but also temporal with a strong seasonal component. Several studies have demonstrated that the trajectory of succession is influenced by the seasonal onset of the disturbance (e.g. Arntz and Rumohr, 1982; Díaz-Castañeda et al., 1989; Lu and Wu, 2007). In addition, the

## Introduction

availability of early colonizers (larvae) is strongly dependent on the season and can conduct to variable onset in the succession (Díaz-Castañeda et al., 1989). Regardless of these sources of variability, the process seems to be directional (thus deterministic), and despite several distinct starting points, a trend towards the resemblance of surrounding communities is often reported (Pearson and Rosenberg, 1978; Roads and Germano, 1986; Díaz-Castañeda et al., 1989; Rosenberg, 2001).



**Figure 2** Synthesis of the three models of mechanisms producing the sequence of species in succession (adapted from Connell and Slatyer 1977).

Succession and, in general, the dynamics of soft bottom macrobenthic communities along the coastal Humboldt Current System have been related to changes in the concentration of dissolved oxygen (Arntz, 1986; Arntz and Fahrback, 1996; Arntz et al., 2006; Tarazona et al., 1988a,b, 1996; Thiel et al., 2007). For example, communities under hypoxia are associated with early successional states with low diversity and high abundance of opportunistic components (e.g. spionid polychaetes) (Arntz et al., 2006). During El Niño events, oxygen concentration is enhanced and species diversity and evenness increase (Arntz, 1986; Tarazona et al., 1988a,b, 1996; Gutierrez et al., 2000; Arntz et al., 2006; Moreno et al., 2008), thus changing macrofaunal communities into a more advanced successional state. However, the succession of macrobenthos distributed in the shallowest

## Introduction

---

fringe between the lower intertidal limit and the upper limit of the oxygen minimum zone, may be related to other factors not necessarily linked to oxygen changes. In this habitat the deposition of important amounts of terrestrial sediments in coastal waters, although infrequently, are sources of new habitats (see also next chapter on the importance of succession in northern Chile). The action of large predators (e.g. large crabs and fishes) also disturbs soft sediment (Publication III). Other disturbances are related to the extraction of biomass by artisanal fishermen. For example, in central Peru suction pumps are used to extract *Ensis macha*, removing sediment (Zavala, unpublished data), impacting and influencing the distribution of communities and succession. However, little is known about this dynamic. This thesis focused on this habitat (at 14m depth) using a temporal controlled experiment designed to identify the mechanisms driving the successional processes (Publication III).

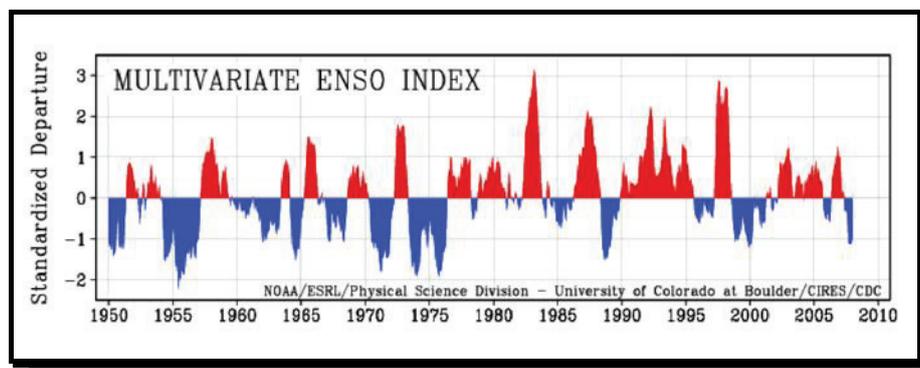
### 1.4 The Humboldt Current System off northern Chile

The northern coastal zone of Chile (18° to 25° S) forms part of one of the most productive Large Marine Ecosystems of the world: the Humboldt Current System (Wolff et al., 2003). This system is predominated by northward flow of surface water of subantarctic origin and by strong upwelling of cool nutrient rich subsurface waters of equatorial origin (Thiel et al., 2007). Upwelling is produced by a combination of trade winds, Coriolis force and Ekman transport, which brings cold and nutrient rich waters from moderate depths to the euphotic zone (Arntz et al., 2006). The resultant high primary production fuels a rich secondary production in the upper pelagic and nearshore zones, but also creates an oxygen minimum zone (OMZ) on the continental shelf and the upper slope (Arntz et al., 2006; Thiel et al., 2007). In northern Chile upwelling cells occur nearly continuously (aseasonally) during the annual cycle (see description for the Antofagasta zone by Escribano et al., 2002) and fuel rich benthic rocky and soft-bottom communities in shallow waters. As a consequence of the high productivity, several benthic organisms from inter- and subtidal habitats develop high abundances and biomasses, which are also subject to intensive artisanal fisheries. Although

## Introduction

---

there are attempts to understand the effects of target species extraction on the community dynamics (e.g. hard-bottom kelp species, e.g. Vásquez and Santelices, 1990; Vásquez, 1995; Ortiz, 2003; soft-bottom scallops e.g. Avendaño and Cantillán 1997), the overall patterns of diversity and the underlying structuring ecological factors are poorly known (Fernández et al., 2000). Benthic communities in this system are not only subject to anthropogenic disturbances such as fisheries, but also the periodical occurrence of El Niño (EN). The warm phase of ENSO (El Niño Southern Oscillation) strongly modifies oceanographic conditions and shallow benthic communities caused by, for example, local extinctions (mass mortalities of invertebrates and kelp beds; Camus, 1994; Martínez et al., 2003; Arntz, 1986; Arntz et al., 2006) or colonisation events (by sub tropical immigrants; Publication IV, Arntz, 1986; Arntz and Fahrback, 1996; Castilla et al., 2005). The magnitude and frequency of the impact of El Niño events are very variable (Fig. 3) and add more complexity to the dynamics of benthic communities (Arntz et al., 2006; Camus 2008). This variation at such long time scales in the system represents an interesting model to study ecological processes such as succession which intrinsically include time as independent variable.



**Figure 3** The multivariate ENSO index from 1959-2007 showing the fluctuations between cold and coldest LN periods and warm EN events (taken from NOAA-University of Colorado, Cooperative Institute for Research in Environmental Sciences (CIRES), Climate Diagnostics Center (CDC)).

### **1.5 The importance of understanding benthic succession in the coastal ecosystem off northern Chile**

In northern Chile, disturbances are recognized (e.g. Vásquez and Santelices, 1990; Vásquez, 1995), but recovery of subtidal epibenthic communities throughout succession has not been documented (see Thiel et al., 2007). During cold and coldest La Niña (LN) conditions disturbances usually occur on a much smaller spatial scale and at higher frequencies than storm-induced disturbances experienced during El Niño (EN). During EN, the combination of reduced nutrients concentrations, strong swell and high temperatures cause mass mortalities of shallow subtidal algae and invertebrates, leaving open primary substratum for recolonization (Arntz, 1986; Arntz and Fahrbach, 1996; Camus et al., 1994; Martinez et al., 2003; Vega et al., 2005; Vásquez et al., 2006). During LN phases, the system is characterized by high biological productivity (Escribano, 1998; Wieters et al., 2003), which is reflected in high growth rates of colonizing species. As a consequence there is a high potential for competitive exclusion between dominant and subordinate organisms (Navarrete and Castilla, 2003; Nielsen and Navarrete, 2004; Valdivia et al., 2005, Publications I and II). Thus, it was assumed that developing communities will quickly resemble the surrounding natural communities, characterized by only a few dominant species (Publications I and II).

In soft-bottom communities, EN events increase wave activity and freshwater runoff with huge loads of terrestrial sediments are frequent sources of disturbance (Arntz, 1986; Arntz and Fahrbach, 1996; Thiel et al., 2007; Thatje et al., 2008), thus creating new spaces in the soft sediment. These effects are likely to modulate the distribution of the communities in space and time, but at present, this topic has not yet been addressed in the well oxygenized part (for the upper OMZ limit see Tarazona et al., 1988a,b, 1996). During cold and coldest LN events, the high level of biological productivity (Escribano, 1998; Wieters et al., 2003) provides a huge supply of organic matter from the upper water layers to the bottom causing oxygen depletion even in very shallow areas such as coastal bays (Escribano and Hidalgo, 2001). Disturbance by input of terrestrial material as well as strong storms are less common

## Introduction

---

during LN periods but, when occurring it can be extremely intense (Thiel et al., 2007). As previously mentioned, small scale biotic disturbance (e.g. predation by fishes and crabs) is thought to be of more relevance (Van Blaricom, 1982; Sousa, 2001), but there is little local evidence about the effects of this type of perturbation in the successional development. Overall in northern Chile there are few studies with relatively limited extension of short and variable duration about soft bottom community dynamics (Laudien et al., 2007b, Carrasco and Moreno, 2007, see review in Thiel et al., 2007).

Even though disturbances occur at different stages along the ENSO, it is more interesting and important to understand community changes in the long term context. The ENSO is not a temporally discrete influence, and its effects do not simply vanish at the end of each event, since such effects are recurrent forces that may generate feedbacks in the structure of a natural system (Camus, 2008; Publication IV). In northern Chile the ENSO has been recorded since the Holocene suggesting that communities evolved and were shaped by the impacts of EN events (Ortlieb et al., 2000; Camus, 2001). Community succession is predicted from the basis of observations on colonization and extinction of species (i.e. species richness turn over). Compositional changes are likely to occur during EN events, but the question would be whether EN can modify the background level of species turnover. Such understanding can only be provided on the basis of understanding turnover rates operating during non-EN periods (Camus, 2008). These approaches are only reliable having detailed knowledge of the structure, dynamics and variability of the study system during non-EN periods.

### **1.6 The effects of seasonality on benthic community development**

As previously stressed a suite of ecological factors are important in community development, but a particular issue in the analyses of successional processes is that experimental studies often confound natural seasonal variability with the time-course of the community development (Osman, 1977, 1978; Arntz and Rumohr 1982, 1986; Underwood and Chapman, 2006). Succession can only be identified when some consistent pattern of

## Introduction

---

temporal change in the composition or relative abundance of species can be observed (Platt and Connell, 2003; Hill et al., 2004). Therefore, community structure must be analyzed at different time intervals along the colonization process, which allows a distinction between the course of the successional development and natural variability (Chapman, 2002). Likewise, effects of different starting points throughout the year must be evaluated in order to disentangle temporal coupling of recruitment events and true successional processes (e.g. Cifuentes et al., 2007; Sugden et al., 2007).

### 1.7 Comparison between hard and soft bottom succession

The bulk of knowledge on benthic ecology is provided by testing hypothesis on either hard- or soft-bottom habitats but rarely evaluating both systems simultaneously (e.g. Thiel and Ullrich 2002, Danovaro and Franschetti 2002). Both habitats differ in several aspects: hard-bottom substrata are characterised by a high substratum complexity, largely comprising habitat-forming sessile organisms (bioengineers), whereas structural complexity of soft bottoms is generally accounted by measures of substratum itself (i.e. sediment texture). In soft sediment, species generally use a three-dimensional habitat, being able to thrive over the superficial layer and bury into the sediment at different depth levels. In hard-bottom habitats, the primary substratum to inhabit is the rock surface. Although species use cavities, crevices and refuges (Publication II) they do only occasionally thrive inside the substratum (e.g. species of the genus *Lithophaga* sp., boring sponges). Thus, strong differences in competitive interactions occur between the two systems. Whereas in intertidal rocky systems dominant competitive organisms exclude subordinate species, in soft sediments competitive interaction has density-dependent effects among populations but generally without exclusion. The resource "space" in sediment habitats overall neither seems to be limited as in the case of hard bottoms nor is the competition as harsh as it usually is on hard bottoms (Gallagher et al., 1990; Lenihan and Micheli, 2001; Witman and Dayton 2001).

## Introduction

---

The wide range of feeding strategies related to soft sediment (e.g. interface feeders, surface deposit feeders and subsurface deposit feeders) is notorious. Several trophic groups use directly or indirectly the organic material deposited on or in the sediment as a food resource. Moreover, through bioturbation using the species' biological capacity to alter the physical and chemical composition of the sediment by their physical and metabolic activities, the fauna strongly modulates the small scale characteristics of the habitat thus modifying community structure. Hard-bottom fauna rarely uses the rock as indirect resource of food. The sessile and motile species generally use the rock surface either as substratum for attachment, displacement or refuge. The spatial configuration is often very variable between systems. Almost all soft-bottom habitats are plain and horizontal with low variations on the inclination. Hard-bottom habitats can be angled covering a large range from horizontal plains, vertical steep walls (Publication I, II, V) to overhangs and cave roofs. This configuration is determinant in the establishment of benthic communities (reviewed by Witman and Dayton, 2001). In both types of habitats, bioengineering species provide habitat to a very diverse and abundant macrofauna (e.g. mussel beds, kelp macroalgae), but functionality of the communities can be different (Thiel and Ulrich 2002). Despite these differences, benthic communities in both systems shared common processes. Successional development from early to late species has been reported for both communities explainable by common factors operating in the supply of colonizers. Larvae and propagules of organisms are transported by similar oceanographic processes operating in both habitats. Surprisingly though, few attempts have been made in comparing processes in benthic communities from hard and soft bottoms. Based on results of individual investigations on community development in hard- (Publication I and II) and soft-bottoms (Publication III) of the same geographical area propose community succession as a good model to highlight generalities and differences of a common ecological phenomenon. A conceptual comparison is approached in the Discussion section.

### **1.8 Aims of this study**

This study aims to understand the ecological succession and the effect of the seasonal onset of the colonization process of benthic communities from hard- and soft-bottom sublittoral habitats off northern Chile.

#### **1.8.1 Hypotheses**

- (i) Community succession is predicted to progress through sequential changes in community composition approaching a resemblance of the natural surrounding communities over time.
- (ii) Communities starting succession at different seasons of the year differ in composition after one year of development.

#### **1.8.2 Specific objectives of this study are**

- (i) To describe the successional development of a subtidal hard-bottom community over a 27 months period.
- (ii) To describe the successional development of a subtidal soft-bottom community over a two years period.
- (iii) To estimate the time necessary for the developing communities to resemble the surrounding natural community.
- (iv) To evaluate the effect of the seasonal starting point of the community succession over a one year period of development.
- (v) To compare and distinguish the mechanisms operating on hard- and soft-bottom community succession.

### 2 Study sites

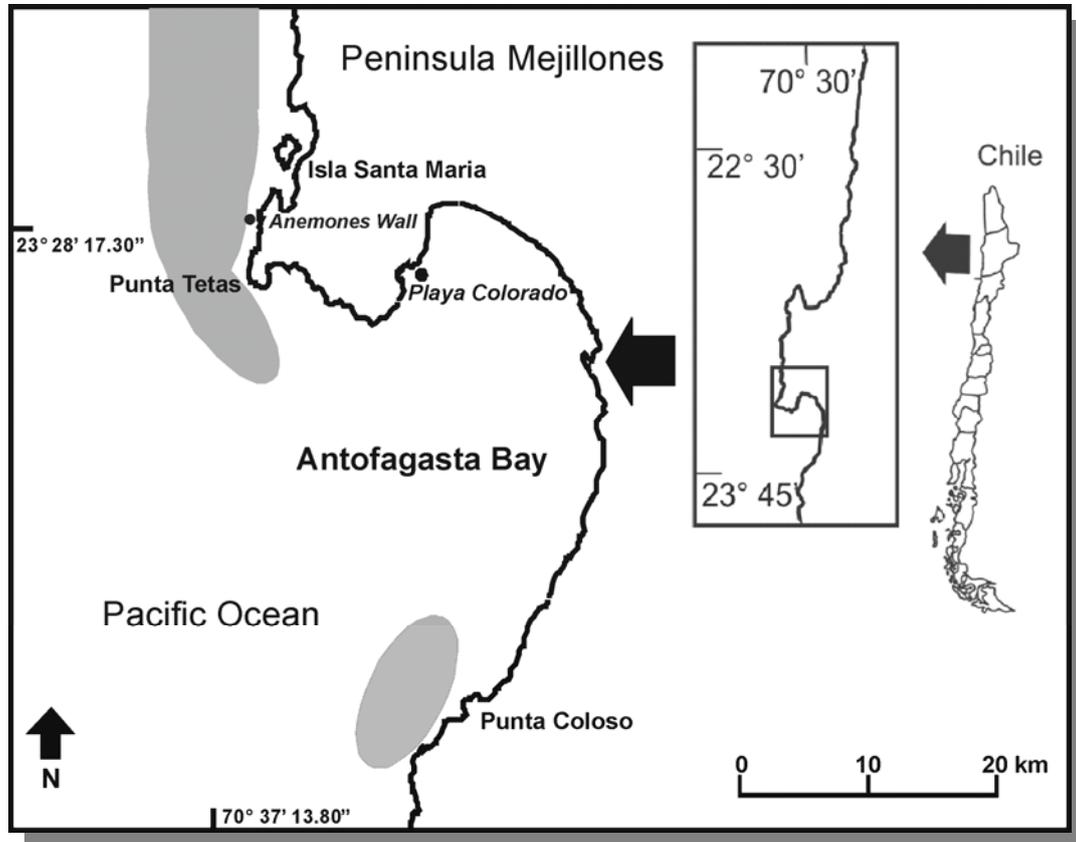
The hard-bottom succession experiment was conducted between January 2006 and April 2008 at Anemones Wall (23°28'S, 70°37'W; Fig. 4, Publication II, III and IV). The soft-bottom succession experiment was conducted between June 2006 and June 2008 at Playa Colorado (23° 30'S, 70° 31'W Fig. 4) (Publication I and V). Both locations are situated at Peninsula Mejillones (Fig. 4). Further information about Anemones Wall is available in Publication II, III and IV, and about Playa Colorado in Publication I and V.

In northern Chile, coastal upwelling produced by the combination of trade winds, Coriolis force and Eckman transport, brings cold, nutrient rich waters from moderate depth to the euphotic zone (Escribano et al., 2002, 2004; Arntz et al., 2006). This promotes high primary production, reflected in high secondary production of the nearshore zone. Upwelling occurs year-round with a maximum and minimum intensity in October and January, respectively (e.g. Marín et al., 2001; Escribano et al., 2002). The upwelling results in cooling of the sea surface temperature, which ranges from 14 to 20°C, even during strong EN events (Vega et al., 2005). A detailed description of the physical oceanography of Peninsula Mejillones was presented by Escribano et al. (2002, 2004). Following the almost straight coast line of Chile from the northern tip towards the south, Peninsula Mejillones seems to disrupt the coast projecting a small part of the continent towards the open sea creating different habitats. Three main areas can be distinguished; Bahía Mejillones at the north tip of the Peninsula, the coastal line and Bahía Antofagasta at the southern part of the Peninsula (Fig. 4). The exposed side of Peninsula Mejillones is thought to be the most productive area off northern Chile.

Playa Colorado is located at the inside part of Bahía Antofagasta. The oceanographic characteristics of this bay are particular because it is the only southwardly oriented bay of northern Chile. Moreover, it is located between two active upwelling centres (Fig. 4). This creates an “upwelling shadow” with an almost constant sea water temperature front crossing the mouth. Thus, upwelled waters are retained inside the bay long enough for temperatures to be elevated by several degrees through surface heating. The bay therefore

## Study sites

exhibits surface temperatures between 2° and 4° C higher than the surrounding waters. Further descriptions of the oceanographic processes of this bay can be found in Escribano and Hidalgo 2001; Castilla et al. 2002; Piñones et al. 2007.

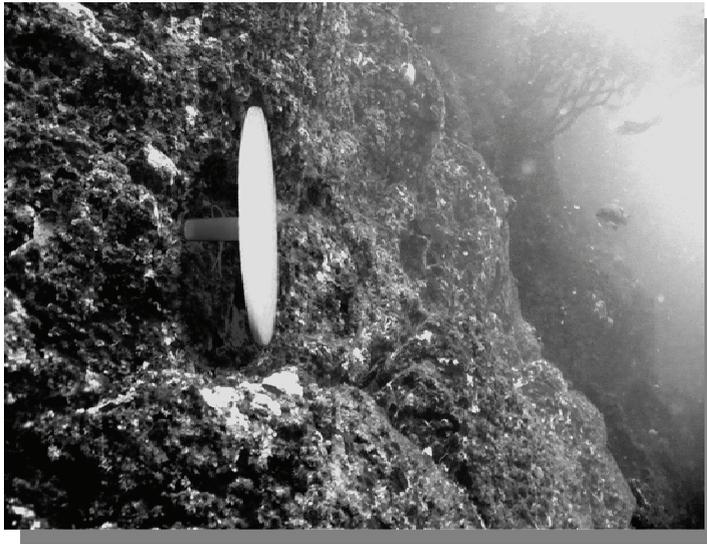


**Figure 4** Study area showing the specific locations of the succession experiments. The main upwelling centres are marked with grey shading.

### 3 Materials and Methods

#### 3.1 *In situ* succession experiment in a hard-bottom subtidal habitat

In order to describe the successional development of subtidal hard-bottom communities and to estimate the time necessary for the developing communities to resemble the surrounding natural community, an experiment using artificial substratum was conducted at Anemones Wall from January 2006 and ending in March 2008. In total, 48 circular polyethylene panels were installed in a horizontal line at 17m depth at a rocky subtidal wall (Fig. 5).



**Figure 5** Installed polyethylene panel used for the hard-bottom succession experiment at 17 m depth of Anemones Wall (Península Mejillones, northern Chile).

Three panels were collected and sampled every three months over a period of 27 months. As a control, the surrounding natural community was surveyed during the same time interval (i.e. every three months) by photographing six haphazardly selected areas (Fig 6).



**Figure 6** View of the photographic device and technique employed to sample natural control hard bottom communities (Photo by Christian Guerra).

## Materials and Methods

---

Organisms from panels, as well as from photographs, were identified to the lowest taxonomic level possible using relevant literature and the assistance of experts. Percentage cover of epibenthic organisms was compared using multivariate analysis and is detailed below (see statistical analysis section page 17). Comparisons were based on data of sessile species, which mainly use primary substratum for attachment, therefore, small motile organisms were excluded from the analysis in order to avoid problems of comparisons of species from different size spectra. Details, experimental set-up and biota quantification are presented in Publication I (page 27-30) and II (page 51).

The experimental set-up was also designed to evaluate the effect of the seasonal starting point on the community succession over a one-year period of development. The assumptions of this experiment were that seasonality may produce: (1) no effect, thus converging to the same structure, (2) slight differences in composition between treatments (e.g. differences in composition accounted for by a single species), or (3) may follow a stochastic pattern (substantially different species richness and composition, thus strong differences between treatments and replicates). Further panels were exposed for a 12 month period of colonization, starting in four different seasons. For each season three panels were collected, percentage of epibenthic species recorded and analyzed accordingly (see sampling scheme in Publication III, page 29).

### **3.2 *In situ* succession experiment in a soft-bottom subtidal habitat**

Similarly an experiment using artificial soft-bottom substratum was conducted at Playa Colorado from June 2006 to June 2008, aiming to describe the successional development of subtidal soft-bottom communities and to estimate the time necessary for the developing communities to resemble the surrounding natural undisturbed ones. In total, 37 containers were installed at the bottom at 14m depth in Playa Colorado (Fig. 7). Three containers were sampled every three months during a two year period using an air-lift device to extract the sediment inside a core (15cm diameter) previously buried 10cm into the experimental container (Fig. 8). As a reference, the surrounding natural community was surveyed at the

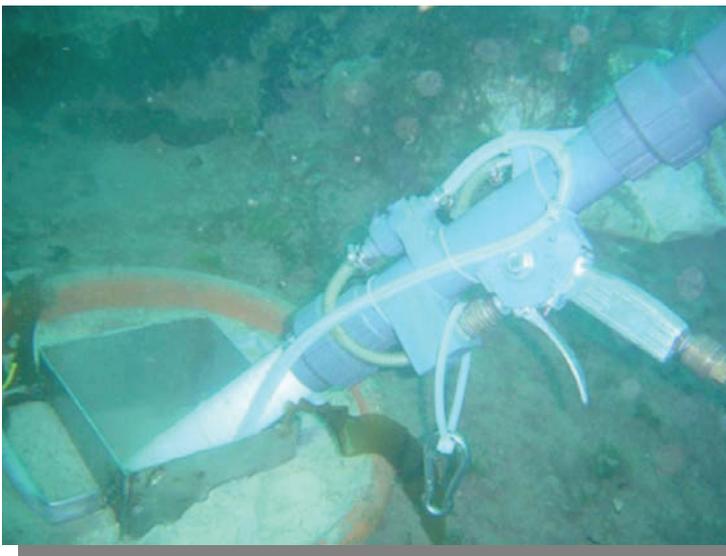
## Materials and Methods

---

same time by sampling four haphazardly selected areas per replicate. Organisms were sieved with a 0.5µm mesh, fixed and preserved in the field. Thereafter, samples were transported to the laboratory where they were identified to the lowest taxonomic level possible using relevant literature (see Publication III, page 67 for details) and the assistance of experts. Data of macrobenthos abundance were analyzed using uni/multivariate analyses which are further explained below (see statistical analysis). Details about the experiment and biota quantification are presented in Publication V pages 74-76.



**Figure 7.** Installed container used for the soft-bottom succession experiment (Photo by Christian Guerra).



**Figure 8.** Air-lift sampling system used in the soft-bottom succession experiment (Photo by Jürgen Laudien).

## Materials and Methods

---

Similar to the hard-bottom experiment, the set-up for the soft bottom was also designed to evaluate the effect of the seasonal starting point on community succession over a one-year period of development. The hypotheses of this experiment were that seasonality would produce: (1) no effect, thus converging to the same structure, (2) slight differences in composition between treatments (e.g. differences in composition accounted for by a single species), or (3) strong differences following a stochastic pattern (substantially different species richness and composition, thus strong dissimilarity between treatments and replicates). Further containers were exposed for a 12 month period of colonization, starting in four different seasons. Per season three containers were collected, macrobenthos abundance recorded and analyzed (see Publication III).

### 3.3 Statistical analysis

In both hard- and soft- bottom experiments, abundance data of taxa for each sampling date, as well as seasonal intervals, were explored and visualized with non-metric multidimensional scaling (nmMDS) ordination plots from a Bray-Curtis similarity matrix calculated after square root transformation. Differences within treatments were tested with one-way analysis of similarity ANOSIM. If R was significant, pair-wise comparisons were conducted to identify treatments responsible for the observed difference. However, the interpretation of the pair-wise comparison was based on R-values as just three replicates for each time interval allowed to only set up a significant level of  $p = 0.1$ . This is totally justified as long as the R-value for the initial ANOSIM test is significant. In addition, nmMDS plots calculated using Euclidian distance from R values of the pair-wise comparison were made in order to obtain visual representation dissimilarities between groups (Publication II and III). The seriation with replication routine implemented in the RELATE analysis was conducted in order to test whether or not succession in hard- and soft-bottom habitats followed a seriation trend, i.e. a consecutive sequence during time. Bray-Curtis and Euclidian distance matrix, nmMDS ordination plots, ANOSIM, RELATE analysis were performed using the PRIMER v6

## Materials and Methods

---

(Plymouth Routines in Multivariate Ecological Research) software package (Clarke and Gorley, 2006).

In the soft-bottom succession experiment differences in species richness, abundance and biomass (wet mass) for between sampling dates and seasonal time intervals were calculated using a two-way analysis of variance (ANOVA). The assumptions of data normality were explored using the Anderson-Darling test (Anderson and Darling, 1952). Data were square root transformed to obtain data normality when it was necessary. When ANOVA detected statistical differences *a posteriori* Tukey test was conducted to evaluate the treatments accounting for the differences. Univariate analyses were conducted using MINITAB Release 14 Statistical software for Windows.

### 4 Results

#### 4.1 Publications

This thesis includes five publications listed below. My contribution to each study is explained.

##### Publication I

Pacheco, A., Laudien, J., Thiel, M., Oliva, M., Heilmayer, O. Early succession and the effects of the seasonal variation in a subtidal epibenthic community off northern Chile. *Marine Ecology Submitted.*

I developed the scientific idea together with the second author. I conducted the field experiment, sampling and sample processing, data analysis and manuscript writing. The final version of the manuscript was achieved considering the comments and recommendations of all co-authors.

##### Publication II

Pacheco, A., Laudien, J., Thiel, M., Heilmayer, O., Oliva, M. 2009. Hard bottom succession of subtidal epibenthic communities colonizing hidden and exposed surfaces off northern Chile. *Scientia Marina. In press*

I developed the scientific idea of this study. I conducted the field experiment, sampling and sample processing, data analysis and manuscript writing. The final version of the article was improved considering the comments of all co-authors.

##### Publication III

Pacheco, A., Laudien, J., Thiel, M., Oliva, M., Arntz, W. Succession and seasonal variation in the development of a subtidal macrobenthic soft-bottom community from northern Chile. *Journal of Sea Research. Submitted*

I developed the scientific idea together with the second author. I conducted the field experiment, sampling and sample processing, data analysis and manuscript writing. The final version of the article was improved considering the comments of all co-authors.

## Results

---

### **Publication IV**

Asthor, T., Riascos, J., Pacheco, A. 2008. First record of *Cymatium keenae* Beu, 1970 (Mollusca: Ranellidae) from Antofagasta Bay, northern Chile, in connection with El Niño events. Helgoland Marine Research 62 (Suppl 1) 107-110.

All authors contributed equally to in this publication.

### **Publication V**

Pacheco, A., Laudien J. 2008. *Dendropoma mejillonensis* sp. nov. a new species of vermetid (Caenogastropoda) from northern Chile (southeastern Pacific). The Veliger 50(3): 219-224.

I conducted the sampling, did the taxonomic work and wrote the manuscript. The final version was achieved considering the revision of the second author.

### 4.1.1 Publication I<sup>^</sup>

#### Succession and seasonal variation in the development of sublittoral epibenthic hard-bottom communities off northern Chile

Aldo S. Pacheco<sup>a,b\*</sup>, Jürgen Laudien<sup>a</sup>, Martin Thiel<sup>c,d</sup>, Marcelo Oliva<sup>b</sup>, Olaf Heilmayer<sup>a,e</sup>

<sup>a</sup>Alfred Wegener Institute for Polar and Marine Research, D-27568 Bremerhaven, Germany. <sup>b</sup>Facultad de Recursos del Mar, Universidad de Antofagasta, P.O. Box 170, Av. Angamos 601, Antofagasta, Chile. <sup>c</sup>Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile. <sup>d</sup>Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile. <sup>e</sup>National Oceanography Centre, Southampton, European Way, SO14 3ZH, Southampton, UK.

**Short running title:** Succession of sublittoral epibenthos off northern Chile

#### Abstract

Succession is an important process modulating the recovery of communities after disturbance. Despite frequent disturbance events caused by El Niño, little is known about the community succession in sublittoral hard bottoms along the Humboldt Current Ecosystem. A field experiment using artificial hard substrata was conducted in a rocky subtidal area off northern Chile and followed at three-month intervals to describe the course and drivers of community succession. The specific aims were (1) to describe successional development in a subtidal hard bottom community over a 27-month period, (2) to estimate the time necessary for developing communities to resemble the surrounding natural community, and (3) to evaluate the effect of the seasonal starting point on community succession over a one-year period of development. Panels were installed on a vertical wall at 17 m depth. Three replicate panels were collected every three months over a period of 27 months. As a reference, the surrounding natural community was surveyed at the same interval by photographing six haphazard areas. In addition, further panels were exposed for a 12-month period, starting in four different seasons. Community succession occurred through progressive changes in which competition for space was identified as the most important factor modulating the processes. After 27 months, the developing communities contained the same species as adjacent communities but did not yet fully converge to the natural community. Seasonality had an effect on successful species settlement, but the final stages of succession were influenced by hierarchical competition for space. This study indicates that succession of epibenthic communities follows a non-rigid, but deterministic pattern, in which colonial suspension-feeding species are hierarchically dominant to solitary species. This dominance of suspension feeders appears to be favored by high levels of primary production associated with upwelling.

**Key words:** Colonization; Epibenthos; Subtidal; Recruitment; Temporal variability, ENSO

---

<sup>^</sup> This is the author's version of a work submitted to Marine Ecology

### **Problem**

Succession describes the process of gradual change in a developing community over time, usually after a disturbance has removed biomass and/or created vacant habitats (Morin 1999; Sousa 1980; 2001; Gutt & Starmans 2001; Conlan & Kvitek 2005; Laudien et al. 2007). Despite major disturbances being well recognized as factors modulating benthic diversity (Gutt & Starmans 2001; Sousa 2001), the processes of colonization and successional development of benthic communities in marine subtidal rocky habitats (e.g. Underwood & Chapman 2006) and sublittoral soft-bottom environments (e.g. Pearson & Rosenberg 1978; Lenihan & Micheli 2001; Zajac & Whitlatch 2003) are still not well understood. Connell & Slayter (1977) proposed three generalized models of succession (inhibition, facilitation and tolerance) upon which predictions can be drawn. However, while recurrent patterns have been noted (Osman 1977, 1978; Underwood & Chapman 2006; Chapman 2007) the processes are diverse and tend to produce variable outcomes, rather than common patterns (Sutherland 1974; Sutherland & Karlson 1977; Vance 1988; Berlow 1997; Wahl 2001; Foster et al. 2003). The frequently observed variability in succession of natural communities seems to be related to the particularities of the observed system and the type of processes involved (Osman et al. 1992; Berlow 1997; Osman & Whitlatch 1998; Underwood & Chapman 2006).

Rocky subtidal habitats can be inhabited with widely dispersed species (e.g. barnacles and mussels with long lived larvae). For those species, the supply of colonizers (i.e. larva) to a new patch of habitat depends on the spatio-temporal variability of oceanographic processes (e.g. upwelling and relaxation events; Navarrete et al. 2005; Narváez et al. 2006; Lagos et al. 2007, 2008) and on the distance from source populations (Pechenik 1999; Grantham et al. 2003). Hence, recruitment in such habitat is not necessarily tightly coupled with reproduction (i.e. production of colonizers) (Keough 1983; Laudien et al. 2001; Navarrete et al. 2002) neither with the occurrence of disturbance (Roughgarden et al. 1988; Morgan 2001; Underwood & Keough 2001, Cifuentes et al. 2007; Sugden et al. 2007). However, there are also a number of important species with short-

## Results

---

distance dispersal stages (Osman 1977; Osman & Whitlatch 1998). These include species such as algae with limited disperse spores, crawling and brooded short-lived larvae (Pacheco & Laudien 2008) and biological processes e.g. colony fission and fragmentation, stolonal growth and benthic egg strands of masses (Osman & Whitlatch 1998) thus, there exists a great potential for localized recruitment (Vance 1988; Todd 1998; Osman & Whitlatch 1998).

The sequence of succession is also mediated by the type of biological interactions between residents and potential colonizers by rejecting or stimulating larvae settlement (Osman & Whitlatch 1995a,b, 2004; Zajac et al. 1989; Bullard et al. 2004). In particular predation (Dean & Hurd 1980; Osman & Whitlatch 2004), which due to its stochastic appearance causes variability in free space (Himmelman et al. 1983; Aguilera & Navarrete 2007; Konar 2007), affects recruitment success of potential settlers and survival of residents (Osman et al. 1992).

In addition to these factors, a particular issue in the analyses of succession experiments is that natural seasonal variability may mask underlying community trajectories, leading to confusion between succession and annual cycles (Osman 1977,1978; Underwood & Chapman 2006). Succession can only be identified when a consistent pattern of temporal change in the composition or relative abundances of species can be observed (Platt & Connell 2003; Hill et al. 2004). Therefore, community structure must be analyzed at different time intervals along the colonization process, allowing a distinction between the course of successional development and natural variability (Chapman 2002).

For communities exposed to the Humboldt Current System the major environmental disturbance is El Niño (EN), the warm phase of the El Niño Southern Oscillation (ENSO) (Arntz et al. 2006; Thiel et al. 2007). During the warm phase (EN), the combination of decreased nutrient concentrations, strong swell and high temperatures cause mass mortalities of subtidal algae and invertebrates, leaving areas of primary substratum available for recolonization (Arntz 1986; Arntz & Arancibia 1989; Camus et al. 1994; Arntz & Fahrback 1996; Vega et al. 2005; Vásquez et al. 2006; Thiel et al. 2007 and references therein).

## Results

---

Resilience time (i.e. the time required for the system to return to the reference state after disturbance, Grimm & Wissel, 1997) was estimated to range from two to three years (Arntz et al. 2006), and the magnitude of the response of benthic communities to the effects of EN depends on the seasonal onset, intensity, and characteristics of the event (Arntz et al. 2006).

In addition to environmental effects such as EN, coastal habitats may also be disrupted by anthropogenic factors. During cold and coldest “La Niña” (LN), the harvesting of marcoalgae by artisanal fishermen leads to further disturbance when kelp holdfasts are dislodged, creating small patches of bare rock (Vásquez & Santelices 1990; Vásquez 1995). Such impacts usually occur on a much smaller spatial scale and at higher frequencies than storm-induced disturbances experienced during strong EN events, but the successional patterns that unfold as the subtidal epibenthic communities recover have yet to be fully documented (see Thiel et al. 2007). During this phase, the system is characterized by high biological productivity (Escribano 1998; Wieters et al. 2003), which is reflected in high growth rates, and as a consequence, a high potential for competitive exclusion (Navarrete & Castilla 2003; Nielsen & Navarrete 2004; Valdivia et al. 2005). Therefore, it is predicted that during LN conditions, successional development will proceed through a sequence of consecutive changes of species, in which the end point is characterized by only a few dominant species.

The objectives of this study were (1) to describe the successional development of a subtidal epibenthic community during a twenty-seven months period, (2) to evaluate the rate of recovery, defined here as the time necessary for developing communities to converge into similar structure of surrounding natural community, and (3) to determine the effect of different seasonal starting points on the community colonization over a one-year period of development.

### Materials and Methods

#### Study site

This study was carried out in the northern-central region of the coastal Humboldt Current Upwelling System (HCUS) at a vertical rock face known as the “Anemone Wall” (AW: 23°28'S; 70°37'W) off Peninsula Mejillones, located near Isla Santa María. The site is exposed to one of the most productive upwelling centers in northern Chile (Escribano 1998; Marín & Olivares 1999; Escribano & Hidalgo 2000; Thiel et al. 2007), and thus the water is comparatively cold, nutrient-rich, and able to sustain high levels of primary production (Escribano 1998). Upwelling occurs year-round with maximum and minimum intensities in October and January respectively (e.g. Marín et al. 2001; Pagès et al. 2001; Escribano et al. 2002), and results in comparatively low sea surface temperatures ranging from 14° to 20 °C (for more details see Escribano et al. 2002, 2004).

AW forms part of a small embayment and extends from the shallow subtidal down to 50 m depth. The upper (down to 13 m) benthic assemblage is dominated by the kelp *Lessonia trabeculata* whose abundance is substantially reduced between 13 m and 25 m where relatively small epibenthic taxa (i.e. filamentous and encrusting red algae, bryozoans, sponges and vermetid gastropods) dominate (Pacheco & Laudien 2008). Similar community composition was observed on surrounding vertical rocky areas (A. Pacheco unpublished data), and the community studied on Anemone Wall can be considered representative for the exposed coast of Peninsula Mejillones and other rocky subtidal areas in northern Chile.

#### Experiment set-up

In January 2006, 48 circular polyethylene panels (white, 40 cm in diameter, 1.5 cm thick and 1256 cm<sup>2</sup> of surface) were installed on AW in an approximately horizontal row between 15 and 17 m depth along a 60 m transect. The distance between panels varied between 1 m and 3 m depending on the relief of the rock wall. Polyethylene® was chosen to avoid selective larval settlement or substratum rejection as it is neutrally charged and thus does not influence natural biochemical conditioning (Dexter & Lucas 1985). Artificial material furthermore provides a clean habitat surface of uniform size, complexity and history (see

## Results

also Underwood & Chapman 2006). Panel surfaces were uniformly roughened with sand paper (grading N°60) to provide a homogeneous surface (Bourget et al. 1994). The circular shape of the panels ensured that border effects were equal at the centered sampling area (38 cm in diameter).

To install the panels, holes were drilled into the bare rock and wall plugs inserted. Thereafter, adaptors (polyethylene cylinders 13.5 cm long and 4 cm in diameter) were screwed onto each wall plug. An external thread was used to fix panels to the adaptors by screwing a nut adaptor, attached in the central rear part of the panel, to the adaptor thread (Fig. 1).

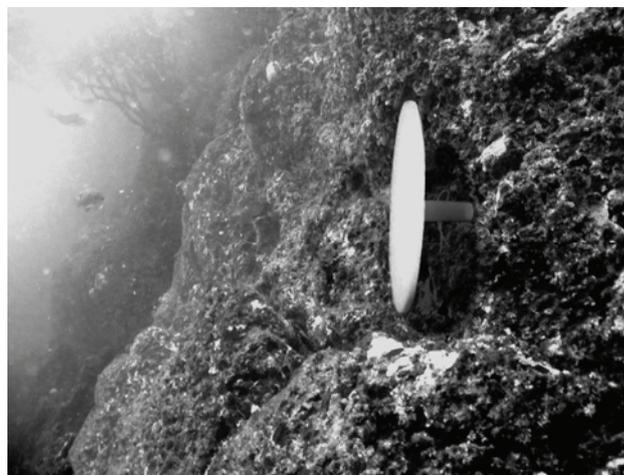
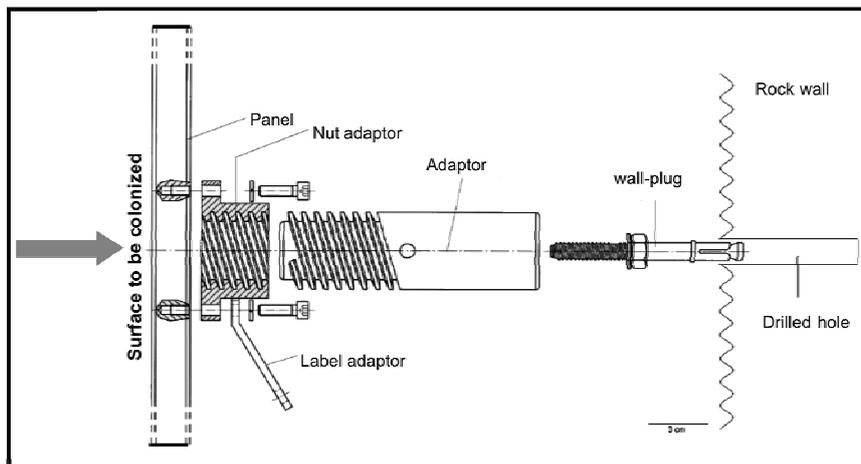


Fig. 1 Design of experimental panel (upper). View of the panel *in situ* (below).

## Results

This allowed easy installation and removal of panels during the experiment. Panels were numbered, monitored monthly by SCUBA divers and analyzed after 3, 6, 9, 12, 15, 18, 21, 24, and 27 months exposure (treatments) (Fig. 2). At each treatment, three replicated panels were detached and carefully deposited into individual mesh bags. Each bag was placed in an individual plastic container filled with filtered seawater in order to allow reallocation of potentially displaced fauna. All panels were treated similarly, and thus the methodological error was equal and allowed comparison.

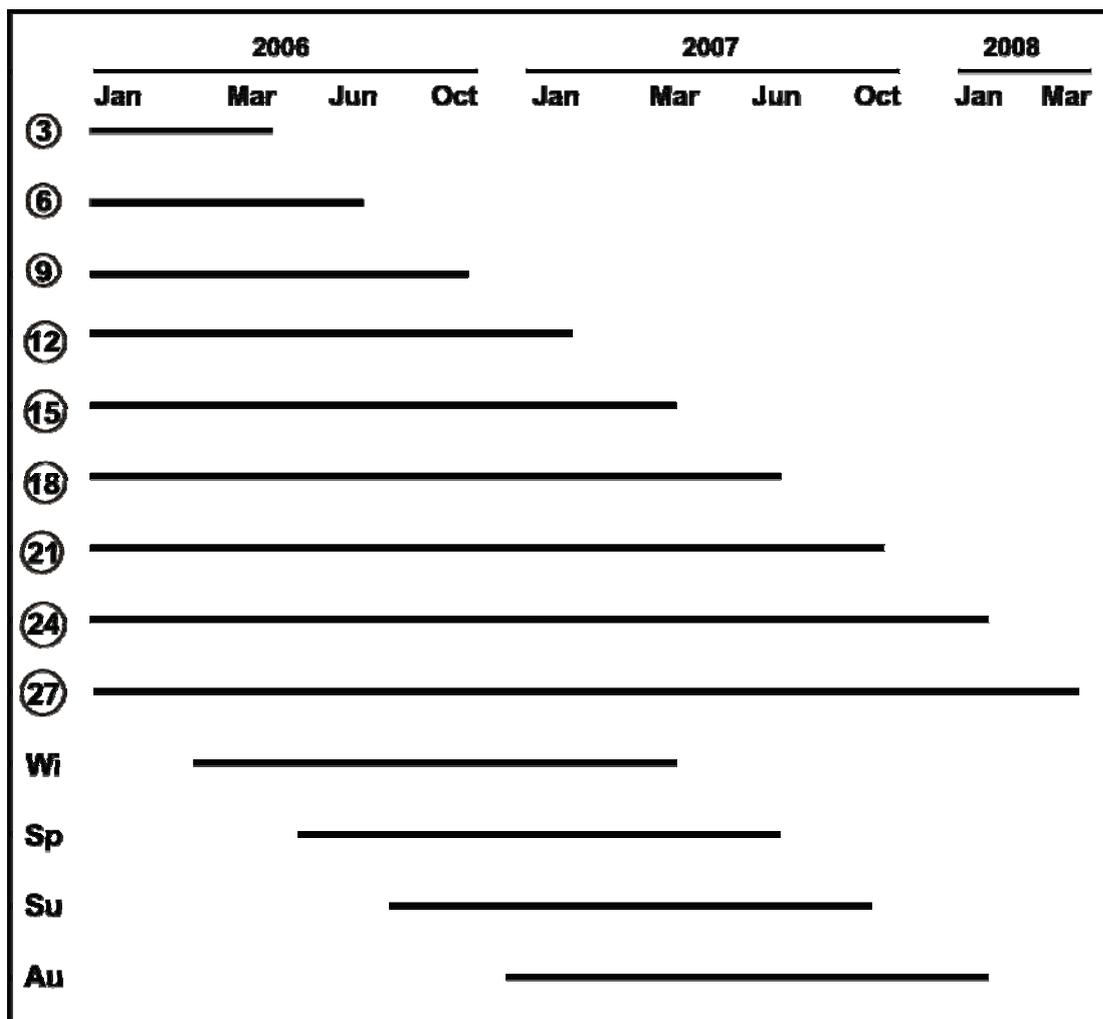


Fig. 2. Experimental design. Three replicate panels were sampled for each time interval (3-27). The abbreviations represent the months/seasons panels were exposed. Panels installed in Au (autumn), Wi (winter), Sp (spring), and Su (summer) were used to evaluate the effect of seasonality on succession.

## Results

---

### ***Species identification and quantification***

Organisms were identified to the lowest possible taxonomic level using a stereomicroscope. *Lithophyllum* sp. and *Lithothamnium* sp. were considered as encrusting coralline algae because their taxonomic status is uncertain for northern Chilean locations (Meneses, 1993). Bryozoans were carefully identified under a stereomicroscope and quantified as number of colonies. Sponges were identified to genus as detailed species information for the locality is not yet available (Desqueyroux and Moyano, 1987). For sessile taxa, percentage cover was estimated by counting 136 intersection points from a circular grid (38 cm diameter) projected centrally on to the front of the panel. In order to reduce methodological bias, identification and estimates were always done by the same person, counting from a fixed position above the panel.

### **Description of the successional sequence and convergence to natural community**

Time intervals (3 – 27, Fig. 2) were designed to describe the successional sequence in 3-month intervals over the entire 27 months of exposure. Data from each interval were compared with reference samples from the natural community in order to evaluate convergence. It was assumed that communities on panels should converge in species composition with the surrounding reference communities. To analyze reference communities from the adjacent natural rocky habitat, six squares (43.5 cm side length and ~1890 cm<sup>2</sup> area) were photographed seasonally using a Nikonos V camera equipped with a 35 mm lens and one Nikonos SB-150 flash, installed on a frame designed to ensure a fixed distance of 64.5 cm from the lens to the target area. Random photo-quadrates of the natural surrounding wall habitat were taken at the same depth as the experimental setup. Slides were projected on a screen and adjusted to match a 1:1 projection so they could be quantified using the same projected grid used for the panels.

### **Influence of seasonality on the onset of colonization**

In order to evaluate the effect of seasonality on the colonization process additional twelve panels were installed in batches of three at seasonal (three month) intervals in March 2006, June 2006, October 2006 and January 2007. After 12 months exposure, the communities were analyzed for differences between seasonal onsets (Fig. 2). To evaluate possible effects of seasonality on community development three categories were defined: (1) no seasonal effect thus converging to the same community structure, (2) slight differences in structure between treatments (i.e. differences in structure accounted for by a single species), or (3) following a stochastic pattern (e.g. substantially different species richness and composition, thus strong differences between treatments and replicates).

### **Data analysis**

Non-metric Multi Dimensional Scaling (nmMDS) conducted from a Bray-Curtis similarity matrix calculated after square root transformation of the data was used to resolve dissimilarities in community structure (i.e. percentage cover of all taxa) associated with different exposure times and between seasons. Differences between exposure times were tested with one-way analysis of similarity (ANOSIM; a non-parametric procedure, which uses the difference between ranked average Bray-Curtis dissimilarity values among replicates, between samples and within samples, Clarke & Gorley 2006). When ANOSIM detected significant differences, pair-wise comparisons were performed. Due to logistic constraints only three replicates were available at each sampling date, resulting in a rather low power to detect high significance levels (i.e.  $p < 0.05$ ) during permutation procedures. Therefore, the interpretation of pair-wise comparisons was based on R-values (rather than  $p$ ) as suggested by Clarke & Gorley (2006). These authors stated that the level of significance is very dependent on the number of replicates in the comparison and is thus always influenced by the sample size, whereas R is 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

## Results

---

communication). To test whether succession followed a constant trajectory or sequential changes through time, a seriation with replication routine was conducted from RELATE analysis. ANOSIM analysis were also used to identify at what point of time panels communities become indistinguishable (in a statistically significant sense) from their respective surrounding communities. Statistical analyses were performed using the PRIMER v6 software package (Clarke & Gorley 2006).

### Results

#### ***Succession and convergence towards natural communities***

After three months of exposure, benthic diatoms (genera; *Navicula* sp., *Nitzschia* sp., *Cocconeis* sp., *Amphora* sp., and *Coscinodiscus* sp.) and small sporophytes of *Rhodymenia corallina* colonized the panels (Fig. 3). Encrusting coralline algae appeared after six months and persisted thereafter at the same percentage cover (26%) throughout the experiment. After nine months the bryozoan *Membranipora isabelleana* and the vermetid gastropod *Dendropoma mejillonensis* were found on the panels. One year after succession began, species richness appeared to have reached a plateau, though abundance continued to increase. After 15 months of exposure, the experimental panels were almost completely covered, mainly due to strong recruitment of the barnacle *Balanus flosculus* (61% of total cover). Three months later, at 18 months, *B. flosculus* decreased in coverage to 40% and the bryozoan *Lagenicella variabilis* began to occupy space. At 21 and 24 months species coverage remained constant between surveys except in the case of *L. variabilis*, which increased considerably (up to 34%). Finally, after 27 months of exposure, *L. variabilis* dominated the community covering > 70% and almost monopolizing the space (Fig. 3). Variations in the percentage of available space during month 18, 21 and 24 resulted from variable predation pressure from the rock snail *Crassilabrum crassilabrum* and the sea star *Stichaster striatus* (personal observations) on *B. flosculus* and *M. isabelleana*.

In general, colonial taxa (e.g. *L. variabilis*) dominated over solitary forms (e.g. *B. flosculus*) (Table 1). Likewise, suspension feeders prevailed over other modes of feeding

## Results

within the community (Table 1). The Kruskal stress level of nmMDS plot indicated a good ordination (Clarke 1993), showing that the differences between communities increased with the time interval separating them (Fig. 4).

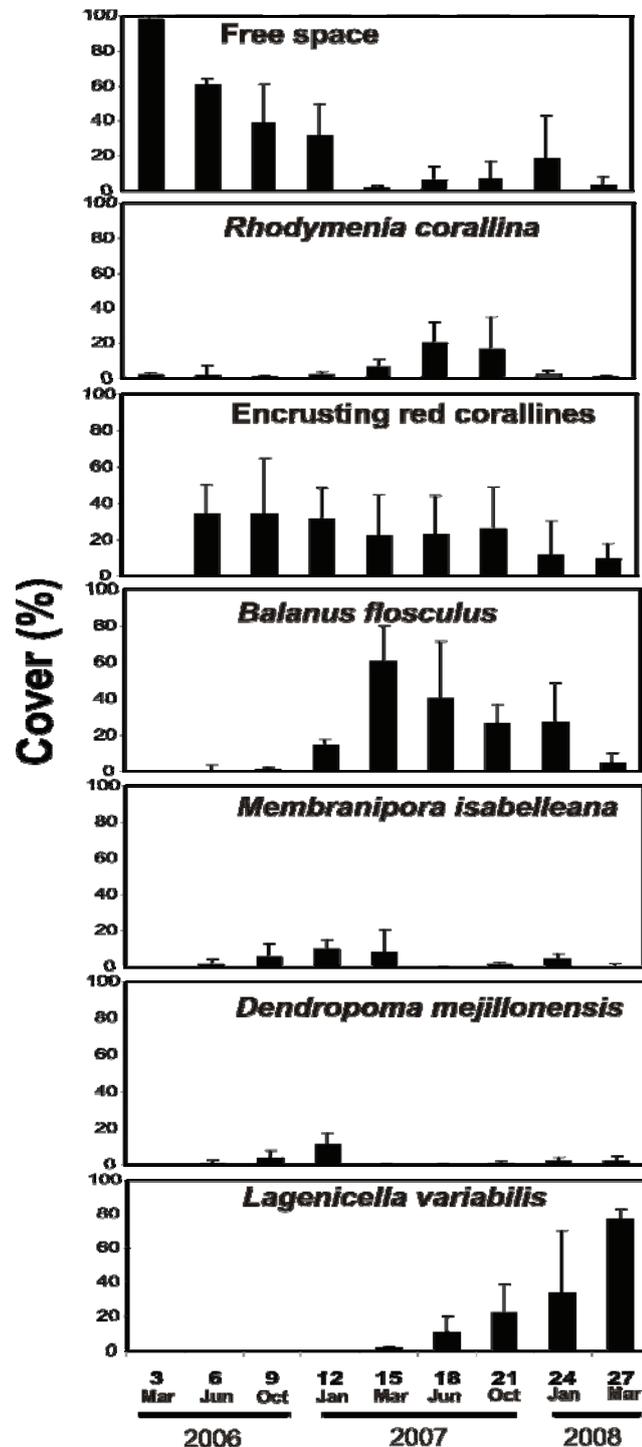


Fig. 3. Mean percentage ( $\pm$  SD;  $n = 3$ ) cover of taxa over the observed 27 month succession period.

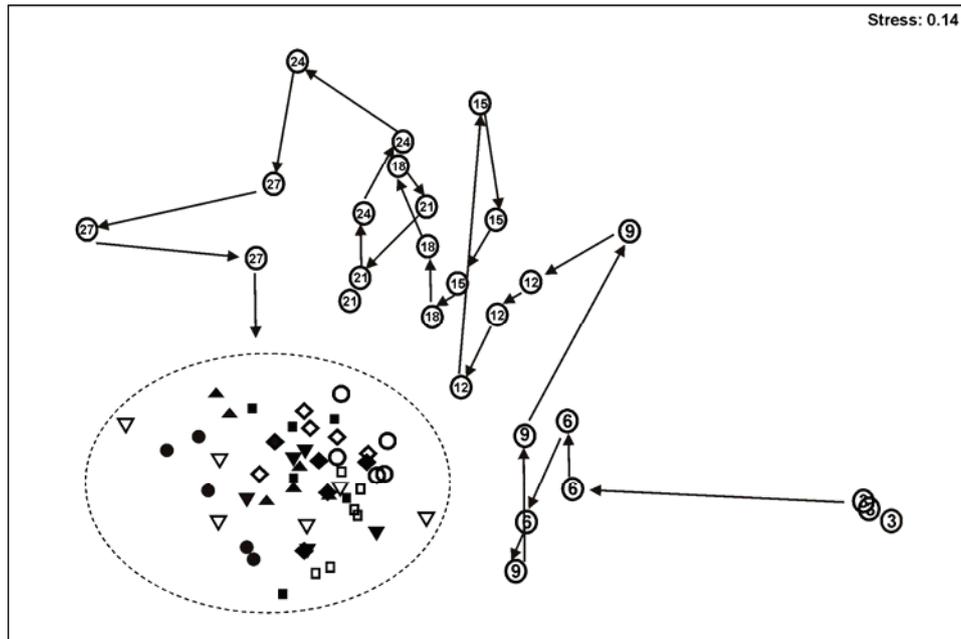
## Results

**Table 1**

Biological traits of taxa encountered (x) on experimental panels and in the natural control community (NC). A: Feeding mode (primary producer: pp, suspension feeder: sf); B: Growth form (solitary: sol, colonial: col); C: Fertilization (external: ext, internal: int); D: Development (spores: spo, larva: la, direct: di); E: Dispersal mode (pelagic: pe, pelagic/benthic: pebe, benthic: be). n.i. = not identified; 3 (March 2006), 6 (June 2006), 9 (October 2006), 12 (January 2007), 15 (March 2007), 18 (June 2007), 21 (October 2007), 24 (January 2008), 27 (March 2008).

	A	B	C	D	E	3	6	9	12	15	18	21	24	27	NC
<i>Rodymenia corallina</i>	pp	sol	ext	spo	pe	x	x	x	x	x	x	x	x	x	x
Red corallines	pp	sol	int	spo	pebe		x	x	x	x	x	x	x	x	x
<i>Balanus flosculus</i>	sf	sol	int	la	pe				x	x	x	x	x	x	
<i>Membranipora isabelleana</i>	sf	col	int	la	pe		x	x	x	x		x	x	x	
<i>Dendropoma mejillonensis</i>	sf	sol	int	di	be		x	x	x			x	x	x	x
<i>Lagenicella variabilis</i>	sf	col	int	la	pe						x	x	x	x	x
<i>Halicondria</i> sp.	sf	col	ext	n.i.	n.i.										x
<i>Clionopsis</i> sp.	sf	col	ext	n.i.	n.i.										x
<i>Hymedesmenia</i> sp.	sf	col	ext	n.i.	n.i.										x

## Results



**Fig. 4. Non-metric MDS plot of community structure calculated from Bray-Curtis measures with square root transformed data showing communities from successional time intervals. Reference communities are surrounded with a dashed line.**

In other words, the community changed gradually from an early towards a more mature late community. This pattern was supported by the seriation analysis from the RELATE routine, which indicated a clear tendency towards seriation ( $\rho = 0.977$ ,  $P < 0.01$ ), implying that succession is sequential. ANOSIM detected significant differences between samplings ( $R = 0.732$ ,  $P < 0.01$ ) thus indicating distinct community composition during the succession period. Pair-wise comparisons (Table. 2) showed clear differences between communities well separated in time (e.g. 6 vs. 15 months, 9 vs. 27 months) while communities from consecutive samplings overlapped in composition (e.g. 12 vs 15 months, 18 vs 21 months), with the 24 and 27-month intervals showing greatest disparity with the rest. It is noteworthy that the 3-month communities were very different from those recorded at all other intervals, indicating that the early stages of succession are relatively slow.

After 27 months' development, communities on the experimental panels contained that same species as the natural control communities, but had not yet reached the same community structure (Fig. 5, Table 1). Accordingly, the ANOSIM analysis comparing data from developing communities with the respective natural control shows significant

## Results

---

differences, confirming that experimental and natural communities were yet to converge fully after 27 months (Table 3).

**Table 2**

**R values resulting from pair-wise comparison of developing hard bottom communities at different stages in their succession (3 to 27 months). Clear differences ( $R > 0.75$ ) are show in bold and underlined, overlapping, but distinct results ( $R \approx 0.5$ ) are underlined, while subtle differences ( $R < 0.25$ ) appear in regular font.**

	3	6	9	12	15	18	21	24
6	<u>1</u>							
9	<u>1</u>	-0.25						
12	<u>1</u>	<u><b>0.96</b></u>	0.25					
15	<u>1</u>	<u><b>0.96</b></u>	<u>0.55</u>	<u>0.74</u>				
18	<u>1</u>	<u><b>0.81</b></u>	<u>0.48</u>	<u>0.74</u>	-0.11			
21	<u>1</u>	<u>1</u>	<u>0.33</u>	<u><b>0.91</b></u>	0.08	-0.41		
24	<u>1</u>	<u>1</u>	<u>0.70</u>	<u>1</u>	<u>0.70</u>	0.37	0.08	
27	<u>1</u>	<u>1</u>	<u>0.66</u>	<u>1</u>	<u>1</u>	<u><b>0.81</b></u>	<u>0.5</u>	<u>0.51</u>

## Results

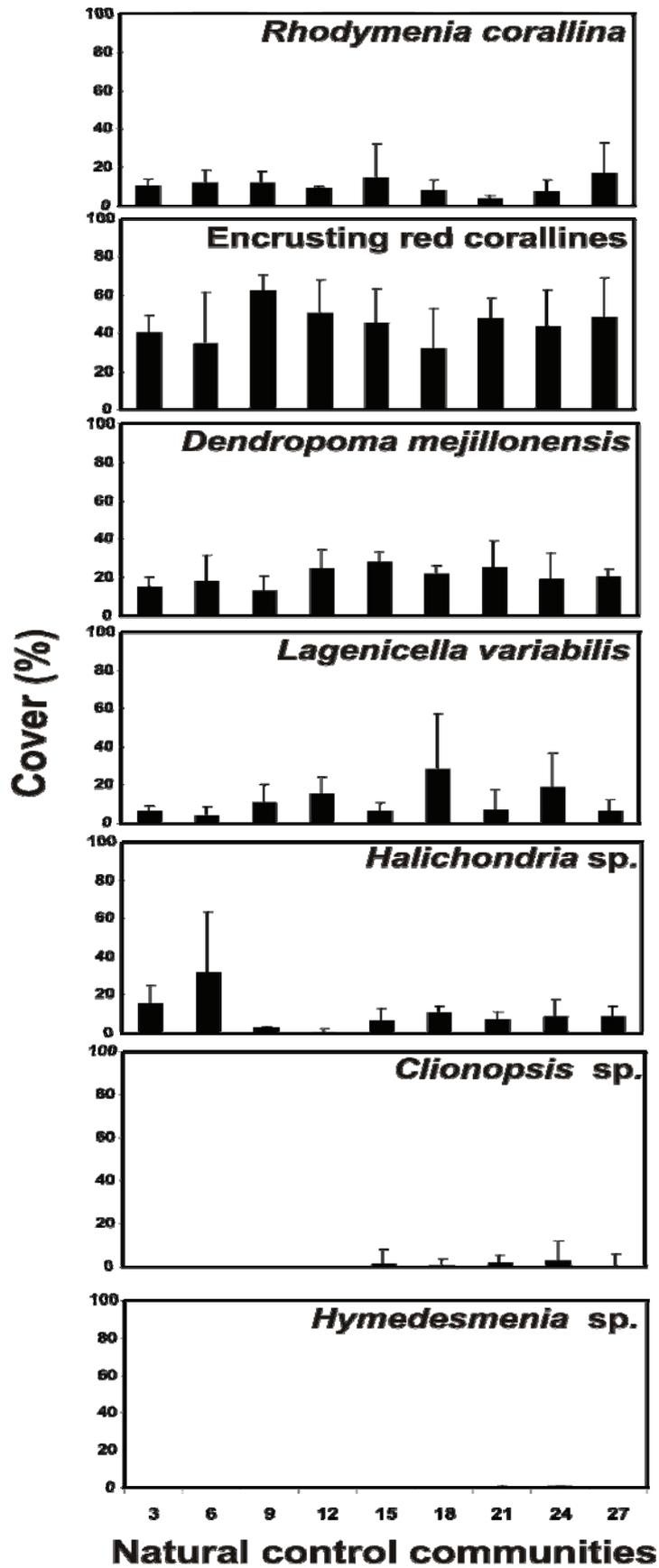


Fig. 5. Mean percentage ( $\pm$  SD;  $n = 6$ ) cover of taxa recorded in the natural control communities for each time interval of the succession experiment.

## Results

---

**Table 3**

**R values from ANOSIM analysis comparing communities from different time intervals with natural reference communities (note that all comparisons were significant at \*  $p < 0.01$ , \*\*  $p < 0.05$ ).**

	R
3 vs RC	0.91*
6 vs RC	1*
9 vs RC	1*
12 vs RC	1*
15 vs RC	1*
18 vs RC	0.95*
21 vs RC	0.93**
24 vs RC	0.97*
27 vs RC	0.99*

### ***Seasonal onset of succession***

Communities in which succession began in different seasons emerged with similar taxonomic composition but distinct abundance ratios (Fig. 6). The nmMDS ordination plot shows seasonal differences in community structure (e.g. winter communities are clearly dissimilar and thus separated from spring communities, Fig. 7). The ANOSIM detected significant differences between seasons ( $R = 0.533$ ,  $P < 0.05$ ). Pair-wise comparisons showed that communities commencing succession in spring accounted for most of the differences between seasons (Table 4).

## Results

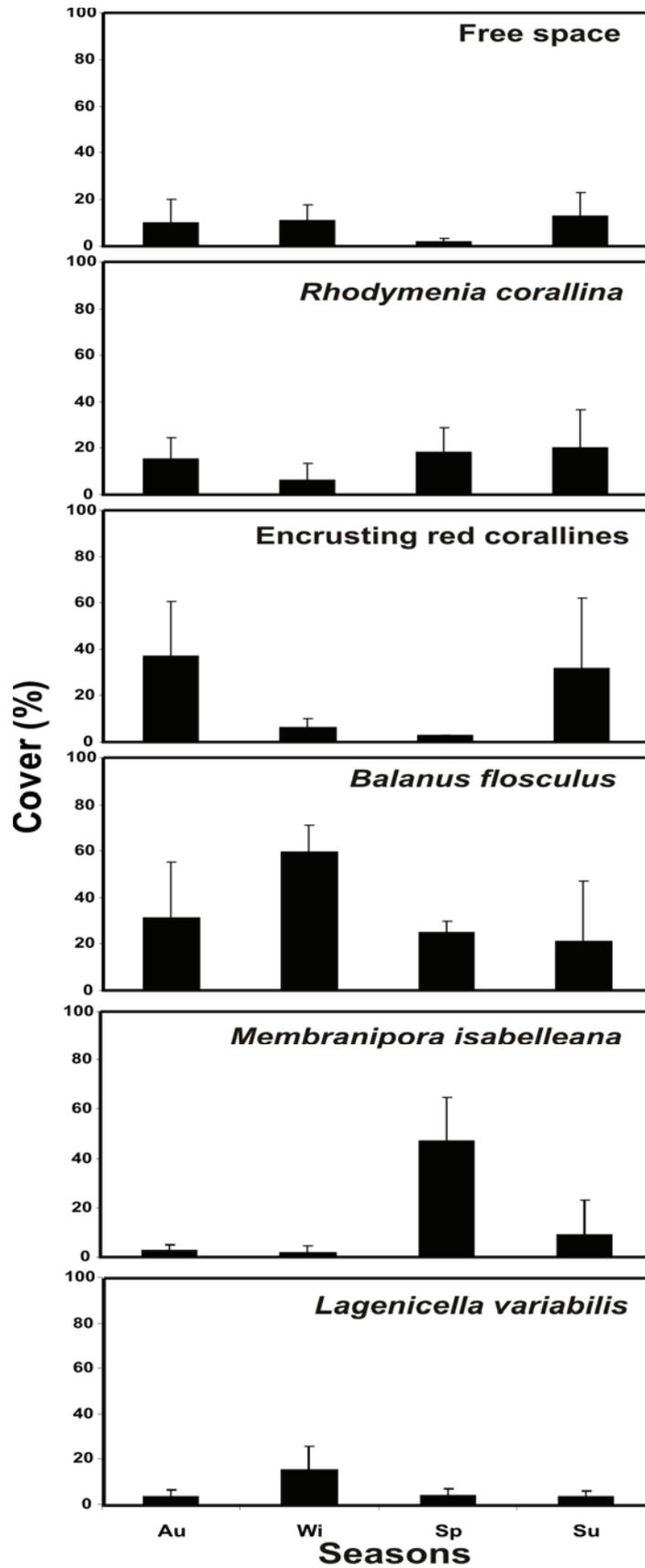


Fig. 6. Mean percentage ( $\pm$  SD;  $n = 3$ ) cover of taxa after different seasonal onset of succession.

## Results

---

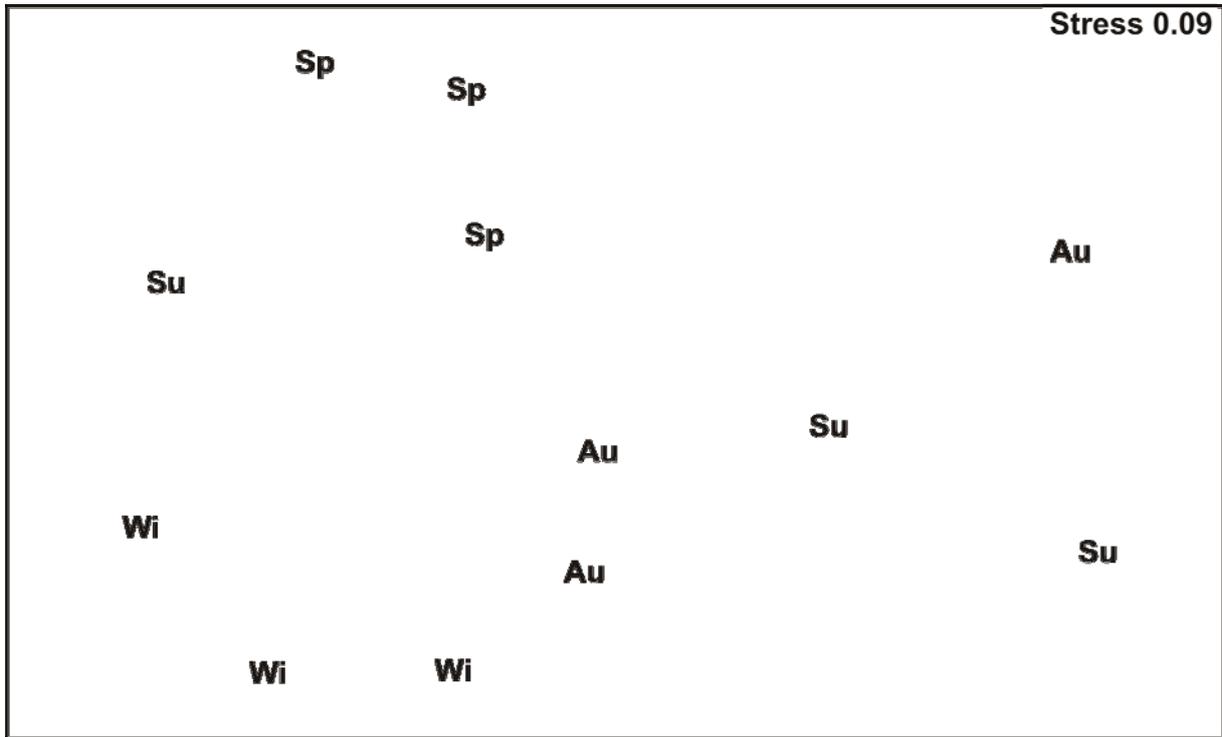


Fig. 7. Non-metric MDS plot of communities with different seasonal onset calculated from Bray-Curtis similarities of square root transformed data; (Su: summer; Wi: winter; Au: autumn; Sp: spring).

Table 4

R statistics resulting from pair-wise comparison of developing hard bottom communities initiated during different seasons (autumn, winter, summer, spring). Clear differences ( $R > 0.75$ ) are shown in bold and underlined, overlapping, but distinct values ( $R \approx 0.5$ ) are underlined, and subtle differences ( $R < 0.25$ ) are shown in regular font.

	Au	Wi	Sp
Wi	0.18		
Sp	<u>0.66</u>	<b><u>0.96</u></b>	
Su	-0.25	0.25	0.25

### Discussion

#### Biotic factors driving community succession

This study is the first to describe the successional development of subtidal hard bottom communities in northern Chile. Observations made during an exposure period of 27 months showed that succession started with a film of benthic diatoms, followed by encrusting red corallines. A subsequent recruitment pulse of the barnacle *Balanus flosculus* partly replaced encrusting corallines. The colonial bryozoan *Lagenicella variabilis*, which appeared later during the course of succession, overgrew space between and over barnacles and subsequently replaced earlier colonizers. Thus, a competitive hierarchy was apparent: benthic diatoms < encrusting red corallines < *B. flosculus* < *L. variabilis*. Comparable sequences of competitive exclusion between species are commonly observed during community development and have been described previously for intertidal hard bottom systems: from the HCS off Chile and Peru a sequence comprising ephemeral algae, long-lived turf or kelp and suspension feeders has been frequently documented (Tarazona & Arntz 2001; Arntz et al. 2006; Thiel et al. 2007). In intertidal habitats along the coast of central Peru, empty space within *Semimytilus algosus* beds is colonized by this mussel itself, which is competitively superior to the barnacles *Jehlius cirratus* and *Notochthamalus scabrosus* and the gallery-building polychaete *Phragmatopoma moerchi*. The latter species are typical early colonizers, but are outcompeted by mussel spat (Tokeshi & Romero 1995). The short succession sequence described in the present study is in line with those observed from hard bottom systems off central Chile, where high levels of primary production permit dominance of superior competitors due to high growth rates and rapid exclusion of inferior competitors (Navarrete & Castilla 2003; Nielsen & Navarrete 2004; Valdivia et al. 2005).

At AW, almost all faunal species encountered during succession were suspension feeders (Table 1). Members of this feeding guild successfully exploit the high primary production (phytoplankton and macroalgae detritus) of the system, which is reflected in rapid overgrowth and lateral expansion, highlighting the importance of competition in these habitats. Suspension feeders suppress other species by overgrowing, competing for food

## Results

---

resources and possibly feeding on early life history stages (see e.g. Paine & Suchanek 1983; Sebens 1982; 1986; Osman & Whitlatch 1995a;b).

Information on succession sequences from subtidal systems of the HCS is scarce (Thiel et al. 2007 and references therein), but initial colonization by encrusting red corallines followed by kelp and the mussel *Aulacomya ater* has been reported from Bahía Independencia off central Peru (Arntz et al. 2006). Although not explicitly described, it is likely that hierarchical dominance and competitive exclusion also occurs in that community. Colonial organisms outcompete solitary species at AW as they do in subtidal hard bottom systems elsewhere (Jackson 1977; Osman 1977; Sebens 1982, 1986). Thus, high growth performance and strong competition for space by lateral growth appears to be more advantageous than abundant initial settlement. These results are in accordance with the prediction that colonial invertebrates will generally dominate over solitary ones in subtidal epibenthic communities (Jackson 1977; Osman 1977; Todd 1998; Witman & Dayton 2001).

### **The predictability of the successional outcome**

The results from AW suggest that succession over 27 months has followed a non-rigid but deterministic pattern, in which the resulting community has a certain level of predictability. Although the developing community showed variation in species richness and cover compared with natural reference communities, fundamental differences in species richness (i.e. multiple state communities) were not observed. The observation of a persistent (i.e. similar community structure through time) natural community supports this notion (Fig. 4). Although substratum heterogeneity is an important factor during settlement and recruitment of epibenthic species (Bourget et al. 1994), the way in which communities develop on our experimental panels mimicked the natural surrounding hard bottom community, suggesting that these were indeed appropriate substrata. With the exception of two species only found on the artificial panels (*B. flosculus* and *M. isabelleana*), the main species recorded from natural reference communities were also present on the colonization panels. The absence on the panels of certain poriferan species that were present in the reference communities

## Results

---

may rather be due to the restricted time allowed for development (here 27 months). The colonization of small patches by lateral growth of dominant competitors accelerates convergence of the resulting community (Osman & Whitlatch 1998; Watson & Barnes 2004). Our panels were elevated above the natural rock, thus lateral ingrowth could not occur, but despite this the results suggest that succession on our panels was representative of the natural communities.

### **Time of convergence towards the natural community**

The observations recorded in the current study indicate that it takes about 15 months for the empty substratum to be completely covered by early colonizers. At the end of the colonization experiment, most of the organisms found in surrounding natural communities were also present on the settlement panels. However, even after 27 months of succession, the experimental communities did not yet fully resemble natural communities, because the proportional coverage of species differed and because one species common in natural communities (Porifera) was not yet found on the settlement panels. Since most species that are important in natural communities had also reached a high percentage of coverage in the experimental communities (e.g. >70 % average cover of *Lagenicella variabilis*), it appears likely that the experimental communities are on a successional trajectory towards a mature community that will ultimately resemble the natural reference communities. Present data do not allow us to predict when convergence between experimental and natural communities will be complete, but based on the preceding considerations we suspect that full convergence will be achieved within 3 or 4 years after the start of the succession.

Late colonizers such as Porifera are likely to appear only during advanced phases of the succession (i.e. Walker et al. 2007). In contrast, the barnacle *B. flosculus* was only recorded in the developing community, which may indicate that this species is a comparatively weak competitor and requires disturbance in order to colonize substrata. *B. flosculus* was not found in natural reference communities, and decreased substantially in abundance on the panels between months 15 and 27, implying an inability to colonize or

## Results

---

persist in mature natural communities. This is in line with earlier observations concluding that barnacles commonly appear in the mid stage of succession but disappear later when overgrown by dominant colonizers (Osman 1977; Paine & Suchanek 1983; Sousa 2001; Cifuentes et al. 2007; Yakovis et al. 2005; 2008).

### **Importance of seasonal onset for composition and structure of developing communities**

Communities initiated in different seasons featured similar taxonomic composition but distinct abundance proportions. This can probably be attributed to seasonality in successful larval settlement by different taxa, repeatedly reported from the coast of northern-central Chile (Nárvaez et al. 2006; Navarrete et al. 2002, 2005; Lagos et al. 2007). Upwelling pulses favor onshore larval transport (Morgan 2001; Nárvaez et al. 2006), and upwelling varies in intensity throughout seasons (e.g. Escribano et al. 2002). The variation in colonization by taxa with long lived pelagic larvae is potentially explained by variations in the supply of colonizers such as *B. flosculus*, (see Table 1 for details). In central Chile, upwelling dynamics seem to be an important factor in the recruitment of intertidal barnacles and mussels (Navarrete et al. 2002, 2005; Lagos et al. 2007). However, such mechanisms cannot explain the variability in the colonization of taxa with short-lived larva such as the bryozoans *M. isabelleana* and *L. variabilis* (see also Osman & Whitlatch 1998), or the brooding vermetid gastropod *D. mejillonensis* (Pacheco & Laudien 2008). Juveniles of *D. mejillonensis* leave the mantle cavity of the adult and crawl for less than one hour before cementing themselves to the substratum. Therefore, the appearance of *D. mejillonensis* in a particular season must reflect peaks in reproduction, rather than a dispersal process.

Regardless of the supply of colonizers, the establishment of the subsequent community structure also depends on the ability of certain species to compete for space (Osman 1977; Sebens 1982, 1986; Walker et al. 2007). As observed in the current study and despite the variation caused by seasonality, the more advanced communities are dominated by late, but apparently competitively superior colonizers. This is especially true for *L.*

*variabilis*, which overgrew other colonizers and dominated the community (achieving 70% coverage) towards the end of the experiment. Thus, although seasonality generates high variability during the early colonization process, the effect is eventually overridden by biological interactions such as competition and growth performances and it is these, which determine the structure and composition of the advanced community.

### **Natural events and succession of subtidal hard bottom communities in the HCS**

The present study was conducted during the cold “La Niña” phase of the ENSO, under which the characteristic communities of the HCS establish. During warm EN events the combination of strong wave swell and high temperatures may cause mass mortalities, reopening swathes of primary substratum for colonization (Arntz 1986; Arntz & Arancibia 1989; Arntz & Fahrbach 1996; Tarazona & Arntz 2001). The experiments described here indicate that the recovery time after severe EN events exceeds two years. Since seasonality has an effect during the early stages of community development, EN events of different seasonal onsets have different impacts (Arntz et al. 2006). For example, the EN of 1982–1983 began during austral spring, while EN 1997–1998 commenced late in austral autumn, i.e. after the main reproductive season. Such differences are likely to influence the supply of colonizers (i.e. larvae) in a given year. In addition, during EN events, planktonic micro-algal communities are impacted in turn, possibly affecting larval survival due to a mismatch in food availability (i.e. Vargas et al. 2006; Thiel et al. 2007). However, as observed in this study, regardless of the early impacts of different starting periods, succession proceeds in the same direction, that is, towards the previous undisturbed condition.

Nearly all marine subtidal hard-bottom communities (if not all) are exposed to disturbance of different extension, frequency and magnitude. But at the same time, these communities, which are often dominated by colonial species, show great capacity of successional recovery as reported from a diverse range of systems such as coral reefs (Connell 1997), antarctic benthos (Teixidó et al. 2004) or from the similar California upwelling system (Day & Osman 1981; Vance 1988). Therefore, it could be predicted that

## Results

---

the mechanism driving succession will favour the persistence and dominance of colonial species in subtidal hard-bottom habitats. In this study we have obtained support for this prediction from one site along the Humboldt Current system. Nevertheless, the ENSO affects a vast region of the eastern Pacific, and enhancing the spatial and temporal scale of this experiment appears necessary to fully assert the aforementioned prediction.

### **Acknowledgments**

We are grateful to T. Ashton, M. Cáceres, I. Fiorillo, C. Guerra, I. Marín, S. Rossi, R. Saavedra, A. Silva, P. Schubert, V. Toro, and J. Velez for their support during diving work. C. Auld and R. Alheit kindly edited the English. This study was conducted in the framework of the EU-funded INCO project, “Climate Variability and El Niño-Southern Oscillation: Implications for Natural Coastal Resources and Management” (CENSOR) and the Programa Bicentenario de Ciencia y Tecnología RUE-02. This is CENSOR publication N°...

### **References ♦**

---

♦ All citation included in this manuscript are compiled in the final list of references

### 4.1.2 Publication II<sup>^</sup>

#### Hard bottom succession of subtidal epibenthic communities colonizing hidden and exposed surfaces off northern Chile

Aldo S. Pacheco<sup>a, b</sup>, Jürgen Laudien<sup>a</sup>, Martin Thiel<sup>c, d</sup>, Olaf Heilmayer<sup>a</sup>, Marcelo Oliva<sup>b</sup>

<sup>a</sup>Alfred Wegener Institute for Polar and Marine Research, D-27568 Bremerhaven, Germany. <sup>b</sup>Facultad de Recursos del Mar, Universidad de Antofagasta, P.O. Box 170, Av. Angamos 601, Antofagasta, Chile. <sup>c</sup>Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile. <sup>d</sup>Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile.

**Running title:** Succession on hidden vs. exposed Chilean hard bottom

#### SUMMARY

The biodiversity of hard bottom substrata comprises species growing on exposed rock and in hidden microhabitats, such as cracks and crevices. This study examines the succession of epibenthic organisms colonizing an artificial substratum with one surface exposed and one hidden face on a vertical wall off northern Chile. At each sampling date species coverage on either surface (exposed and hidden) of three replicate panels was assessed. Hidden surfaces were dominated in terms of coverage by the bryozoans *Membranipora isabelleana* and *Lagenicella variabilis*, while algae were absent. In contrast, the most important components of communities colonizing exposed surfaces were encrusting red corallines and the red alga *Rhodomyenia corallina*. At the end of the experimental period both surfaces were dominated by colonial suspension feeders, but showed different community structure and successional pattern. On exposed surfaces, competitive exclusion was identified as an important aspect of succession, whereas on hidden surfaces this pattern was not observed. This has implications for overall biodiversity, because pioneer species that are not able to survive long periods on exposed surfaces become restricted to hidden surfaces, from where they spread laterally. Thus hidden microhabitats provide important refuges for certain species, and may play an important role in the overall succession on rock faces. Examination of hidden microhabitats is necessary to fully understand succession on hard bottoms habitats.

**Keywords:** Habitat complexity, epibenthic hard bottom communities, Succession, Peninsula Mejillones, Humboldt Current Upwelling System

---

<sup>^</sup> This is the author's version of a work accepted for publication in Scientia Marina

### RESUMEN

La biodiversidad en sustratos de fondo duro esta compuesta de especies que crecen en las superficies expuestas de las rocas así como también aquellas presentes en microhábitats ocultos como grietas y cavidades. Este estudio examina el proceso de sucesión de organismos epibentónicos que colonizan un sustrato artificial presentando una superficie expuesta y una oculta en una pared vertical en la Península de Mejillones en el norte de Chile. Cada tres meses, tres paneles fueron colectados y en el laboratorio se cuantificó la cobertura de especies de ambas superficies. Durante la sucesión en las superficies ocultas los briozoos *Membranipora isabelleana* y *Lagenicella variabilis* dominaron la comunidad en términos de cobertura notándose una ausencia total de algas. En contraste, las algas coralinas custrosas y *Rhodymenia corallina* fueron componentes importantes de las comunidades que colonizaron las superficies expuestas. La estructura comunitaria y los patrones de sucesión fueron diferentes en ambas superficies, observándose una tendencia a la dominancia de los animales coloniales suspensorios. En las superficies expuestas se identificó a la exclusión competitiva como un proceso importante durante la sucesión, mientras que en las superficies ocultas este patrón no se observó. Esto tiene implicaciones en la biodiversidad general, debido a que las especies pioneras que no pudieron sobrevivir periodos largos en las superficies expuestas, se restringen a los hábitats ocultos desde donde pueden crecer lateralmente. Los microhábitats ocultos proporcionan refugios para algunas especies lo cual puede afectar la sucesión en hábitats rocosos. Es necesario examinar los microhábitats ocultos para poder tener un total entendimiento de la sucesión en hábitats de fondos duros.

**Palabras clave:** Complejidad del hábitat, comunidades epibentónicas de fondos duros, Sucesión, Península Mejillones, sistema de surgencia de la corriente de Humboldt

### INTRODUCTION

Natural shallow subtidal rocky habitats are structured heterogeneously. Variable slope, topography, orientation, angle and the characteristics of the substratum have drastic consequences for the small-scale variability of abiotic and biotic factors (i.e. light intensity, currents, sediment and detritus accumulation, barriers to predators), and thereby influence the establishment of epibenthic organisms (Witman and Dayton, 2001; Miller and Etter, 2008). In temperate zones, subtidal vertical rocky walls are often dominated by epibenthic suspension feeders while numerous macroalgal species flourish on horizontal substrata, where they benefit from high levels of incoming light (Baynes, 1999; see review in Witman and Dayton, 2001). A range of distinct microhabitats can be noted, from fully exposed horizontal and vertical plain surfaces (Glasby, 2000; Glasby and Connell, 2001) to completely sheltered or hidden habitats such as shaded surfaces, crevices, undersides of boulders, cracks, cavities and even large caves (Jackson, 1977; Glasby, 1999a,b; Richter et al., 2001). Hidden microhabitats also occur beneath or within biogenic substrata, such as kelp canopies (Melville and Connell, 2001; Villegas et al., 2008), or foliose corals (Jackson, 1977; Richter et al., 2001). These hidden microhabitats can be important for the survival of poorly competitive epibenthic species. Firstly they provide refuge from consumers during settlement, post settlement and juvenile growth (Coyer et al., 1993; Raimondi and Morse, 2000; Roleda et al., 2007). Secondly, hidden microhabitats may alleviate competition, both from species that dominate in more exposed habitats (Irving and Connell, 2002; Miller and Etter, 2008) and between congeners (Navarrete et al., 2008). Thirdly, such habitats may serve as refuges from harmful abiotic conditions such as strong currents or solar radiation (e.g. Burnaford, 2004). The vast majority of studies analyzing the main factors influencing subtidal rocky community composition have been conducted using plain, exposed surfaces (e.g. Sebens, 1986; Siddon and Witman, 2004). Nevertheless, species that first settle on inner (hidden) rock surfaces, from which they later spread onto exposed surfaces, form an important component of the community.

## Results

---

Succession on exposed, hard bottom epibenthic communities off the coasts of northern and central Chile typically follow a sequence of early, mid and late colonization in which competitive exclusion is an important driving factor (Navarrete and Castilla, 2003, Valdivia et al., 2005, Cifuentes et al. 2007). Hidden habitats are likely to be colonized by different communities but species interactions and processes involved in shaping such communities are not well known. Previous studies mentioned a conspicuous absence of macroalgae in hidden and shaded habitats, which leads to a dominance of invertebrates (Irving and Connell, 2002). In such sites competitive exclusion might be limited or masked by other limitations such as restricted food supply (Baynes, 1999; Richter et al., 2001). Settlement in hidden habitats can be species- or site-specific but the type and strength of post-settlement interactions might also depend on the species composition of adjacent exposed surfaces. Differences between hidden and exposed communities are to be expected, but the interactions and processes involved require evaluation.

To analyze whether the succession process differs between hidden and exposed microhabitats, artificial substratum units with hidden and exposed surfaces were installed on a vertical rock wall off northern Chile. Communities developing on the exposed and hidden surfaces were analyzed sequentially over a 27 month period. The aims were (i) to describe the succession of epibenthic organisms colonizing the distinct substratum surfaces, and (ii) to identify the mechanisms driving the community pattern.

## MATERIALS AND METHODS

### Study site

This study was carried out in the northern-central region of the coastal Humboldt Current System (HCS) at a vertical rock face known as the “Anemone Wall” (AW) at 23°28'S, 70°37'W off Peninsula Mejillones (near Isla Santa María), northern Chile. Peninsula Mejillones is one of the most productive upwelling centers along the northern coast of Chile. A detailed description of the physical oceanography of the area is available in Escribano et al. (2002). Forming part of a small embayment, AW extends from the shallow subtidal down

## Results

---

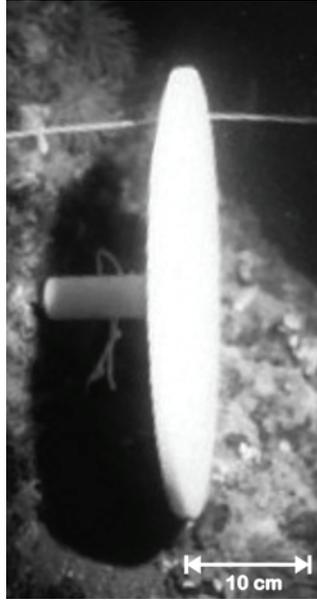
to 50 m depth. From the surface to 13 m the benthic community is dominated by the kelp *Lessonia trabeculata*. From 13 m down to 30 m kelp abundance is substantially reduced and dominant organisms are relatively small epibenthic taxa, such as filamentous and encrusting red algae, bryozoans, sponges and vermetid gastropods (Pacheco and Laudien, 2008). Since a similar community composition was observed on surrounding vertical rocky areas, the community studied on Anemone Wall can be considered representative of the exposed coast of Peninsula Mejillones (A. Pacheco unpublished data).

### Experimental design

In January 2006, 24 circular Polyethylene® panels (white, 40 cm in diameter, 1.5 cm thick, Fig. 1) were installed at AW. This material was chosen because it provides a clean habitat surface of uniform size, complexity and history (see also Underwood and Chapman, 2006). Polyethylene® has been shown to avoid bias due to selective larval settlement or substratum rejection, because its neutral charge does not influence natural biochemical conditioning (Dexter and Lucas, 1985; Rodriguez et al., 1993). The experimental panels were installed in an approximately horizontal line along a 60 m section of wall between 15 and 17 m depth. The distance between panels varied from 1 to 3 m depending on the relief of the rock wall. Panels were roughened with sand paper (grade N°60) in order to provide a homogeneous surface structure (Bourget et al., 1994). The circular shape ensured that edge effects were equal along the border of the circular sampling area. To install panels at AW, holes were drilled and wall plugs inserted. Thereafter, adaptors (a polyethylene cylinder 13.5 cm long and 4 cm in diameter) were screwed into each wall plug. The distance between panels and the rock wall was approximately 16 cm. At regular intervals of 3, 6, 9, 12, 15, 18, 21, 24, and 27 months, three panels were randomly chosen, detached and placed carefully into individual mesh bags. Each bag was deposited in an individual plastic container filled with seawater and carefully transported to the laboratory. All panels were treated in the same way, and thus the potential methodological error was equal and allowed comparison.

## Results

---



**Fig. 1 Experimental Polyethylene ® Panel installed at 17 m depth.**

### **Species quantification**

All taxa found on the exposed and hidden surface of the experimental panels were individually identified to the lowest taxonomic level possible. Benthic diatoms were registered and identified at the beginning of the experiment but were excluded from further analysis in order to avoid possible problems due to comparisons of species from very different size spectra. The percent coverage by sessile taxa was estimated counting 130 intersection points from a circular grid (38 cm diameter) projected onto the centre of both panel surfaces. The circular central area covered by the nut-adaptor (50.2 cm<sup>2</sup>) was excluded from analyses of both surfaces. Quantification and identification was always conducted by the same person, counting from a fixed position above the panel, in order to reduce methodological bias.

### **Abiotic factors**

Light intensity readings for both sides of the panels were obtained with a HOBO light data logger (MicroDAQ Ltd, USA). The logger was fixed with cable ties to the respective panel surface where it recorded light intensity for three successive days of full sun (24-27th of April 2008) using three different panels. Differences in light intensity between hidden and exposed surfaces were evaluated using the non-parametric Mann-Whitney test.

## Results

---

Current velocity was assessed for both surfaces by measuring the mass loss from dissolution of gypsum half-spheres (3 cm diameter, 2 cm radius, initial dry masses ranging between 9.45 and 12.24 g). The mass loss has been shown to be directly proportional to current velocity (Yund et al., 1991). Three pairs of gypsum blocks were attached to three newly installed panels, one block on each side. The panels were placed haphazardly along the experimental row. Gypsum blocks were retrieved after 24 h exposure time, dried and their mass recorded. Differences in percent mass loss per block between exposed and hidden surfaces were evaluated with a t-test. Statistical analyses were conducted using the software Minitab, release 14 for MS Windows.

### **Statistical analysis**

Differences in community composition between distinct sampling dates (months 3 to 27) and surfaces were tested using one-way analysis of similarity, ANOSIM. This is a non-parametric procedure, in which the difference between average ranked Bray-Curtis dissimilarity values among replicates, between treatments and within treatments, is used to calculate an R statistic (Clarke, 1993). When the global R-value of the ANOSIM test was significant, pairwise comparisons were conducted. Therefore, the interpretation of pairwise comparisons was based on R-values (rather than p) as recommended by Clarke and Gorley (2006), because with three replicates for each sampling date the significance level cannot be lower than  $p=0.1$ . These authors stated that the level of significance is very dependent on the number of replicates in the comparison, and thus always influenced by the sample size. R on the other hand, is largely unaffected by the number of replicates (i.e. possible permutations) and gives an absolute measure of differences between two (or more groups) in the high-dimensional space of the data. In order to facilitate and visualize the interpretation of pairwise comparisons, an nmMDS plot was constructed from a dissimilarity matrix calculated from Euclidian distances between R-values. To test whether community succession on the different panel surfaces underwent trajectory or sequential changes over time, a seriation with replication routine was run using the RELATE analysis. Dissimilarity

## Results

---

matrix, nmMDS ordination plots, ANOSIM and RELATE seriation analyses were performed using the PRIMER v6 software package (Clarke and Gorley, 2006).

### RESULTS

#### Measurements of light and currents

During the three 24 h cycles, hidden surfaces received only 9% of the light intensity measured at exposed surfaces ( $1.2 \pm \text{SD } 5.19 \text{ lum m}^{-2}$  compared to  $13.01 \pm \text{SD } 75.62 \text{ lum m}^{-2}$ ). The difference was significant (Mann-Whitney U-test;  $U = 346.57$ ,  $df = 1$ ,  $p < 0.05$ ). Mass losses of gypsum half-spheres installed at exposed ( $6.46 \pm 1.11 \text{ g}$ ) and hidden ( $7.05 \pm 5.24 \text{ g}$ ) sides of the panels were not significantly different (t-test;  $T = 0.92$ ,  $p > 0.05$ ).

#### Species cover during succession on exposed versus hidden panel sides

On both surfaces, succession started with benthic diatoms (*Navicula* sp., *Nitzschia* sp., *Cocconeis* sp., *Amphora* sp., and *Cocinodiscus* sp.). From the beginning, young sporophytes of *Rhodymenia corallina* were only present on the exposed surface. Here, encrusting red corallines appeared after six months and persisted with about 30% coverage for most of the experiment, while abundances of the bryozoan *M. isabelleana* were lower (Fig. 2). For these two species coverage on exposed surfaces remained constant with a slight increase in abundance after one year. After 15 months, a strong recruitment of the barnacle *Balanus flosculus* (60.8% of total cover) was observed (Fig. 2). Three months later, abundance of *B. flosculus* on exposed surfaces was reduced to 40% and the bryozoan *Lagenicella variabilis* occupied most of the space. *L. variabilis* abundance increased progressively from 33.8% at 24 months to 70% at the end of the experiments, finally monopolizing the available space on the exposed experimental substrata (Fig. 2). Thus, on exposed surfaces, community succession occurred in a clear transitional manner from early (encrusting red corallines and *M. isabelleana*), via mid (*B. flosculus*) to late (*L. variabilis*) colonizers (see below).

In contrast to exposed surfaces, hidden surfaces lacked macroalgae and were colonized instead by the bryozoan *M. isabelleana* after three months. Coverage by this

## Results

---

species increased progressively to a maximum of 67.2% cover after one year of exposure. *Lagenicella variabilis* appeared after 9 months and achieved 18.9% coverage before it decreased to 5.4%, and then resurged at month 18 to reach 20% after 27 months of exposure (Fig. 2). *Balanus flosculus* recruited after one year and reached its maximum coverage (29.9%) after 18 months, before decreasing to 8.8% towards the end of the experiment. The vermetid gastropod *D. mejillonensis* was present in low abundance over the entire course of the experiment (Fig. 2). The gastropod *Trochita calyptraeiformis* and the white actinia *Anthotoe chilensis* occurred in very low percentages of cover and only on hidden surfaces. Overall during the experiment, succession on hidden surfaces did not follow a clear sequence of development, as no substantial replacement of species was observed. The early colonizing *M. isabelleana* occupied most of the available substratum throughout the experiment, even though it appeared to be overgrown by the late colonizer *L. variabilis*.

### **Temporal variation during successional development on exposed and hidden surfaces**

The nmMDS ordination plot derived from the communities of exposed and hidden surfaces showed two clearly separated groups (Fig. 3). ANOSIM indicated differences in community composition both between sampling dates and between exposed and hidden surfaces ( $R = 0.71$ ,  $p < 0.05$ ).

For exposed communities, the one-way ANOSIM analysis detected significant differences in composition at different sampling dates ( $R = 0.732$ ,  $p < 0.05$ ). Pairwise comparison nmMDS plot (Fig. 3) showed that the dissimilarities were larger between well-separated sampling dates (e.g. 3 vs. 12 or 9 vs. 24 months) than consecutive samplings (6 vs. 9, 12 vs. 15, 15 vs. 18, 18 vs. 21, 24 vs. 27 months). The community compositions observed at consecutive samplings mostly overlapped, indicating that the community developed through progressive changes. The modification in taxonomic composition (i.e. arrival of colonizers) takes at least 6 months. The seriation analysis (RELATE routine),

## Results

indicated a clear tendency towards seriation ( $\rho = 0.977$ ,  $p < 0.05$ ) confirming a sequential pattern of succession.

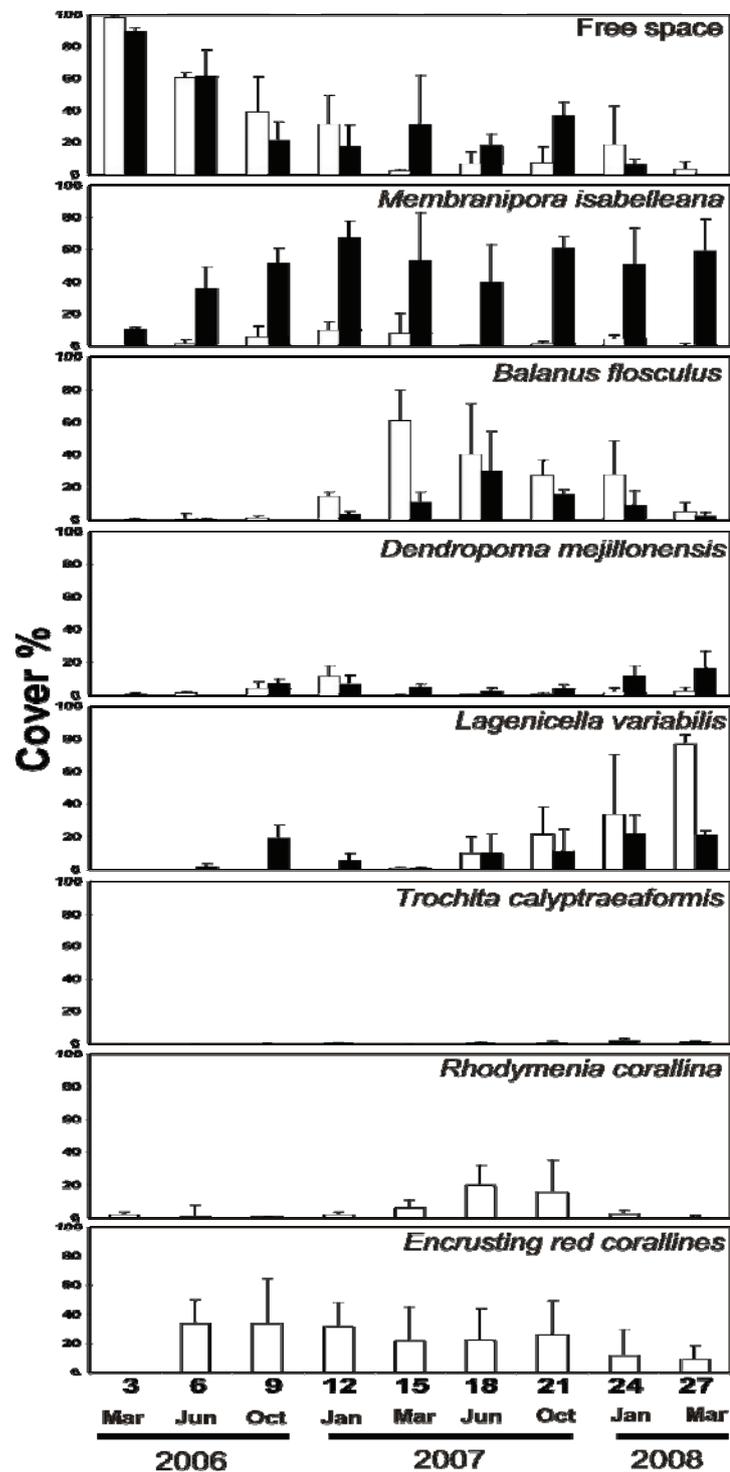


Fig. 2 Mean percentage ( $\pm$  SD,  $n = 3$ ) cover of epibenthic species colonizing exposed (white bars) and hidden (black bars) surfaces during successional development.

Communities found on hidden surfaces also showed significant differences between sampling dates (ANOSIM  $R = 0.47$ ,  $p < 0.05$ ). The nmMDS plot of pairwise comparisons (Fig

## Results

3) indicated that the developing community recorded early in the experiment (months 3 and 6), was highly dissimilar to the ones observed in established stages. Some overlap in composition between the community snapshots recorded at 12, 15, 18 and 21 months was observed, but there were distinct differences in composition between these and the more established community that emerged after 24 and 27 months but also with 9 months. The RELATE seriation analysis indicated a tendency towards a sequential pattern ( $\rho = 0.421$ ,  $p < 0.05$ ) though less clearly than for communities of exposed surfaces.

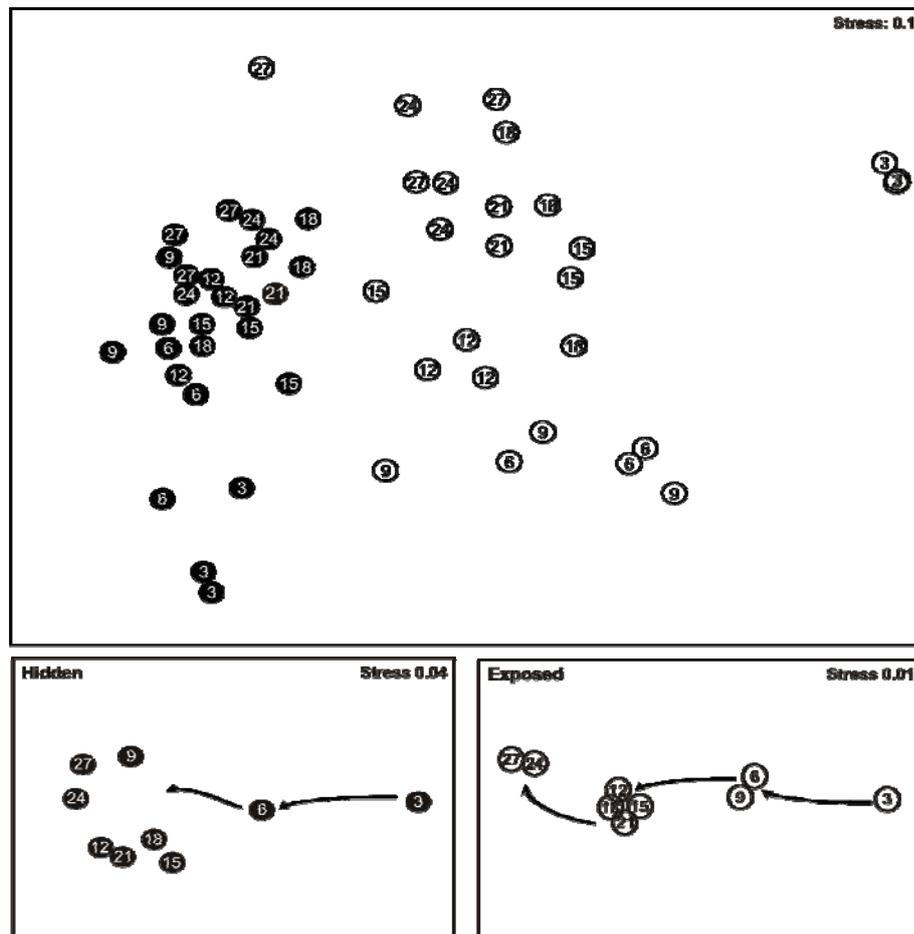


Fig. 3 Non-metric MDS plot (upper) derived from Bray-Curtis measures with square root transformed data of communities developed on exposed surfaces (open circle) and hidden surfaces (filled circle). Non-metric MDS plot derived from Euclidian distance calculated from the R values resulting from pair-wise comparisons after ANOSIM analysis from communities developed on exposed surfaces and hidden surfaces.

### DISCUSSION

Natural rock surfaces are topographically heterogeneous, commonly including a high proportion of hidden microhabitats. These are subject to distinct environmental conditions, and contribute to the diversity of the subtidal landscape. While most ecological studies have focused on exposed substrata, hidden surfaces may support different assemblages, potentially contributing to substantial differences in function and diversity (Richter et al., 2001).

During the 27-month in situ experiment described above, exposed surfaces were colonized by algae and several invertebrates. Colonial forms were dominant in terms of coverage at the end of the experiment. In contrast, hidden surfaces consistently failed to be colonized by any type of algae. Other studies have demonstrated similar reduced algal coverage in hidden and shaded habitats (e.g. Duggins et al., 1990; Glasby, 2000), and the reduced light intensity is mentioned as a likely cause. However, on artificial plots installed in the temperate subtidal system off southern Australia encrustations of corallines have been thriving, even under shaded conditions (Connell, 2005). This may be due to the relatively shallow deployment of artificial substrata in the latter study, at just 3-5 m water depth. Light intensity may not have fallen below the physiological threshold of algal survival in that particular case.

In the present study bryozoans dominated the hidden substratum, which is in agreement with observations from other experiments using hidden plots, where bryozoans were conspicuous settlers (e.g. Duggins et al., 1999; Glasby, 1999b). This distributional pattern reflects the negative phototactic behavior of bryozoan larvae during settlement (Duggins et al., 1999; Glasby, 1999b).

The limpet *Trochita calyptraeiformis* was observed exclusively on hidden surfaces. This may be explained by the behavior of the juvenile (Navarro and Chaparro, 2002; Chaparro et al., 2004), which crawls and grazes on biofilm and detritus deposited on rock surfaces, before settling down to begin life as a sessile and suspension feeding adult (Navarro and Chaparro, 2002; Chaparro et al., 2004). The hidden surfaces on which *T.*

## Results

---

*calyptraeaformis* were found exclusively were dominated by the flat bryozoan *M. isabelleana*. On exposed surfaces the presence of the large, mound-shaped barnacle *B. flosculus* and the erect bushy bryozoan *L. variabilis* may hinder the movements and grazing of juvenile limpets. Another factor in the preference of *T. calyptraeaformis* for cryptic habitats, suggested by our observations on inter- and subtidal rock habitats, may be the protection offered by such cracks and crevices from predatory seastars. Future studies are needed to show whether early settling *T. calyptraeaformis* may attract further specimens to form aggregations, which are frequently observed under boulders in the intertidal and shallow subtidal zone (Gallardo, 1977; Chaparro et al., 1998).

Another notable difference between the two microhabitats is the strong preference of the barnacle *B. flosculus* for exposed surfaces. Settlement on the hidden side of the experimental panels was very scarce. In general, barnacle larvae exhibit positive phototaxis (Barnes and Klepal, 1972) and thus prefer open and exposed surfaces for settlement (e.g. Connell, 1985). The initial abundance is further enhanced by a gregarious tendency whereby larvae from subsequent waves of recruitment are encouraged to settle amongst conspecifics (Matsumura et al., 2000). Differences in species composition on exposed and hidden surfaces lead to dissimilar patterns of coverage during the successional sequence. On exposed surfaces, the pioneer bryozoan *M. isabelleana* was subsequently outcompeted by encrusting red corallines and the barnacle *B. flosculus*. Thus exposed communities display a competitive hierarchy, eventually dominated by the late colonizing *L. variabilis*, whose ability to suppress competitively inferior organisms is an important factor in the late successional sequence. This is in line with observations from other subtidal habitats, in which dominant colonial species (e.g. poriferans, hydrozoas, and corals) overgrow subordinate species by lateral expansion (Jackson, 1977; Teixidó et al., 2007). On hidden surfaces, the bryozoan *M. isabelleana* benefitted from the absence of competitively superior taxa throughout the experiment, despite the subsequent recruitment of *D. mejillonensis* and *B. flosculus*. No overgrowth was observed and thus competitive exclusion was not detected. *Lagenicella variabilis* was recorded on hidden surfaces at the end of the experiment but in

## Results

---

much lower abundance than on the exposed surfaces. However, it is likely that over time colonies will continue to grow and spread out, and that ultimately, overgrowth may occur. This would indicate a slower successional sequence in hidden habitats compared to that on exposed substrata. Likewise, the interactions between algae and invertebrates are critical in the dynamics of space occupancy, but in hidden habitats the absence of algae can alleviate competition for space (Glasby, 1999a,b; Baynes, 1999; Miller and Etter, 2008), which presumably is another factor slowing down the rate of succession.

In conclusion, the successional sequences differed substantially between exposed and hidden habitats during the 27-months in situ experiment. In natural systems, such differences will contribute to overall biodiversity, as pioneer species unable to survive long periods on exposed surfaces may be able to persist on hidden surfaces, from where they may expand by lateral growth to exposed surfaces or migrate when size-specific thresholds are overcome (e.g. Sommer et al., 1999). In particular, hidden communities may also be part of important energy and material pathways (Richter et al., 2001) but they are often ignored, as most succession studies focused on exposed plain surfaces. We suggest that future studies on ecological processes and community succession on hard bottom substrata should also include hidden communities, because these may have an important influence on local community composition and structure.

### ACKNOWLEDGMENTS

We are grateful to T. Ashton, M. Cáceres, I. Fiorillo, C. Guerra, I. Marín, S. Rossi, R. Saavedra, P. Schubert, A. Silva, V. Toro, J. Velez and M. Weiss for their support during diving. Two anonymous reviewers provided constructive comments on the manuscript. This study was conducted in the framework of the EU-funded FP6-INCO-STREP project, "Climate Variability and El Niño-Southern Oscillation: Implications for Natural Coastal Resources and Management" (CENSOR-\-CT-2004-511071) and the Programa Bicentenario de Ciencia y Tecnología RUE-02. This is CENSOR publication N° 380.

### References ♦

---

♦All citation included in this manuscript are compiled in the final list of references

### 4.1.3 Publication III<sup>^</sup>

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

Aldo S. Pacheco<sup>a,b\*</sup>, Jürgen Laudien<sup>a</sup>, Martin Thiel<sup>c,d</sup>, Marcelo Oliva<sup>b</sup>, Wolf Arntz<sup>a</sup>

<sup>a</sup>Alfred Wegener Institute for Polar and Marine Research, D-27568 Bremerhaven, Germany. <sup>b</sup>Facultad de Recursos del Mar, Universidad de Antofagasta, P.O. Box 170, Av. Angamos 601, Antofagasta, Chile, <sup>c</sup>Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile. <sup>d</sup>Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile.

#### Abstract

Community recovery through succession is an important process modulating the composition of benthic soft-bottom communities. Despite frequent disturbance caused by El Niño events, little is known about the community recovery in sublittoral sediments off northern Chile (Humboldt Current Ecosystem). 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 evaluate 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. Forty-one containers with sediment were buried at 14 m water depth off Playa Colorado, Bahía Antofagasta, Chile. During a two year period three replicate containers were sampled every three months using an air-lift device. This allowed to extract the sediment inside a round core (15 cm diameter) previously buried 10 cm deep at the centre of the experimental container. As a reference, the surrounding natural community was surveyed at the same time by taking four haphazardly placed samples. In addition, three containers were installed in each of the four seasons, and the community development described along a one-year period. 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. Seasonality had no evident effect, as all establishing communities converged to the similar composition after one year, regardless when the containers had been installed. This study highlights the strong resilience of northern Chilean sublittoral benthic communities to environmental variations during the cold conditions of the El Niño Southern Oscillation.

**Key words:** Disturbance, colonization, macrozoobenthos, seasonality, soft-bottom community recovery, tolerance succession model

---

<sup>^</sup> This is the author's version of a manuscript submitted to Journal of Sea Research

### 1. Introduction

Although the knowledge on recovery 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 can be much more variable in inter- and subtidal sandy habitats, involving several successional pathways and different endpoints (Zajac et al., 1998; Zajac and Whitlatch, 2003). Thus, recolonization and succession in these highly dynamic systems is complex and hence requests 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 a 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-Gomez, 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 latter species. The sharp abundance decline of opportunistic species is generally a result of biological 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 large and long-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

## Results

---

succession is not 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 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 of juvenile and small adult soft-bottom inhabitants (Armonies, 1994; Zühlke and Reise, 1994; Cummings et al., 1995). Both, larval supply and post-settlement dispersal mechanisms 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; Ólafsson, 1988; Marinelli 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. 1988a,b; 1996; Arntz et al., 2006). During cold and coldest La Niña (LN) conditions, shallow soft-bottoms are typically hypoxic and the community is composed by few species. The intrusion of warm and oxygen-rich waters during El Niño (EN) triggers the development of a much richer and diverse community, suggesting progression towards an advanced successional state (Tarazona et al. 1988a,b; 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

## Results

---

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), however there is no local information on the macrobenthic recovery. The published information on shallow macrobenthic dynamics off northern Chile describes only changes in community diversity and structure during and after EN events (Carrasco and Moreno, 2006; Laudien et al., 2007; Moreno et al., 2008; see review in Thiel et al., 2007) while other important ecological aspects (e.g. succession, colonization processes) have not been studied yet. The present temporal experiment was conducted in a northern Chilean subtidal soft-bottom in order to understand the processes driving community development.

The objectives of this study were (1) to describe the recovery and successional development of the subtidal soft-bottom macrobenthic community over two years, (2) to evaluate 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 in different seasons differ in their community structure after one year of succession.

### **2 Material 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 at the south part of the upwelling influenced Peninsula Mejillones, where cold water with a high nutrient content is present. 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 (< 5 ml O<sub>2</sub> L<sup>-1</sup>, Escribano and Hidalgo, 2001) and below this depth the oxygen minimum zone (< 0.5 ml O<sub>2</sub> L<sup>-1</sup>) extends to deeper waters (~200 m, Escribano et al., 2002). With the intensification of upwelling during summer months the oxygen depleted water can ascend to shallow waters close to the coast (Thiel et al., 2007). Further descriptions of the physical oceanography (e.g. circulation patterns) of the area were described by Escribano and Hidalgo (2001) and Escribano et al. (2002, 2004).

#### **2.2. Experimental set-up**

Forty-one labeled round containers (conical terracotta flowerpots; 40 cm upper diameter, 30 cm lower diameter and 48 cm height) were installed at 14 m water depth by SCUBA divers in June 2006. To allow vertical exchange processes, 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 bays adjoining Peninsula Mejillones (Rojo and Laudien, 2005). We used Calcium-Bentonite (IBECO® AGROMONT S&B Industrial Minerals GmbH, Oberhausen, Germany), which is calcium phyllosilicate generally impure 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 to be

## Results

---

effective in previous colonization studies (e.g. Arntz and Rumohr, 1982, 1986; Veit-Köhler et al., 2008) and avoids environmental impact due to a potential extraction of large in situ quantities of natural sediment.

The distance between containers was  $\geq 1.5$  m and thus adequate to guarantee interspersed (Quinn and Keough 2002). Containers were deployed in two parallel lines and were 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 simultaneously opened the bags and filled the containers. During the course of the experiment, the fouling attached to the exposed 5 cm rim of the containers was removed every month. Every three months three containers were randomly assigned to be sampled.

### ***2.3. Description of the 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) centrally deployed into the experimental container. Each container was sampled just one time. The material retained in the mesh bag (0.5 mm) of the air-lift was further sieved on a 0.5 mm mesh in the field before preservation in a 10% formalin-methanol solution stained with Bengal rose. In the laboratory, organisms were sorted, identified under a stereo microscope to the lowest taxonomic level possible and counted. Taxa were identified using the following references: Polychaeta (Rozbaczylo, 1980), Mollusca (Keen, 1971; Marinovich, 1973; Guzman et al., 1998), Crustacea (Zuñiga, 2002), Urochordata (Sielfeld, 2002). Taxa were identified to either genus or species level, but polychaetes were grouped into families. Such taxonomic resolution has been proven to be adequate in benthic studies (e.g. Warwick 1988). Biomass was recorded as wet mass with a 0.01g 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

## Results

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.



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).

### 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). It was expected that the resulting community shows (1) no seasonal effect, thus the developing communities converged to the same structure, (2) subtle differences in structure (i.e. same abundant species but differences accounted by single components), or (3) substantial differences (different abundant species and structure for each season).

### 2.6. Data analysis

Differences in species richness, abundance and biomass (wet mass) were examined using two-way analysis of variance (ANOVA) with origin (two levels, succession and reference) and time intervals (eight levels, 3, 6, 9 ... 24 months) as fixed factors plus the interaction factor. Prior to the analysis the assumptions of data normality were explored using the Anderson-Darling test. Abundance and biomass data were log transformed to obtain data normality, while values of species richness were processed without transformation. When 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 (nMDS) ordination plots, conducted from a Bray-Curtis similarity matrix after square-root transformation of the data, were used to visualise 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 intervals were compared with their respective reference samples also using ANOSIM. When ANOSIM detected differences, pair-wise 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 pair-wise 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 pair-wise comparisons an

## Results

---

nMDS plot (based on a dissimilarity matrix calculated from Euclidian distances between R-values) was prepared. The nMDS 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, numerically abundant taxa included the cephalochordate *Branchiostoma elongatum*, the bivalves *Tagelus dombeii*, *Linucula pisum*, *Mysella* sp., polychaetes from the families *Cirratulidae* and *Spionidae*, the amphipods *Ampelisca* sp., *Eudevenopus* sp., and ostracods (Table 1). There were no significant differences in species 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 within origin ( $F = 19.46$ ,  $p < 0.001$ ) and within time intervals ( $F = 2.73$ ,  $p < 0.05$ ) but also the interaction factor was significant ( $F = 8.82$ ,  $p < 0.001$ ). The 12-months value accounted for the differences (Tukey test  $p < 0.05$ ). 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 within origin ( $F = 1.18$ ,  $p > 0.05$ ) neither time intervals ( $F = 3.49$ ,  $p > 0.05$ ) and the interaction factor was not significant ( $F = 1.23$ ,  $p > 0.05$ ). Biomass from reference communities showed only minor fluctuations over time and was lower compared to experimental communities (Fig. 2).

## Results

**Table 1. Total abundance (individuals m<sup>-2</sup>) of macrofaunal taxa in experimental containers exposed to different time intervals (in months).**

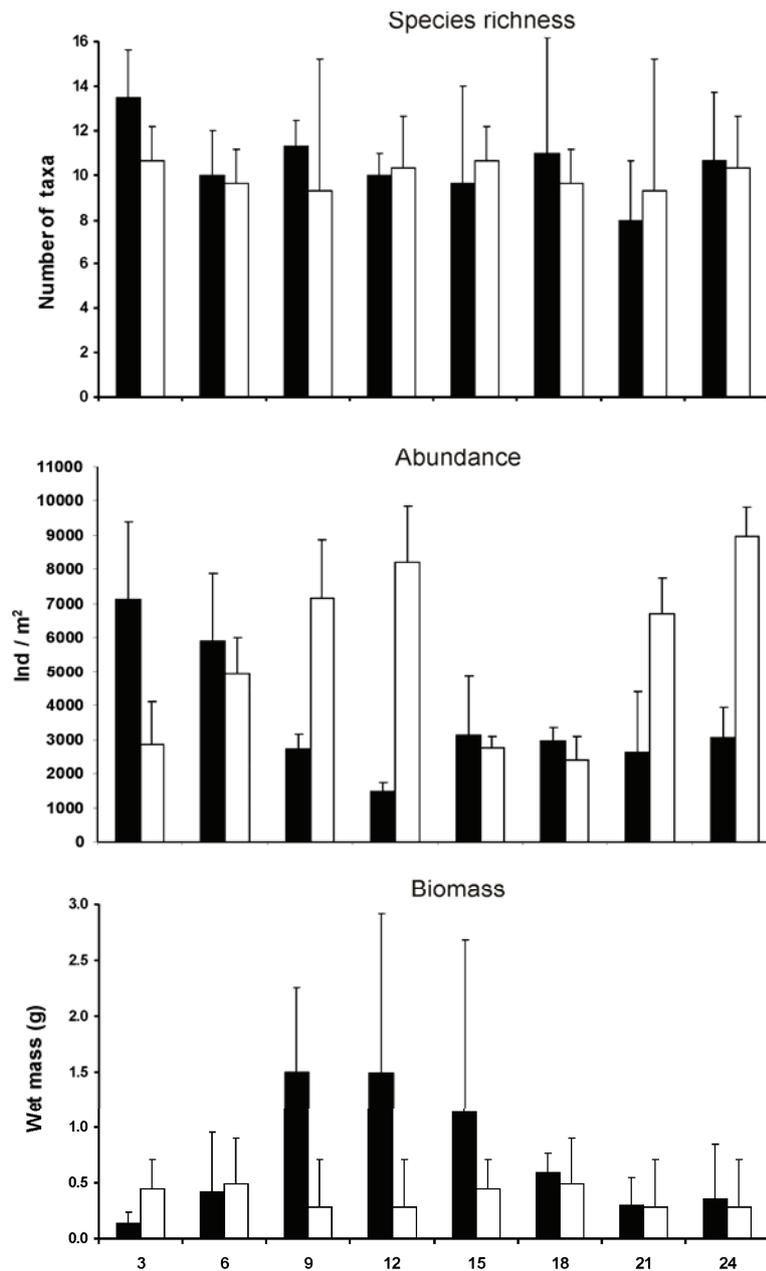
<b>Taxa</b>	<b>3</b>	<b>6</b>	<b>9</b>	<b>12</b>	<b>15</b>	<b>18</b>	<b>21</b>	<b>24</b>
<b>Polychaeta</b>								
Arabellidae	-	-	56	-	-	-	-	-
Cirratulidae	1169	2300	113	94	18	282	-	75
Glyceridae	-	-	-	18	-	-	-	-
Goniadidae	-	-	37	-	-	-	-	-
Lumbrineridae	-	-	18	18	-	-	-	-
Magelonidae	-	-	18	-	-	-	-	-
Maldanidae	-	-	18	-	-	-	-	377
Nephtyidae	-	-	18	56	37	-	-	-
Nereidae	37	-	-	-	-	-	-	-
Orbinidae	-	-	37	-	-	-	-	56
Paraonidae	-	-	37	-	-	-	-	-
Polynoidae	-	-	18	56	37	-	-	-
Spionidae	3225	2093	829	94	2018	1112	1791	1075
<b>Crustacea</b>								
<i>Ampelisca</i> sp.	339	75	37	-	56	-	18	94
Aoridae	-	-	-	-	264	113	18	94
<i>Biffarius pacificus</i>	75	-	-	37	18	18	-	18
<i>Cancer coronatus</i>	94	37	-	-	-	-	-	-
Dyastilidae	56	18	-	-	-	18	-	-
<i>Eudevenopus</i> sp.	961	169	245	37	75	226	245	94
Gammaridae indet.	75	18	-	-	-	-	-	-
<i>Harpinia</i> sp.	18	-	-	18	-	94	-	-
<i>Latreutis antiborealis</i>	-	-	-	-	-	-	-	18
Ostracoda	207	207	-	132	37	226	94	282
<i>Pagurus edwardsii</i>	18	-	18	-	-	-	-	-
<i>Pagurus gaudichaudii</i>	-	-	-	-	56	56	-	-
<i>Pagurus perlatus</i>	37	-	-	-	-	-	18	-
<i>Pagurus villosus</i>	-	-	-	-	56	18	-	56
<i>Pinnixa transversalis</i>	-	-	56	-	18	-	37	-
<i>Platyxanthus orbigny</i>	-	-	-	-	-	18	-	-
<b>Gastropoda</b>								
<i>Cancellaria buxinoides</i>	-	-	-	18	18	-	-	-
<i>Crucibulum</i> sp.	-	-	-	-	-	-	-	18
<i>Fissurella</i> sp.	-	-	-	18	-	-	-	-
<i>Mitrella unisfaciata</i>	-	-	-	-	-	37	-	-
<i>Nassarius gayi</i>	37	169	37	37	18	226	75	113
<i>Oliva peruviana</i>	-	-	-	-	-	-	18	-
<i>Polinices uber</i>	-	18	-	-	-	-	-	-
<i>Priene scabrum</i>	-	-	-	-	-	37	-	-
<i>Tegula luctuosa</i>	-	-	-	18	-	-	-	-
<i>Xanthochorus cassidiformis</i>	-	-	-	-	-	18	-	-
<b>Bivalvia</b>								
<i>Argopecten purpuratus</i>	-	-	37	-	-	18	-	18
<i>Choromytilus chorus</i>	-	-	18	-	-	-	-	-
<i>Linucula pisum</i>	169	37	-	75	37	282	-	18
<i>Macoma</i> sp.	-	37	-	-	-	-	-	-
<i>Mysella</i> sp.	-	37	18	75	18	18	18	358
<i>Semelle solida</i>	-	-	18	-	-	-	-	-
<i>Tagelus dombeii</i>	37	94	867	641	207	18	113	207
<b>Nemertina</b>								
Indeterminate	-	-	-	-	-	-	18	56
<b>Chordata</b>								
<i>Branchiostoma elongatum</i>	546	584	169	-	132	94	169	-
<b>Total</b>	<b>7110</b>	<b>5903</b>	<b>2734</b>	<b>1489</b>	<b>3130</b>	<b>2942</b>	<b>2640</b>	<b>3036</b>

## Results

**Table 2. Total abundance (individuals m<sup>-2</sup>) of macrofaunal taxa recorded from the control community at distinct time intervals (in months) resembling the sample intervals of the succession experiment.**

	3	6	9	12	15	18	21	24
<b>Polychaeta</b>								
Capitellidae	141	-	-	-	127	-	-	-
Cirratulidae	-	14	42	84	-	14	42	84
Glyceridae	-	28	-	-	-	-	-	-
Lumbrineridae	28	-	42	-	28	-	28	-
Nephtyidae	84	28	28	-	84	28	42	-
Orbinidae	-	28	-	-	-	28	-	-
Polynoidae	14	-	-	-	28	-	-	-
Spionidae	2051	1315	5221	5702	2122	990	5037	6579
<b>Crustacea</b>								
<i>Ampelisca</i> sp.	113	-	226	226	99	-	198	240
Aoridae	56	452	28	56	56	283	14	42
Decapodito (Brachyura)	28	-	-	-	14	-	-	-
Dyastilidae	14	-	14	-	14	-	14	-
<i>Eudevenopus</i> sp.	-	2264	1061	1400	-	707	933	1174
<i>Harpinia</i> sp.	-	212	-	-	-	70	-	-
Ostracoda	28	42	99	226	28	42	70	254
<i>Pagurus gaudichaudii</i>	-	169	-	-	-	-	-	-
<i>Pagurus villosus</i>	-	28	28	28	-	28	14	28
<b>Gastropoda</b>								
<i>Cancellaria buxinoides</i>	28	-	-	-	28	-	-	-
<i>Oliva peruviana</i>	-	14	-	-	-	-	-	-
<i>Polinices uber</i>	-	14	28	42	-	-	14	42
<b>Bivalvia</b>								
<i>Linucula pisum</i>	-	28	28	28	-	28	42	28
<i>Macoma</i> sp.	-	-	14	14	-	-	42	14
<i>Mysella</i> sp.	212	198	56	183	127	99	14	240
<i>Tagelus dombeii</i>	-	28	127	141	-	28	127	141
<b>Nemertina</b>								
Indeterminate	56	14	42	14	14	14	14	14
<b>Chordata</b>								
<i>Branchiostoma elongatum</i>	-	28	70	56	-	28	56	70
<b>Total</b>	2858	4910	7159	8207	2773	2391	6707	8956

## Results



**Fig. 2 Summary of the changes of primary community parameters detected during the colonization experiment. Data from the experimental containers shown in black bars (mean  $\pm$  SD; n = 3) and respective controls are in white bars (mean  $\pm$  SD; n = 4).**

Comparisons of the community structure from 3 to 24 months showed significant differences between treatments (one-way ANOSIM,  $R = 0.51$ ,  $p < 0.05$ ). Clearly only 15 and 21 months old experimental communities were overlapping, while the rest indicated high 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

## Results

---

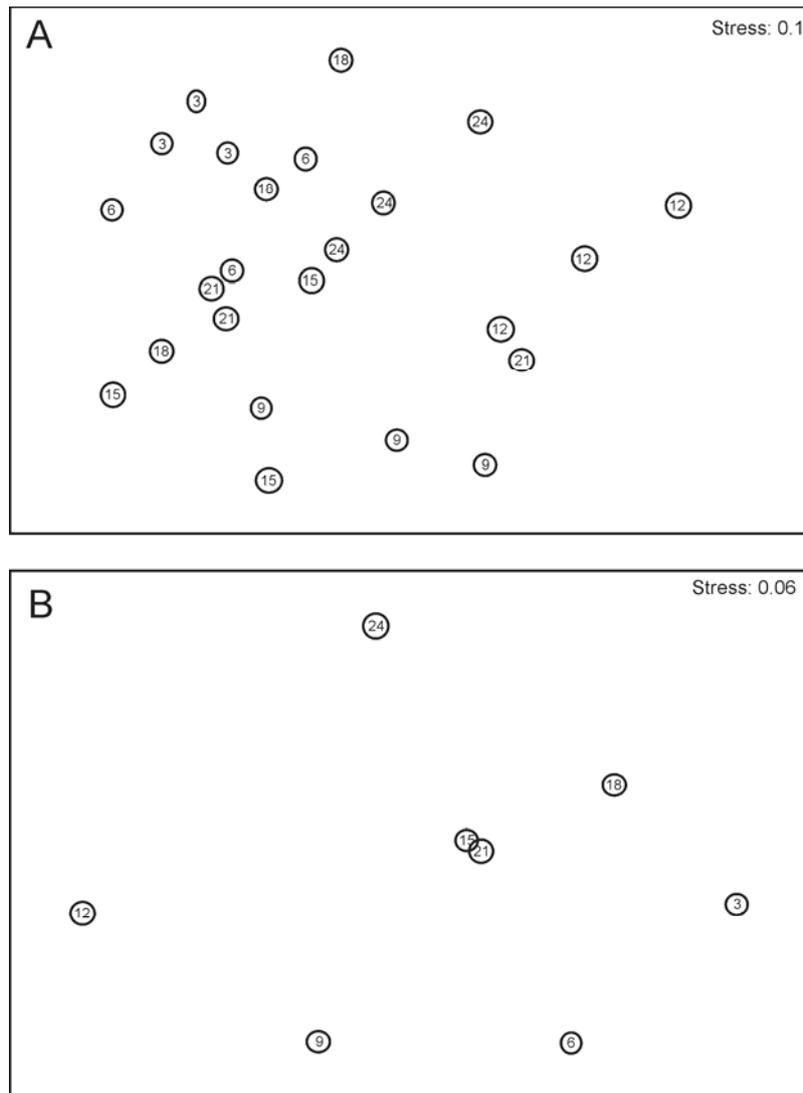
stages did not differ from the dissimilarity detected between 9- and 21-month-old stages. The absence of a consecutive pattern was supported by the RELATE analysis, which did not show any tendency of seriation ( $\rho = 0.105$ ,  $p > 0.05$ ). The proportions of distinct feeding groups encountered during 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 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.

**Table 3. R-values resulting from ANOSIM comparing community stages of different developmental time intervals (in months) and reference from respective surrounding community (C) (\*  $p < 0.05$ ).**

	R	p
3 vs C	0.833	0.02*
6 vs C	0.704	0.05
9 vs C	0.778	0.02*
12 vs C	1	0.02*
15 vs C	0.63	0.02*
18 vs C	0.315	0.08
21 vs C	0.389	0.02*
24 vs C	0.648	0.02*

## Results



**Fig. 3 (A) Non-metric MDS plot of community structure calculated from Bray-Curtis measures after square root transformation showing the community after distinct time intervals. (B) Non-metric MDS plot of community structure calculated from Euclidian distance from pair-wise R-values after ANOSIM from communities after distinct development times.**

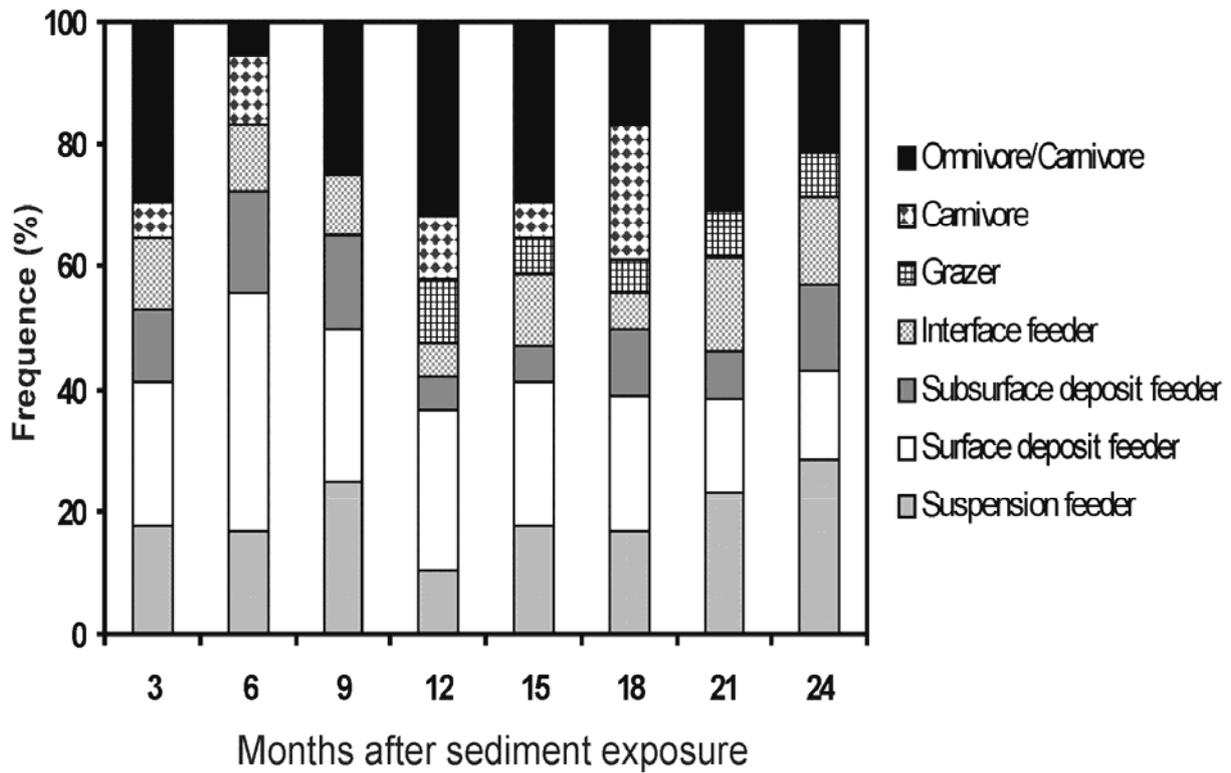


Fig. 4 Feeding groups proportional to the total abundance distributed throughout the colonization experiment.

### 3.2. Seasonal onset on soft-bottom colonization

The seasonal onset showed no effect in any of the parameters analyzed: there were no detectable effects on number of taxa, 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.

## Results

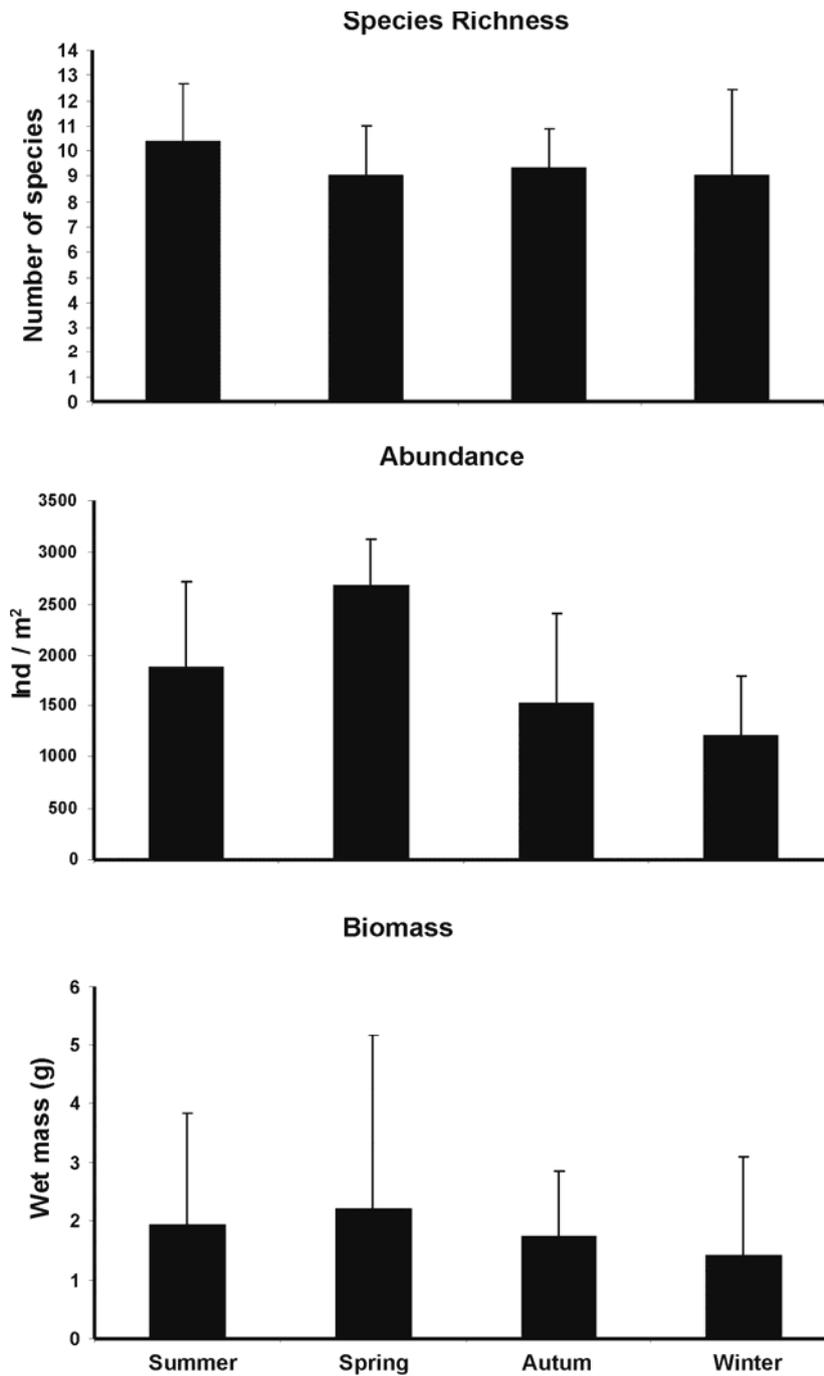


Fig. 5 Summary of the changes on primary community parameters after distinct seasonal onsets of the colonization.

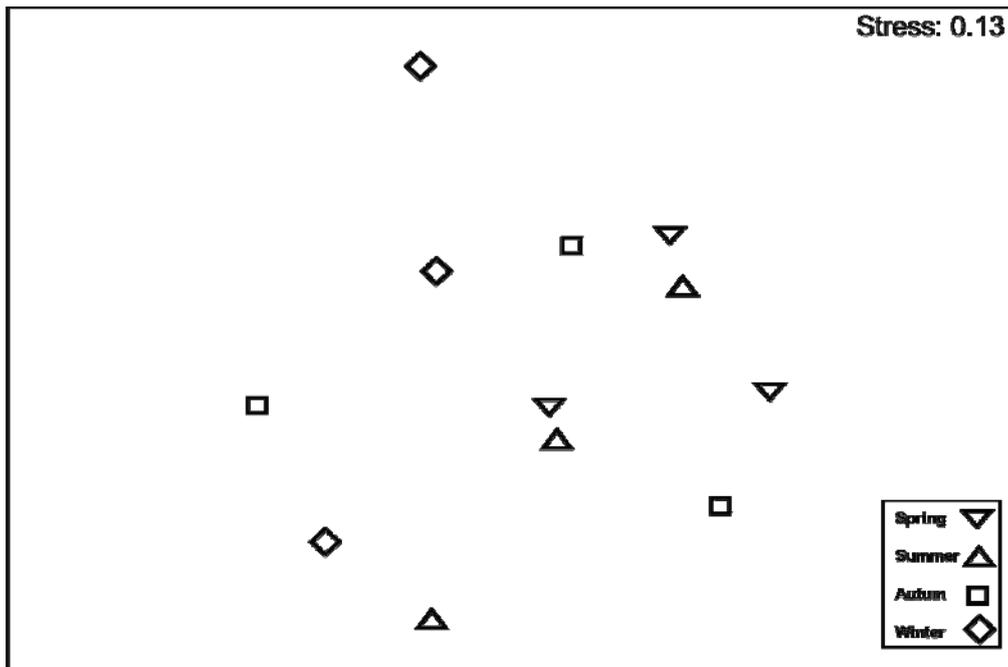


Fig. 6 Non-metric MDS plot of community stages starting to develop after different seasonal onsets and calculated from Bray-Curtis similarities of square root transformed data; Su: summer; Wi: winter; Au: autumn; Sp: spring.

#### 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; Berger, 1990). Our study provides evidence that succession in northern Chilean sandy subtidal habitats are more variable and does not include distinguishable seral stages, which are more 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,

## Results

---

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, *Eudevenopus* sp., Ostracoda, *Nassarius gayi*, *Mysella* sp. and *Tagelus dombeii*) were present since the beginning and persisted throughout the entire 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 recovery through succession after 3 disturbance (hypoxia) events and concluded that there are no successive patterns in species composition or densities during recolonization. This is in accordance with Zajac and Whitlatch (2003), who suggested that the dynamics of succession in sandy intertidal flats are complex due to the highly variable responses of species populations to disturbances, obscuring the identification of clear stages. 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 response, which is reflected in a variable community structure (Zajac and Whitlatch, 1991) and thus the observed successional pathway.

### **4.2 Succession and feeding groups**

Distinct feeding groups encountered during the colonization process occurred at equal proportions throughout the experimental time, which again is in contrast to most

## Results

---

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; Nilsson and Rosenberg, 2000; Zajac et al., 1998; Van Colen et al., 2008). Changes 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). This result provides support for the tolerance model (discussed below), because the distribution of the feeding groups suggest that the community is composed of species capable to efficiently exploit resources, presumably each specialized on different kinds of resources (Connell and Slatyer, 1977).

### **4.3 Resemblance to the surrounding community**

Resemblance to the reference communities (in this case, equal or very similar species richness and 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 month 9, 12 and 15 due to the presence of the comparative large bivalves *Argopecten purpuratus* and *Tagelus dombeii*. In absence of these large species, biomass values from experimental and reference communities were similar. Arntz and Rumohr (1982) showed that during succession biomasses of experimental communities remained lower than those of the natural communities, while species richness and abundance displayed a fast recovery. Hence, it is suggested that biomass, is not an

optimal indicator of recovery, and that species richness and abundance can be more informative.

Experimental studies examining the recovery of small patches of disturbed sediment have shown that recovery depends on local environmental characteristics. While shallow subtropical areas recover through succession 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 four years (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 produce a resemblance with the environmental conditions in temperate zones. Under colder conditions convergence of experimental and natural communities requires even more time. In Polar regions, several decades are necessary to develop mature macrobenthic communities after severe iceberg scouring (e.g. Conlan and Kvitek, 2005; Bowden et al., 2006; Teixidó et al., 2007).

#### **4.4 Soft-bottom succession follows the Tolerance Model**

Connell and Slatyer (1977) mentioned that the Tolerance Model will be 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 benthos of Antofagasta Bay. Similar to other areas of the Humboldt Current System, shallow macrobenthic communities are principally controlled by oxygen concentration and water temperature (Tarazona et al., 1988a,b, 1996; Gutiérrez et al., 2000; Palma et al., 2005; Sellanes et al., 2007). Particularly, the rise of the oxygen minimum zone ( $< 0.5 \text{ ml O}_2 \text{ L}^{-1}$ ) to shallow water depths is an important factor modulating the bathymetric distribution of

## Results

---

benthic communities in this region (see review in Thiel et al., 2007). In the area around Peninsula Mejillones waters with low oxygen concentrations can be found as shallow as 10 m depth (e.g. Escribano et al., 2002; Laudien et al., 2007), thus potentially impacting normally oxygenated benthic communities. According to Escribano and Hidalgo (2001), the shallowest waters of Antofagasta Bay are poor in oxygen content, especially during summer months when upwelling is more intense and upwelled waters can bring low oxygen to the shallow bottoms impacting benthic communities. 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. flatfishes *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. For example, in the common crab *Cancer setosus* prey consumption rates decrease about 3-fold under hypoxic conditions (Cisterna et al., 2008; see also Bernatis et al., 2007 for a similar case with *Cancer magister*). It is likely that communities at El Colorado are adapted to resist hypoxic events and therefore the assumptions of the model are fulfilled.

### **4.5 Effect of the season during 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 succession, but a convergence towards a similar composition at later stages (Diaz-Castañeda et al., 1989; Rosenberg, 2001; Lu and Wu, 2007). In the same area 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

## Results

---

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). Further north in Iquique Bay (20°11'S; 70°10'W) shallow macrobenthic communities between 9 and 30 m depth also showed persistence in structure with spionid polychaetes as abundant components (Quiroga et al., 1999).

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; Zühlke and Reise, 1994; Cummings et al., 1995; Reise, 2002; Zajac and Whitlatch 2003). Motile taxa such as amphipods *Eudevenopus* sp., *Harpinia* sp., *Ampelisca* sp., the lancelet *Branchiostoma 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 larval settlement events (Van Colen et al., 2008), and both colonization mechanisms are important even at small new habitats patches.

In conclusion, macrobenthic development of small azoic sediment patches located in shallow northern Chilean habitats follows 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 composition 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.

### ***Acknowledgments***

We are grateful to T. Ashton, M. Cáceres, I. Fiorillo, P. Lira, C. Guerra, I. Marín, S. Rossi, R. Saavedra, P. Schubert, A. Silva, J. Velez and M. Weiss for their support during diving work. We thank Guillermo Guzman for his help in identifying crustaceans and polychaetes. This study was conducted in the framework of the EU-funded FP6-INCO-STREP project, “Climate Variability and El Niño-Southern Oscillation: Implications for Natural Coastal Resources and Management” (CENSOR-CT-2004-511071) and the Programa Bicentenario de Ciencia y Tecnología RUE-02. This is CENSOR publication N°...

### **References ♦**

---

♦All citation included in this manuscript are compiled in the final list of references

## 4.1.4 Publication IV

Helgol Mar Res (2008) 62 (Suppl 1):S107–S110  
 DOI 10.1007/s10152-007-0084-5

SHORT COMMUNICATION

## First record of *Cymatium keenae* Beu, 1970 (Mollusca: Ranellidae) from Antofagasta Bay, northern Chile, in connection with El Niño events

Tom Ashton · Jose M. Riascos · Aldo Pacheco

Received: 12 May 2007 / Revised: 21 June 2007 / Accepted: 26 June 2007 / Published online: 13 October 2007  
 © Springer-Verlag and AWI 2007

**Abstract** *Cymatium (Monoplex) keenae* Beu, 1970, the neopolitan triton, is a Ranellidae predator distributed in tropical and subtropical waters. In this study we report this species for the first time in Antofagasta Bay, northern Chile. Adult specimens have been found since June 2003 at depths ranging from 5 to 15 m in La Rinconada Marine Reserve (23°28'18"S, 70°30'46"W) in Antofagasta Bay, near a scallop farming facility. The present findings clearly extend the geographic range of *C. keenae*, which previously had been reported from La Paz, Gulf of California (Mexico) to Galápagos Islands (Ecuador) in the SE Pacific. Previous evidence strongly suggests that the intrusion of this tropical immigrant can be related to warm El Niño episodes. We analyze the key role of the oceanographic characteristics of Antofagasta Bay as potential temporal refuge for this species.

**Keywords** ENSO · Geographic distribution · Ranellidae · Antofagasta Bay · Range extension

Communicated by Sven Thatje.

Special Issue: S. Thatje (ed.), Climate variability and El Niño Southern Oscillation: implications for natural coastal resources and management.

T. Ashton  
 Gatty Marine Laboratory, School of Biology,  
 University of St. Andrews, Fife KY168LB, UK

J. M. Riascos (✉) · A. Pacheco  
 Instituto de Investigaciones Oceanológicas,  
 Universidad de Antofagasta, Av. Angamos 601,  
 Casilla 170, Antofagasta, Chile  
 e-mail: josemar.rv@gmail.com

### Introduction

The marine fauna of the Chilean coast is characterized by a complex interaction of tropical, subtropical and sub-Antarctic elements, a high level of endemism and a close association to climate and oceanographic features, notably sea surface temperature (Castilla 1979; Camus 2001). Particularly the northern and central Chilean coast (between 18° and 36°S) has been under the disturbing influence of the El Niño-Southern Oscillation (ENSO) since its mid-Holocene development (Moy et al. 2002). Indeed, ENSO now constitutes a critical component for defining the current biogeography of this area (Fernández et al. 2000; Camus 2001).

During warm episodes, warm water masses of low oxygen concentration from oceanic and equatorial regions enter the upwelling zones of Peru and Chile, bringing a variety of tropical immigrants (Arntz et al. 2006). These episodic incursions of tropical species during the warm El Niño (EN) phase of ENSO has been well described (e.g., Díaz and Ortlieb 1993; Paredes et al. 2004; Castilla et al. 2005) and seems to be a common characteristic of those regions in the past (De Vries 1987; Guzmán et al. 2001). However, little is known about how long these temporal invaders thrive after EN conditions and which environmental setting could allow those species to persist. In this study, we report the presence of the tropical gastropod *Cymatium (Monoplex) keenae* Beu, 1970 for the first time for Chilean waters. We discuss the role of El Niño as the mechanism explaining the extension of its distributional range and the importance of the oceanographic characteristics of Antofagasta Bay as a refuge for this species under La Niña conditions.

## Methods

Specimens of *Cymatium keenae* were collected in February and November 2006 at La Rinconada Marine Reserve (23°28'18"S, 70°30'46"W), Bay of Antofagasta (Fig. 1). The samples were taken during SCUBA diving expeditions, at a depth ranging between 15 and 5 m near a scallop farming facility. Two divers covered about 600 m<sup>2</sup> area during 2 h immersion each time. The collected specimens were brought to the laboratory and the shell length (SL: length from the apex to the end of the siphonal canal) was measured to the nearest 0.1 mm.

Local collections of shells in Antofagasta were checked to assess previous occurrences of this species. The taxonomic determination was confirmed by C. Paredes (Laboratorio de Biología y Sistemática de Invertebrados Marinos, Universidad Nacional Mayor de San Marcos, Lima, Perú).

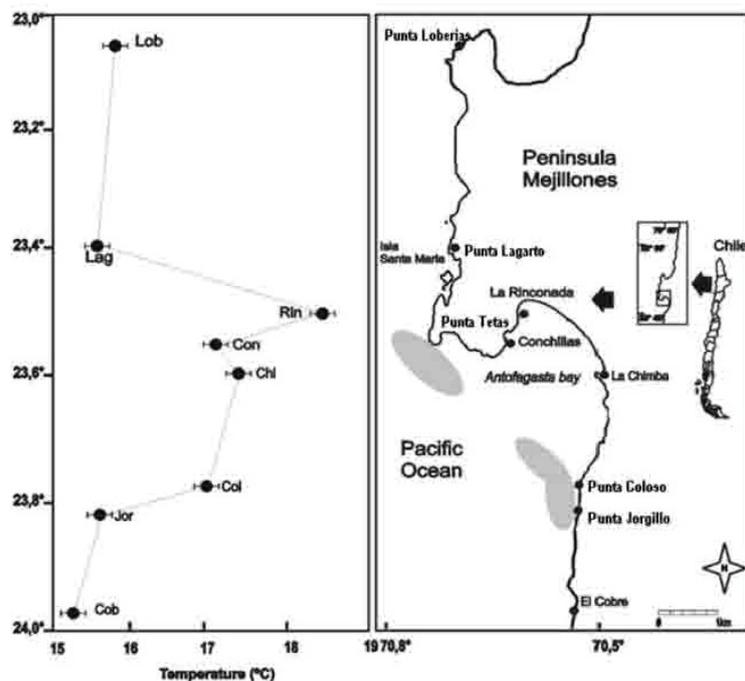
## Results and discussion

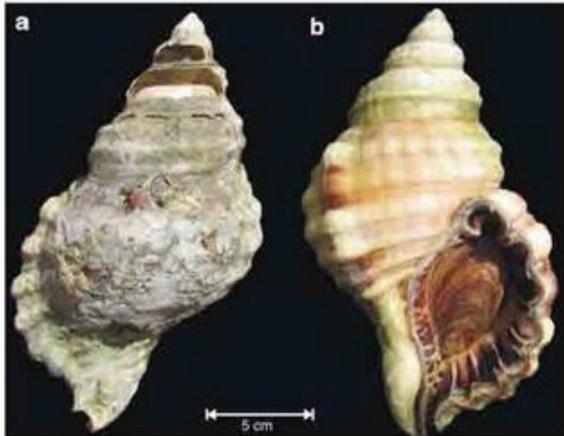
*Cymatium keenae* was found in a soft-bottom community dominated by the scallop *Argopecten purpuratus*, and the bivalves *Transennella pannosa* and *Tagelus dombeii* as well as predatory gastropods, such as the muricids *Stramonita chocolata* and *Xanthochorus cassidiformis*. Two adult specimens of *C. keenae* were found in February 2006: a live specimen (SL = 134.0 mm) and an empty shell (SL = 142.9 mm). A second live specimen was found in

November 2006 (SL = 115.4 mm). One of the live specimens was extremely eroded on the dorsal surface and bore evidence of polychaete infestation, the second and third whorls were broken open and showed signs of internal repair (Fig. 2) while the other one did not show erosion evidence. Review of local collections rendered an additional adult shell (SL = 153 mm; Miguel Avendaño private collection, Universidad de Antofagasta). The specimen, without erosion evidence, was collected alive in June 2003 at the La Rinconada, and it was observed among three other adult specimens while performing an annual survey of the scallop bed (M. Avendaño, personal communication).

Species of *Cymatium* Röding, 1798 are widely distributed marine gastropods belonging to the family Ranellidae and inhabiting warm waters around the world (Skoglund 2002). This genus is known as a predator of wild and farmed bivalve species in a variety of tropical locations (Perron et al. 1985; Urban 2000; Freitas et al. 2000). Formerly recognized as *Cymatium (M.) parthenopeum keenae* (Keen 1971), *C. keenae* has been recorded as living in warm-water environments in the tropical eastern Pacific with a southern limit in Galápagos at 1°S (Keen 1971; Skoglund 2002) although it has been occasionally found in Pucusana (12°28'S) and Paracas (13°50'S) at the Peruvian coast (Diaz and Ortlieb 1993). The present findings add an additional 10° of latitude (about 1,300 km coastal distance) to the occasional report of *C. keenae* from Pucusana, and 22° of latitude to the species previous southern limit at the Galápagos Islands.

**Fig. 1** Map of La Rinconada, in Antofagasta Bay in northern Chile. Upwelling centres in front of Punta Tetras and Punta Coloso are marked with grey shading. The left graph shows mean sea surface temperature (and standard errors) from 1997 to 2003 obtained from thermistors placed inside and around the bay (adapted from Piñones et al. 2007; Castilla et al. 2002)





**Fig. 2** *Cymatium (Monoplex) keenae* (SL = 134.0 mm) collected in Antofagasta Bay in November 2006. **a** Dorsal view showing erosion and polychaete infestation. **b** Ventral view without shell damage

mouth. Thus, upwelled waters are retained inside the bay long enough for temperatures to be elevated by several degrees through surface heating. The bay therefore exhibits surface temperatures between 2° and 4° higher than surrounding waters, (Castilla et al. 2002; Piñones et al. 2007) allowing it to act as an isolated refuge for occasional arrivals from warmer waters.

**Acknowledgments** The authors would like to thank Carlos Paredes for providing important assistance regarding the taxonomy of the reported species. Miguel Avendaño is thanked for allowing access to his collection. Marcela Clarke and Ricardo Guíñez provided useful literature. Thanks to Sven Thatje, Martin Thiel, Javier Calcagno, and an anonymous reviewer for providing constructive comments on the manuscript. This study was conducted in the framework of the EU-funded INCO project, “Climate Variability and El Niño-Southern Oscillation: Implications for Natural Coastal Resources and Management” (CENSOR) and Programa Bicentenario de Ciencia y Tecnología RUE-02. This is CENSOR publication No. 115.

The arrival of *C. keenae* in Peruvian waters was attributed to EN, as it was only observed after major EN episodes (Diaz and Ortlieb 1993). During these events, warm water masses from oceanic and equatorial regions enter the upwelling zones, thus transporting meroplanktonic larvae of tropical origin (Arntz et al. 2006). This is most likely the mechanism explaining the arrival of *Cymatium keenae* to Antofagasta Bay. This species has been shown to have the potential for long-distance trans-oceanic larval dispersal and the possibility to delay metamorphosis in order to facilitate long distance larval transport (Pechenik et al. 1984).

Although these are the first reported findings of this species at La Rinconada, adult *C. keenae* have been found since June 2003. This, and the fact that *C. keenae* is commonly known by local fishermen, who recognize it as “Caracol Perro”, indicate that at least some specimens are capable of long term persistence in this bay. Viable populations of the tropical gastropods *Aplysia juliana* and *Linaetella weigmanni* have been established in Antofagasta Bay after their arrival during EN (Tomacic 1985; Guzmán et al. 1998; Castilla et al. 2005). The question remains if this is the case for *C. keenae*. So far only adult specimens have been found, which would suggest that a reproductive population has not yet formed.

Antofagasta Bay has been shown to play a critical geographical distribution “stepping stone” role for sub-tropical invaders into Chilean waters (Castilla et al. 2005). The oceanographic characteristics of this bay are unique, since it is one of the few bays in Chile facing southward. On the other hand, it is located between two active upwelling centres (Punta Tetos and Punta Coloso, Fig. 1). This creates an “upwelling-shadow” with an almost constant sea water temperature frontal oceanographic structure crossing the

## References<sup>♦</sup>

<sup>♦</sup> All citation included in this publication are compiled in the final list of references

## 4.1.5 Publication V

THE VELIGER

© CMS, Inc., 2007

The Veliger 50(3):000–000 (July XX, 2008)

*Dendropoma mejillonensis* sp. nov. a New Species of Vermetid (Mollusca: Caenogastropoda,) from Northern ChileALDO PACHECO<sup>1,\*</sup> AND JÜRGEN LAUDIEN<sup>2</sup><sup>1</sup> Universidad de Antofagasta, Facultad de Recursos del Mar, Av. Angamos 601, PO Box. 117, Antofagasta, Chile<sup>2</sup> Alfred Wegener Institute for Polar and Marine Research, D-27568 Bremerhaven, Germany

**Abstract.** *Dendropoma mejillonensis* sp. nov. is described based on morphology for the first time. This vermetid gastropod inhabits the rocky subtidal zone of Península Mejillones in northern Chile. In July 2006, specimens were collected by SCUBA divers from the rocky “Anemones Wall” (23°28'17.30"S, 70°37'13.80"W) at 17 m depth. The morphology of *D. mejillonensis* is distinguished from that of other members of the family by its pointed lip on the external border of the protoconch and the two white bands on the head tentacles. This extends the geographical range of the genus *Dendropoma* into the Southeastern Pacific. The present species *D. mejillonensis* is the only known vermetid gastropod able to thrive under the cold upwelling conditions of the Humboldt Current ecosystem off northern Chile.

## INTRODUCTION

Marine gastropods of the family Vermetidae are sessile organisms with an irregular, uncoiled shell providing a three-dimensional biogenic habitat for associated species. Their distribution is restricted to tropical and subtropical latitudes (Mexico, California and West Africa) as well as to locations in the warm Mediterranean Sea (Keen, 1961, 1971; Schiaparelli et al., 2003). Habitats are rocky intertidal and subtidal zones with warm and oxygenated waters (Keen, 1961; Calvo et al., 1998). Due to the irregular tube form, taxonomic identification has commonly been confused with *Vermicularia* (Turritellidae) (Bieler, 1996) and Serpulid polychaetes (Keen, 1961, 1971) resulting in a confused taxonomic status. The morphological characters deemed useful for taxonomic identification have changed over time (Bieler, 1995; Schiaparelli & Métivier, 2000). A genetic study further concluded that disjunct populations of *Dendropoma* species are close phylogenetic relatives (Rawlings et al., 2001), thus suggesting that taxonomic determination should be approached carefully.

The genus *Dendropoma* (Mörch, 1861) was reviewed by Keen (1961) on the basis of 10 species distributed among tropical and subtropical locations. Distinctive morphological characteristics for this genus are planorboid early whorls that become more loosely coiled in later stages; and the sculpture of lamellar growth-striations that may or may not be intersected by longitudinal lines, sinuous and rising toward a crest near the outer edge of the whorl in most species. The

operculum is well developed and equal in diameter to the aperture. At present, the genus *Dendropoma* covers intertidal and sublittoral species and can be gregarious or solitary. So far, the most comprehensive information about *Dendropoma* spp. taxonomy is provided by Hadfield et al. (1972) for specimens found off Hawaii.

Information on the distribution of vermetids off continental Chile and its offshore islands is scarce and the taxonomic status is still uncertain (Rehder, 1980; Ramírez & Osorio, 2000; R. Bieler pers. comm.). In fact, extensive reviews of gastropod taxonomy and studies of invertebrate biogeographic patterns available from this coast do not mention the family in the region (Marincovich, 1973; Guzmán et al., 1998; Brattström & Johanssen, 1983; Valdovinos, 1999; Lancellotti & Vásquez, 2000). Anecdotally, vermetids have been observed associated with holdfasts of the kelp *Lessonia trabeculata* Villouta & Santelices, 1986 off central Chile (Vásquez & Vega, 2004). With the exception of the latter observation, there is no published evidence from the Chilean coast. Nonetheless, *Dendropoma platypus* Mörch, 1861; *Dendropoma* spp. and *Serpulorbis* Sassi, 1827 have been recorded from Easter Island (Rehder, 1980; Ramírez, 1987; Valdovinos, 1999) and *Serpulorbis* sp. was also observed at Robinson Crusoe Island (Juan Fernández archipelago) (Ramírez & Osorio, 2000), both insular Chilean locations.

Northern Chile forms part of the Humboldt Current upwelling ecosystem, which is characterized by year-round high levels of primary production due to wind-driven cold upwelling water, which returns nutrients to the euphotic zone (Barber & Smith, 1981). There is a shallow oxygen minimum zone (OMZ) and only the upper 40 m are well oxygenated (Arntz et al., 2006).

\* Tel.: 056-55-637404, Email: babuchapv@yahoo.com

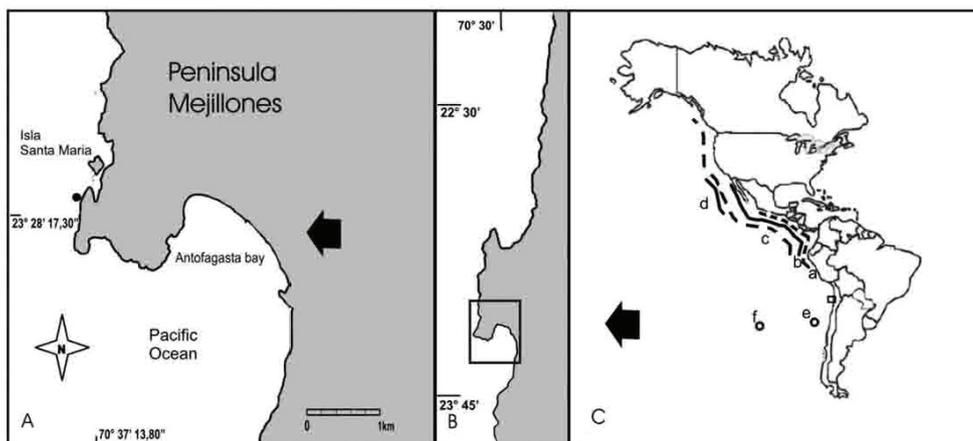


Figure 1. A. Sampling location "Anemones Wall" ( $23^{\circ}28'17.30''\text{S}$ ,  $70^{\circ}37'13.80''\text{W}$ ) opposite the southeastern side of Isla Santa Maria. B. Peninsula Mejillones. C. Distributional range of related vermetid species (a) *Petalonchus innumerabilis* (b) *Serpulorbis squamigerus* (c) *Vermetus compta* (d) *Dendropoma rastrum* (e) *Serpulorbis* sp. (f) *Dendropoma platypus*.

This habitat is very different from that of warm-water subtropical and tropical vermetid species. In this study *Dendropoma mejillonensis* sp. nov. is described from Peninsula Mejillones, a location within this particular upwelling system. A detailed morphological characterization is provided.

#### MATERIAL AND METHODS

Individuals of *Dendropoma mejillonensis* sp. nov. colonizing a vertical rock wall in the subtidal zone (17 m depth) of Peninsula Mejillones ( $23^{\circ}28'17.30''\text{S}$ ,  $70^{\circ}37'13.80''\text{W}$ ) were photographed and collected by SCUBA divers on July 11th, 2006 (Figure 1A, B). Several vermetid clusters were scratched from the rock with a knife and maintained in the laboratory for observations. Measurements were taken with a digital caliper or by using calibrated eyepieces on a dissecting microscope. Photographs were taken with a Canon Power Shot S50 camera connected to a binocular microscope Olympus SZ61. Animals were anesthetized by adding methanol drops in the small examination containers before sacrificing. Soft bodies were removed from the shell after cracking with a small clamp. Gross anatomy of the soft parts was studied under a dissection microscope. Air-dried shells, radula, protoconch and opercula were observed and photographed, using the scanning electronic microscope JEOL, model JSM- 6360LV.

#### Diagnosis

##### Genus *Dendropoma* Morch 1861

Solitary to colonial forms, corroding a trench in the substrate, in which the lower part of each volution is

embedded; coiling planorboid in early whorls, becoming looser in later whorls, with tendency toward right-angle turns. The color of the adult is mostly white, intermittently stained with dark brown, especially within. The sculpture of lamellar growth-striations, that may or may not be intersected by longitudinal lines, is sinuous and rises toward a crest near the outer edge of the whorl in most species. Two nuclear whorls are dark brown in color, inflated, smooth to malleated or axially ribbed, and the aperture lip is pointed or claw-like in some species. The operculum is well developed, as large as the aperture, its inner surface having a distinct central attachment scar that is somewhat button-like, and its exterior composed of chitinous plates in a spiral arrangement, either compactly welded to form a smooth surface or variously agglutinated with foreign materials.

##### *Dendropoma mejillonensis* sp. nov.

**Type locality:** Live-taken syntypes collected from a large aggregation colonizing Anemones wall at 17 m depth, Peninsula Mejillones, northern Chile ( $23^{\circ}28'17.30''\text{S}$ ,  $70^{\circ}37'13.80''\text{W}$ ) were deposited in the Field Museum of Natural History, Chicago, Illinois, U.S.A. (FMNH N<sup>o</sup>-312172 and N<sup>o</sup>-312173). Additional samples were deposited in the Museo Nacional de Historia Natural de Santiago de Chile (paratype MNHNCL N<sup>o</sup>-5159 and syntypes MNHNCL N<sup>o</sup>-5160, 5161, 5162)

**Teleoconch (Figure 2a, b):** The tubes form continuous and compact colonies, which are grey to faintly green in the field, but white after cleaning. *In situ*, the tubes are slightly nested in the rocky substrate. The attached part of the tube appears eroded, and thus is thinner

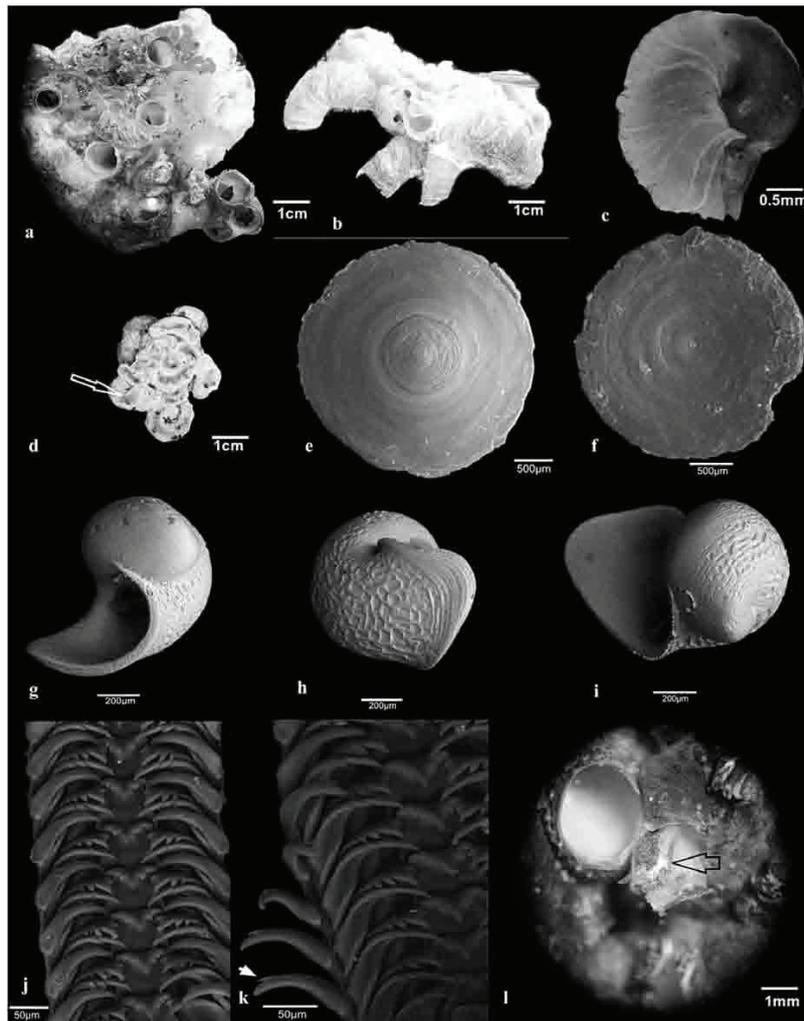


Figure 2. *Dendropoma mejillonensis* sp. nov. (a) Mass of living adult tubes. (b) Lateral view (c) Teleconch of juvenile showing concentric growth striations. (d) Smooth eroded part showed from the attached part of the tubes. (e) Operculum dorsal view. (f) Operculum ventral view. (g) Protoconch aperture. (h) Protoconch; detail of the sculpture and pointed lip-like external border. (i) Protoconch in ventral position, the earliest whorl is noted. (j) Radula displacement. (k) Detail of the cusp on the marginal teeth. (l) View of the animal head, the arrow points to the distinctive white mark.

(Figure 2d). The aperture is circular and its mean diameter in adults is 4.29 mm (SD = 0.37; n = 16). The tube exhibits sinuous growth lines and the sculpture of lamellar growth-striations is not intersected by longitudinal lines (Figure 2 c). The periostracum is white and the intermediate layer slightly cream. Observing from a cross-longitudinal section, three layers of the conch are present. The interior part is cream porcelain, darker towards the interior tube. Only under magnification are very soft longitudinal lines observed. There is no internal shell lamellar structure. The proximal

part of the tube slightly tends to vertically rise from the rest of the mat. The coiling pattern is variable. Early whorls are like Planorbidae, coiling counterclockwise, followed by a very loose coiling or irregular pattern. The shell of the juvenile is white and translucent with clear axial ribs (Figure 2c).

**Operculum (Figure 2e, f):** The form is circular and concave, slightly flattened and reddish in the center, brown-orange to colorless towards the external border. The diameter is 2.7 mm (SD = 0.2; n = 10) in adult

specimens and about 1/5 of the length of the relaxed pedal disk diameter. The operculum is composed of concentric layers of chitinous material with visible concentric irregular lines, notably in juveniles. The small mamilla is inserted in the pedal surface. Almost 90% of the studied opercula were fouled with bryozoans.

**Protoconch (Figure 2g, h, i):** Globular, brown or colorless, white towards the earliest whorl. The shell shows 1 to 1.5 nuclear whorls, ornamented with longitudinal grooves. The grooves show no evident axial pattern, are variable in size and present a slightly rectangular or triangular shape with no marks at the corners. The external border presents a pointed lip shape and growths striations are present. At hatching, shell length (the distance from the external lip border to the opposite whorl margin) is 0.77 mm (SD = 0.07; n = 10).

**Radula (Figure 2j, k):** Taenioglossan type, similar to the description of other vermetids (i.e., *Vermetus triquetrus* Bivona-Bernardi, 1832 and *Thylaeodus rugulosus* Monterosato, 1878; Bieler, 1995), transparent, consisting on average of 39.8 (SD = 6.06) rows of teeth (counts and measurements based on adult animals of 4 mm shell aperture, n = 10, no differences between sexes were noted). Total length of radular ribbon is 2.35 mm (SD = 0.34) and 0.196 mm width (SD = 0.011, mid ribbon). A trapezoidal rachidian tooth with a strong main cusp and 4–5 flanking cusps on either side (diminishing toward margin), basal denticles strongly developed. Lateral tooth cusp arrangement of triangular cutting shape, as in the central tooth, with two flanking cusps on either side. The inner marginal tooth is slender with a strong main cusp and the inner marginal with one flanking cusp on inside and two on outside. The outer marginal teeth present a single flanking cusp smooth on outside. Radular formula: 2+1+R+1+2.

**Animal:** Removed from the shell the body is short and narrowest towards the terminal part, which is slightly coiled. The average length of relaxed large adult specimens is 18.66 mm (SD = 1.68; n = 10). The head is mainly light grey or reddish with black, white and yellow specks. The posterior part is reddish or dark brown in color. Two white bands on the head tentacles are distinctive appearing as a white eyebrow (Figure 2l). The head tentacles are brown or light grey in color with black and yellow dots, no distinctive marks at the tips are visible. The pedal tentacles are light grey with yellow specks. In both sexes the light orange/melon mantle is entire and is characterized by a light brown border. The foot is a similar color to the mantle; however it has a white band around the operculum insertion. The gill filaments are about 1/3 of the size of

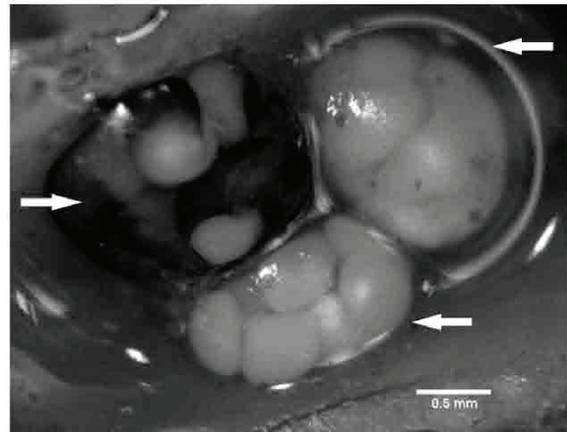


Figure 3. Capsules of *Dendropoma mejillonensis* sp. nov. containing juveniles (arrow left side) and nurse yolk (arrows right side).

the mantle and slightly triangular in shape. The columellar muscle appears as a white triangular narrow strip, enabling the animal to retreat deeply into its shell. Female's broods comprise three to four egg capsules, which are ovoid and the membrane is translucent. Each capsule contains between three to ten juveniles. Early capsules contain nurse yolk (Figure 3). Feeding is carried out by mucous threads.

**Habitat:** The specimens were attached to a vertical rock wall, which extends from the shallow subtidal down to 50 m depth. In the field, colonies showed a light grey to white color and were commonly fouled by calcareous algae causing a red/purple coloration. The surrounding benthic community is dominated by the kelp *Lessonia trabeculata* from 13 m depth down to 25 m. Below 25 m, kelp abundance is substantially reduced and relatively small epibenthic taxa such as calcareous algae (*Lythothamnium* sp. and *Lithophyllum* sp.), red algae (*Rhodomenia corallina* Bory de Saint Vincent & Greville), bryozoans (*Membranipora isabelleana* D'Orbigny, 1847 and *Lagenicella variabilis* Moyano, 1991), and Porifera cover the substrate. *Dendropoma mejillonensis* sp. nov. colonies were observed between 15 and 25 m.

**Etymology:** The species is named *Dendropoma mejillonensis* in reference to the discovery location Peninsula Mejillonnes.

## DISCUSSION

### Taxonomic remarks

The morphological classification of the species to the *Dendropoma* genus was carried out following Keen (1961). *Dendropoma mejillonensis* sp. nov. shows

similarities to *Dendropoma gregaria* Hadfield & Kay, 1972 (Hadfield et al., 1972) from Hawaii, sharing the circular pattern in the operculum and dense white pigmentation around the eyes. The most noteworthy difference is in the protoconch sculpture, while *D. gregaria* has light axial ribs crossed by finer spiral striations, *D. mejillonensis* shows soft grooves without evident design shape and pattern.

#### Distributional remarks

As already mentioned, the presence of vermetid gastropods is limited along the Pacific coast of South America. Alamo & Valdivieso (1997) reported *Petalonchus innumabilis* Pilsbry & Olsson 1935 from Mazatlán (México) to Bocapan and Huacho (Peru), *Serpulorbis squamigerus* Carpenter, 1857 from San Diego (California) to Paita (Perú) and *Vermetus compta* Carpenter, 1857 from British Columbia (Canada) to Paita. Keen (1971) recorded *Dendropoma lituella* Mörch, 1861 and *Dendropoma rastrum* Mörch, 1861 from the northern part of the Eastern Pacific; both were found from southern California to the southern Gulf of California at La Paz, Baja California (see also Figure 1c).

The presence of *Dendropoma mejillonensis* in the rocky subtidal zone of Peninsula Mejillones clearly extends the geographic range of the family into the Southeastern Pacific, almost 2000 km southwards. According to the literature the closest distribution limit of vermetids is Huacho (11°6'56.21"S, 77°37'9.46"W) (Alamo & Valdivieso, 1997). Easter Island and Juan Fernández may be source locations if *Dendropoma* sp. is *D. mejillonensis*, in this case the range would be extended from insular to continental Chile. However, it is not possible to define the biogeography of this species, as we did not sample south or north of the type locality.

Our record provides evidence that *D. mejillonensis* is able to thrive under cold upwelling conditions. The observed recruitment at Anemones Wall (A. Pacheco unpublished data) indicates that this species has the capacity to adapt to cold upwelling conditions. The species' distribution may be limited by the presence of a short larval stage. As in the case of many other vermetids (Keen, 1961; Hadfield et al., 1972; Calvo et al., 1998), larvae of *D. mejillonensis* leave the female mantle cavity well developed and crawl around for less than one hour before cementing themselves to the substrate. The recent discovery from Peninsula Mejillones suggests that several unexplored areas with unreported species may still exist along the northern Chilean coastline, particularly in zones difficult to reach (Camus, 2001). Furthermore, distributions of rafting species (a dispersal mechanism suggested for vermetids (Bieler, 1995)) may extend quickly with an

increasing amount of anthropogenic floating material, facilitating the supply of sessile species to new regions (Thiel & Haye, 2006). A genetic study is necessary to reveal linkages between *D. mejillonensis* and other vermetids.

**Acknowledgments.** We are grateful to Christian Guerra and Ivan Marin for their support during diving. Martha Calvo provided useful literature. Jose Riascos, Olaf Heilmayer, Ricardo Guíñez are thanked for their suggestions on an earlier version of the manuscript. Carrie Auld and Ruth Alheit kindly edited the English. Pabla Vega helped with the SEM photographs. Rüdiger Bieler provided the taxonomic advice. We appreciated the comments made by two anonymous reviewers. This study was conducted in the framework of the EU-funded INCO project, "Climate Variability and El Niño-Southern Oscillation: Implications for Natural Coastal Resources and Management" (CENSOR) and Programa Bicentenario de Ciencia y Tecnología RUE-02. This is CENSOR publication N° 341.

#### References♦

♦ All citations included in this publication are compiled in the final list of references

### 5 General discussion and conclusions

In the following chapter, I summarize and discuss the main results obtained during the realization of this thesis. Detailed discussions related to relevant topics are available in the respective publications.

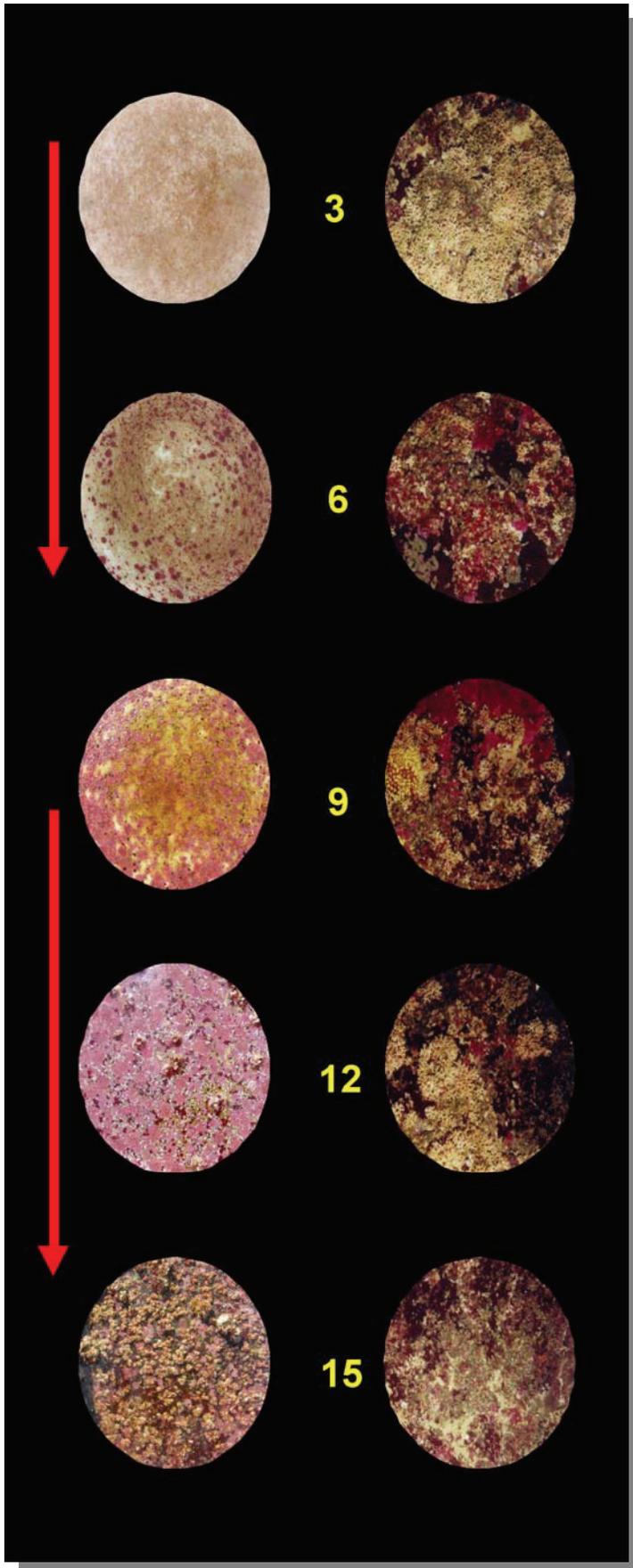
#### 5.1 Succession and convergence towards natural communities of hard-bottom habitats

The results of the hard-bottom experiment revealed a successional sequence between encrusting red corallines < the bryozoan *Membranipora isabelleana* < the barnacle *Balanus flosculus* < the bryozoan *Lagenicella variabilis* (Publication I and II). The barnacle *Balanus flosculus* covered early encrusting red corallines and *Membranipora isabelleana* by a strong pulse of recruitment. Thereafter, *Lagenicella variabilis* settled and overgrew barnacles by lateral expansion thus becoming the dominant component after 27 months of time exposure (Fig. 9). This sequence of replacement suggested that competition for space was the most important factor driving the successional development. After 27 months of exposure, the experimental communities did not yet resemble natural communities, because the proportional coverage of species differed and because one phylum common in natural communities (Porifera) was not yet found on the settlement plates. However, it appeared likely that the experimental communities were on a successional track towards a mature community that will ultimately resemble the natural controls. Based on these results it was predicted that at least 3 or 4 years are necessary to achieve full resemblance (Publication I page 42).

Observations of epibenthic succession on hidden surfaces of the panels showed a slower process compared to the exposed surfaces. Species replacement was less intense because some superior competitor taxa did not colonize this type of habitats (e.g. macroalgae). The lack of organisms apparently alleviated space competition and allowed pioneer species (e.g. *Membranipora isabelleana*) to survive long periods (Publication II). In

## General discussion

natural systems, hidden habitats will contribute to overall biodiversity and may also be part of important energy and material pathways (Richter et al., 2001).



**Figure 9** Left row, view of the panels with respective epibenthic community from each sample date. The yellow numbers indicate the number of sampling months. The right row is a view of the surrounding community taken at the respective sampling date.

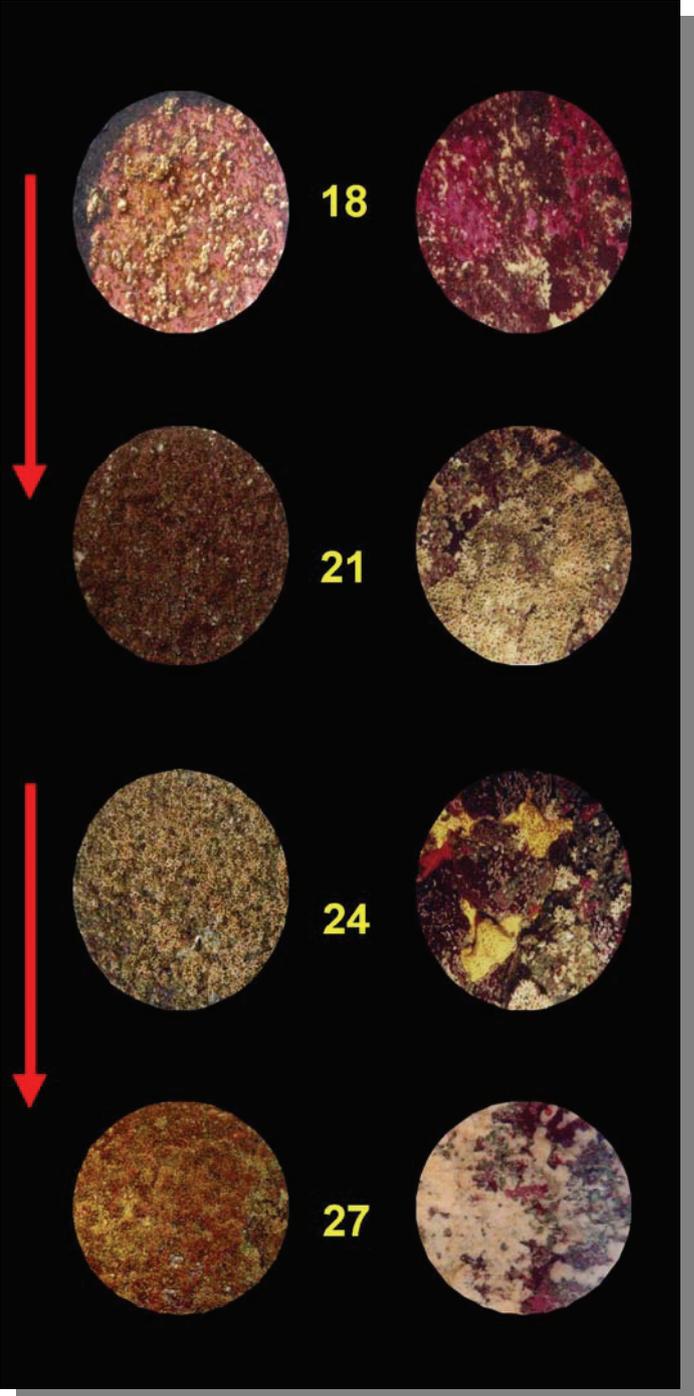


Figure 9 Continuation.

## General discussion

---

Succession on the examined subtidal habitat followed a non-rigid but deterministic pattern, indicating that developing communities tend to resemble natural communities. In other rocky systems succession can lead to different community states to which communities diverge during development (see fig. 1 and references therein). In the present study succession was deterministic thus the outcome community can be predicted from an eventual start point in time (e.g. Underwood and Chapman 2006). The strength of the interactions between early and middle colonizers adds variability to the successional process (Berlow, 1997; Underwood and Chapman, 2006), but the results of this study suggest that despite the potential variability during the process, succession can lead to a predictable outcome community.

The implications of this result are relevant in the context of the dynamics of the ENSO in northern Chile. After massive mortality of invertebrates and macroalgae populations on rocky shores caused by the strong impact of El Niño events, communities are capable to recover within three years after the event (Tarazona and Arntz, 2001) thus indicating the high resistance of this benthic system.

### Conclusion

- Succession in subtidal hard bottom habitats follows a deterministic pattern through consecutive species replacement towards the composition of the natural surrounding communities.
- The late dominant species are colonial forms able to suppress inferior competitors by lateral expansion thus covering space.
- Hard bottom subtidal communities from northern Chile are resistant to small scale perturbations, and potentially to higher magnitude disturbing events (i.e. El Niño).

### 5.2 Succession and convergence to natural communities in soft-bottom habitats

Macrobenthic succession in soft sediments did not follow a sequence of consecutive replacement from early to late colonizers. During succession communities were composed

## General discussion

---

by the same dominant colonizers and the variations were accounted for by the less abundant species but finally resembling natural surrounding communities. Instead of replacement of opportunistic species by late successional organisms, the process observed here is in agreement with the prediction of the “tolerance succession model” (Connell and Slatyer, 1977) stating that organisms occurring in the undisturbed community can colonize at the same time as species normally associated with the beginning successional stages (Publication III). Several studies on succession have shown the early arrival of opportunistic species such as spionid or capitellid polychaetes, which were thereafter displaced by late colonizers, often long-lived organisms (reviewed by Lenihan and Michelli, 2001). However, macrobenthic succession does not necessarily follow this deterministic sequence, at least not with a so called peak of opportunistic species during the beginning of the process (Santos and Bloom, 1980, 1983; Publication III). The arrival of colonizers may be due to larval settlement, passive migration of juveniles by swimming and crawling and bed load transport. Regardless of the mechanisms of arrival in the present experiment early and late colonizers were capable to use the resources offered by the new patch of substratum as no indication for competitive exclusion was detected.

Despite the non-sequential succession observed, resemblance to natural surrounding macrobenthos occurred already after 18 months, which supports the notion that benthic communities can return to an almost identical faunal structure with the same dominants after severe disturbance events (Santos and Bloom, 1980 and Rosenberg, 2001). This study is the first experimental approach demonstrating biotic recovery in soft bottom habitats of northern Chile. As addressed for hard bottom communities, this result highlights the resistance capacity of this community at least to small scale disturbances as suggested elsewhere for the Antofagasta area (Carrasco, 1997; Carrasco and Moreno, 2006), possibly also to severe ones associated with strong EN events.

## General discussion

### Conclusion

- Succession in sublittoral soft-bottom habitats develops through non consecutive changes in community structure.
- The developing community resembled the natural surrounding communities after 18 months.
- The findings support the “tolerance successional model” (Connell and Slatyer, 1977) stating that species associated with late successional stages can colonize and coexist with species from the early stage.
- Soft-bottom subtidal communities from northern Chile are resistant to small scale perturbations but potentially also to higher magnitude disturbing events (i.e. El Niño).

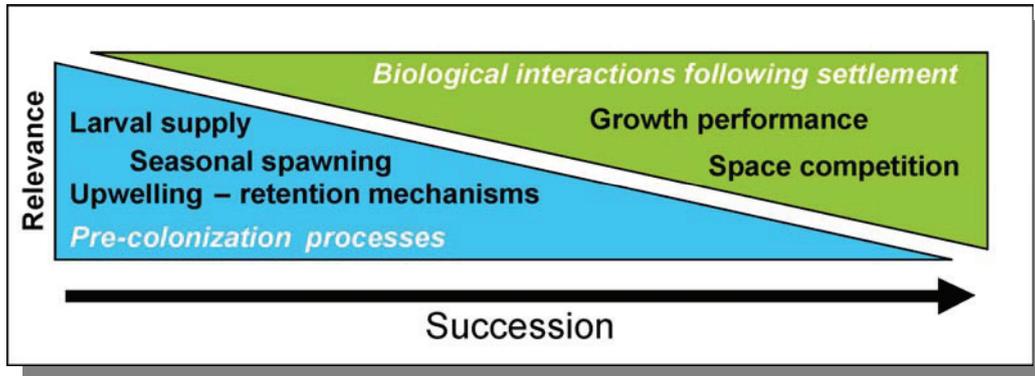
### 5.3 The effects of seasonality during the onset of successional development

#### 5.3.1 Seasonality in hard-bottom communities

Communities starting the succession in different seasons showed different composition after one year of development. However, the taxonomic composition was similar and only the different proportions in abundance accounted for the differences. This variability was attributable to the mechanisms of dispersion and arrival of invertebrate propagules. Upwelling is the main oceanographic component in the study area and its intensity varies between seasons (Escribano et al., 2002). Species with free living larval stages can be transported onshore but also be retained in nearshore areas depending on the intensity of the upwelling pulses (Castilla et al., 2002; Narváez et al., 2006; Lagos et al., 2008). Thus, this can explain the between-seasons variation of species with pelagic larvae (e.g. barnacles), however, this process is less important for taxa such as the vermetid gastropod *Dendropoma mejillonensis* (Publication V), which have direct development. Therefore, the effect of seasonality is related to reproduction peaks. Regardless the settlement of species in different seasons, this effect may be overridden by biological interactions such as competition and growth performances which seem to be the determinant factors modulating

## General discussion

the structure and composition of the community at the advanced stages (Fig. 10). These results also supported the notion of the non-rigid but deterministic type of succession model.



**Figure 10** Summary of important processes modulating the successional development on hard-bottom communities.

### Conclusion

- Seasonality had an effect on the early stages of hard-bottom succession as this factor has an impact on the supply of propagules (i.e. spores and larvae) reflected in different community structures.
- Despite these early variations, community succession was also driven by species interactions.
- This supports the non-rigid deterministic succession model, where different start points produce a predictable end point.

### 5.3.2 Seasonality in soft bottom communities

The appearance of fresh sediment in different seasons had no effect on the resulting community after one year of exposure. Despite the different onset during succession, communities converged to a similar composition. The effect of seasonality has been shown to be marked in early states of succession but convergence towards a similar composition appears to be characteristic in several soft-bottom systems (Diaz-Castañeda et al., 1989; Rosenberg 2001). Seasonality seems to have a strong effect principally on species with opportunistic life traits such as small, short lived animals, highly fecund with larvae that are dispersed widely in high numbers (Lenihan and Michelli, 2001) and are able to settle over

## General discussion

---

great part of the year (e.g. Arntz 1981). Thus, a new substratum can be colonized quickly with this species depending on the available pool of colonizers in each particular season. However, early opportunistic species are generally weak resource competitors and are subsequently replaced by later colonizers, being the bulk of the taxa of the surrounding sediment. Seasonality may have influenced the early colonization, but the outcome community after one year did not show a different structure compared to the natural community.

The lack of a seasonal signal on communities' composition may be in part attributable to some of the oceanographic characteristics of Bahía Antofagasta. The bay is influenced by two active upwelling centres, one located in front of Punta Coloso towards the south of the bay and the second located in the northern end of the bay in front of Punta Tetas (Fig. 4). This creates an "upwelling shadow" with an almost constant sea water temperature front across the mouth, thus upwelled water is retained inside the bay and presents a high residence time (Escribano and Hidalgo, 2001; Castilla et al., 2002; Piñones et al., 2007; see also Publication IV). Retained larvae have a higher probability to settle and successfully recruit in any particular time of the year compared to recruitment outside the bay (Lagos et al., 2008). Additionally post-settlement movements by juveniles and adults by swimming, drifting or crawling from the surrounding area is another determinant factor. Migration from adjacent areas to a new small patch of habitat has been demonstrated to be an important factor explaining quick benthic recovery in sedimentary areas (Publication III, Zajac et al., 1998).

### Conclusion

- North Chilean soft-bottom macrobenthic communities converged in a similar structure when starting colonization at different seasons of the year.
- The lack of a seasonal signal and the return to previous undisturbed conditions suggested a high resistance of the benthic system off northern Chile.

### 5.4 Succession in subtidal benthic habitats: hard- vs soft-bottom processes

This study focussed on community succession using the same time intervals and similar spatial scales but analyzing two different benthic habitats. This offers the opportunity for a conceptual comparison between the successional processes. Succession in hard-bottom habitats occurred through consecutive replacement of species throughout time, whereas sequential changes were not observed in the soft bottom experiment. In the former case biotic interactions such as competition for space between dominant solitary and colonial species made the sequence evident. In soft bottoms, changing numbers of species were observed, but the dominants maintained their abundances consistently during time. Thus, species replacement was not observed. There were no indications of any particular biological interaction leading to a complete or partial displacement of species. Whether or not competitive exclusion occurs between infaunal species remains a matter of debate but in the present case it did not seem to be an important factor.

Elsewhere community succession on hard- and soft-bottom habitats shows common characteristics at late stages of the community development. For instance, Antarctic soft-bottom benthos is dominated by colonial growth forms at late successional stages (i.e. long lived hexactinellids and demosponges, Teixidó et al., 2002) as is the case for soft bottom corals in the tropics (Knowlton and Jackson, 2001). Similarly the dominance of colonial species was observed in the present study of the hard-bottom habitat (Publication I and II). Why does succession not lead to the dominance of colonial growth forms in soft bottom habitats of temperate regions such as northern Chile? A comparative view on the evolution of benthic fauna of different geographical areas may provide insights and this should be addressed in future studies.

In soft bottoms the resemblance to natural communities occurred faster than on hard bottoms. Eighteen months were necessary to achieve resemblance, whereas hard-bottom communities were approaching but not fully resembling natural communities after twenty-seven months. Thus at least 3 to 4 years are necessary. This difference can be attributed to the fact that juveniles and adults of soft-bottom species can quickly immigrate into and thrive

## General discussion

---

in the new sediment patch, while few hard-bottom invertebrates directly migrate to a new open space. In the later case the community mainly depends on successful larva and spore settlement.

Another reason for the faster colonization in soft bottoms may be that animals present shorter life spans and, therefore, more colonizers are available in a certain time period. Despite the time lag between habitats, both communities tended to resemble natural surrounding communities, indicating the capacity of the overall benthic system to recover from disturbances to the previous undisturbed state.

These differences of the habitats in recovery through succession call the attention of management issues. Off northern Chile and particularly in coastal bays, port activities such as harbour construction, dredging and shipping are activities, which are gradually increasing and changing the sublittoral realm by two marked types of disturbances. The first is the removal of sediment by dredging (for example 1,200,000 m<sup>3</sup> sea floor were dredged for the construction of the Angamos port in Bahía Mejillones (Allan et al., 2008)), and the second is the subsequent construction of large concrete piles and the appearance of other newly available primary substrata. As demonstrated here the eventual biotic recovery of the bottom and the colonization of hard substratum will differ, therefore the monitoring programs should be adequate to substratum specific approaches in order to obtain a better understanding of how human constructions can alter biodiversity in different benthic habitats.

## General discussion

---

### Conclusion

- Benthic succession on small patches of habitat occurred faster in soft-bottom compared to hard-bottom subtidal habitats off northern Chile.
- Small patches of habitat in soft-bottom sediments are colonized by both larvae and juvenile recruitment while larval settlement is the only important factor for hard bottom colonization.
- Hard-bottom succession progresses by consecutive sequence of species replacement, in which species interactions such as competition for space are relevant for development.
- Soft-bottom succession is non consecutive and factors other than interactions like adaptation to external factors (e.g. hypoxia) seem to be operating the process.

### 6 Future perspectives of research

There is still a lack of knowledge on the community succession and other processes modulating the structure and diversity of subtidal benthic communities off northern Chile. Here I would like to outline some future research aspects which can contribute to a better understanding of these communities.

- **Enhancing temporal and spatial scales** – The study of successional processes of benthic communities requires observations encompassing long time periods (several years) to register the entire sequence. This is particularly relevant in the Humboldt Current System off northern Chile where the ENSO can substantially change the structure of benthic communities. Enhancing the temporal and spatial scale (e.g. during EN conditions) of the present experiments could provide a better knowledge about community organization, diversity and the driving forces behind the variability.
- **Area size effects** – Further studies could focus on the effect of the area size (small vs. large) to be colonized. This feature has been reported as the main factor conducting divergent succession (i.e. alternative states) in benthic realms (Petraitis and Dudgeon, 2005). At present, the presence of barren grounds and kelp beds in the same areas have been proposed to be alternative states along the Humboldt Current system (Thiel et al., 2007) but, to this date, there is little empirical evidence to support this (Villegas et al., 2008).
- **Settlement vs. migration** – Colonization by larval settlement or lateral migration seems to be dependent on the area size in soft-bottom habitats (Zajac and Whitlatch, 1991). Patch size experiments could be conducted in order to distinguish between processes and their relevance for community succession.

## Future perspectives of research

---

- **Early colonization** – The variability of sedimentation rates, food supply and chemical properties of the sediment (in hours, days) just after disturbance can influence early colonization (larval settlement) and subsequent successional development. More information is needed at this finer resolution which can be addressed with field and laboratory experiments.
- **Hypoxia responses and adaptation** – There is evidence that very shallow and usually normoxic benthic communities can undergo periods of hypoxia related to rises in the upper limit of the oxygen minimum zone (Publication V), but the implications on community structure and organism responses (mortality or tolerance) are not well understood. Future studies should address this issue together with research on physiological adaptations of benthic organism to hypoxic events.
- **Soft-bottom disturbances** – Soft-bottom predators (e.g. *Cancer* spp. crabs and fishes) are responsible for small scale disturbance in soft sediments, however the magnitude and the extension of this type of disturbance and the subsequent community recovery have not been documented. Future studies should cover this topic and also the impact of large scale disturbances such as the anthropogenic sediment dredging areas.
- **Ecosystem properties** – Ecosystem properties (persistence, resilience) are linked to community succession. Therefore, it should be investigated whether the variation of these properties are locally dependent or can be generalized on larger latitudinal and bathymetric scales within the Humboldt Current System. For instance, are the assemblages of clonal organisms (sponges and bryozoans) observed at 30 meters depth at Anemonas wall, as persistent as the polychaete assemblage in soft bottoms off Punta Coloso (40 m depth, Carrasco, 1996)?

## Future perspectives of research

---

- **Biodiversity inventory** – The discovery of new species showing wide (Publication IV) and short (Publication V) larval dispersion mechanisms calls for a better inventory of the organisms and therefore their role on ecological processes. This can furthermore, improve our knowledge of the species turnover (Camus, 2008) within the system.
- **Oceanographic variability and geographical complexity** – The area of Peninsula Mejillones is a system that includes sheltered bays and exposed rocky coast with variable upwelling intensity and extension (e.g. upwelling shadows, Castilla et al., 2002). These features seem to affect the supply of colonizers (i.e. larvae) to benthic habitats. So far, examples of these dynamics have been observed in rocky intertidal zones, being necessary similar observations but for subtidal hard- and soft-bottom habitats.
- **Improving the basic biological information** – There is a concerning lack of information about many biological traits of many benthic species, e.g. taxonomy, reproduction, dispersal mechanisms, patterns of recruitment as well as bathymetric and latitudinal distribution. In particular, this is true for hard bottoms; Bryozoans (taxonomy, reproduction, distribution), sponges (taxonomy, dispersion, reproduction, growth), encrusting corallines (taxonomy, dispersal mechanism). In soft bottoms, Urochordata (reproduction, growth), Polychaeta (reproduction, distribution, recruitment), Mollusca (reproduction, dispersal mechanisms), Crustacea (taxonomy, reproduction, dispersal mechanism) are groups that need further investigation. Furthermore, the small scale interactions among species (e.g. consumption of larvae by suspension feeders) must be studied.

## Acknowledgements

---

### 7 Acknowledgements

This doctoral thesis was conducted as part of the EU – funded FP6-INCO project: “Climate Variability and El Niño Southern Oscillation: Implications for Natural Coastal Resources and Management” CENSOR, and the Programa Bicentenario de Ciencia y Tecnología RUE – 02 from Comisión Nacional de Investigación Científica y Tecnología CONICYT, Gobierno de Chile. I’m deeply thankful for the scholarship received during my stay and field work at Universidad de Antofagasta, Antofagasta, Chile, as well at the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany. I’m particularly thankful for the support I received in order to present preliminary results of this thesis at several conferences in Chile (Iquique and Concepción), Brasil (Florianopolis) and Perú (Lambayeque and Lima).

I wish to express my deepest gratitude to everybody who was directly and indirectly involved in the realization of this thesis over the past 3.5 years:

To Dr. Wolfgang Stotz and Dr. Jaime Mendo for provided me with letters of recommendation for this position in the CENSOR project.

To my “Doktorvater” Prof. em. Dr. Wolf Arntz, for me it was a privilege to be one of your last PhD students, but more importantly, thank you for making possible the important research along the South American coast.

This thesis would be not possible to achieve without the tireless help of Dr. Jürgen Laudien. Thanks Jürgen for your true commitment in this project and for your participation in the diving operation to install the experiments. I really appreciate your generous contribution in all documents included in this thesis. Thanks also for your hospitality in Bremerhaven.

I will never stop learning thoughtful lessons about benthic ecology from Prof. Dr. Martin Thiel. Thanks Martin for taking the job of the external supervisor and for your enormous help in the written part of this thesis. I really appreciated your “to the point” corrections and suggestions. After your comments I always feel like “I could and must do better science”!!!!

A special thank goes to Dr. Marcelo Oliva, who supported this work from the basic logistics to conceptual ecological discussion. Thanks Marcelo for keeping the work running.

## Acknowledgements

---

Thanks to Dr. Olaf Heilmayer for his constant support and critical review over this thesis.

Thanks to all the people in Antofagasta for sharing friendship and support: Tom Ashton, José “Froggy” Riascos, Daniel Carstensen, Rodrigo Saavedra, Sönke Fisher, Miguel “Cutu” Cuturrufo, Maria Jose “La polola” Guiñez, Fernanda “Feri” Orellana, Rosita Chavez, Alex “Satan” Maffet, Monika “Moni” Weiss, Karen Chamblas, Christina “Christinita” Vargas, Besty Maluenda, Omar “el flaco” Larrea, Soledad “Sole” Morales, Sofia Salazar, Cecilia Avalos.

Thanks also to UA secretaries; Blanca “Blanquita” Vergara, Paulina Lopez, Maria Raquel “Rachel” Perez whom were always there to give me a helping hand.

This research owes it's results to the labor of several mutual divers and friends: Cristian Guerra, Ivan Marin, Arami “Aramir” Silva, Francisco “Pacho” Lira, Espiridion “Espiri” Montanares, Mauricio “Mauro” Caceres, Monika Weiss. Thanks in particular to Cristian Guerra and Ivan Marin with whom I shared many hours of diving and fascination for underwater life;jj

I deeply thank the work of the scientific German diving Team: Jose Velez, Sergio Rossi, Ida Fiorillio, Phillip Schubert who installed most of the material used during the experiments.

Thanks to my friends in Bremen and Bremerhaven: Kelly Ortega; special thanks to you “charapita” for helping me with my German confusion during the early days in Bremen;jj. Tania “Tita” Mendo, Ricardo “Richi” Chero, Maria Isabel Criales, Laura “Laurita” Wollheim and Sophie “Tofi” Streck, they were lovely friends to have around during the last stage of this work.

Many thanks also go to several colleagues who either discussed or advised me in many topics about benthic ecology, taxonomy and statistics: Dr. Maria Teresa Gonzales, Dr. Ricardo Guiñez, Dr. Cecilia Osorio, Dr. Rüdiger Bieler, Dr. Julie Bremner, Dr. Ruth Desqueroux, Dr. Hugo Moyano, MSc Guillermo Guzman, Dr. Marco Ortiz, Dr. Miguel Avendaño, Dr. Thomas Brey, Dr. Ricardo Sahade, Dr. Gerry Quinn and Dr. Robert Clarke.

## Acknowledgements

---

Special thanks go to my parents Sergio and Magda, to my brother Sergio his wife Male and the two little beauties Lucianita and Chiarita for the constant support.

To my wife Carrie, thank you for making our little nest the most delightful oasis in the middle of the Atacama dessert. Thank you for all your unconditional love and support!!

Halifax, In a lucky dayjj

## 8 Appendix

### List of conference contributions

**Pacheco A., Laudien J., Thiel, M., Oliva M., Heilmayer, O., Arntz W. 2008.** Successional development of hard and soft bottom benthic communities: a comparative view of a single ecological process on different subtidal habitats off northern Chile (Humboldt Current ecosystem). CENSOR Endterm Symposium 9-11 September, Lima, Peru. **Talk**

**Pacheco A., Laudien J. 2008.** A new species of vermetid *Dendropoma mejillonensis* sp. nov. (Mollusca, Caenogastropoda, Vermetidae) from northern Chile. CENSOR Endterm Symposium 9-11 September, Lima, Peru. **Poster**

**Pacheco A., Laudien J., Oliva M. 2007.** Sucesión temprana en comunidades macrobentónicas de fondos duros y blandos en el norte de Chile: diferencias y similitudes. 1er Congreso de Ciencias del Mar del Perú, November 27-30, Lambayeque, Perú. **Talk**

**Pacheco A., Laudien J. Riascos J. 2007.** First record of specimens belonging to the genus *Dendropoma* sp. (Mollusca, Caenogastropoda, Vermetidae) from the rocky subtidal zone of Peninsula Mejillones, northern Chile World Malacology Conference, Jul 27-31, Amwark, Belgum. **Poster**

**Pacheco A., Laudien J., Heilmayer O., Oliva M., Thiel M., Arntz W. 2007.** Colonization time and early sucesión in hard and soft bottom habitats off northern Chile. XXVII Congreso de Ciencias del Mar, May 27-31, Iquique, Chile. **Talk**

**Pacheco A., Laudien J. 2007.** First record of specimens belonging to the genus *Dendropoma* (Mollusca, Caenogastropoda, Vermetidae) from the rocky subtidal zone of Peninsula Mejillones, northern Chile XXVII Congreso de Ciencias del Mar, May 27-31, Iquique, Chile. **Poster**

**Pacheco A., Laudien J., Heilmayer O., Oliva M., Thiel M., Arntz W. 2007.** Tiempo de colonización y sucesión temprana de las comunidades macrobentónicas de fondos duros y blandos en el norte de Chile. XVI Congreso Latinoamericano de Ciencias del Mar COLACMAR, April 14-19, Florianópolis, Brasil. **Talk**

**Pacheco A., Laudien J., Heilmayer O., Oliva M., Thiel M., Arntz W. 2006.** Colonization timing and early succession of hard and soft bottom subtidal macrobenthic assemblages off northern Chile. CENSOR Midterm Symposium 5-8, Concepción, Chile. **Talk**

## References

---

### 9. References<sup>▲</sup>

- Aguilera MA, Navarrete SA 2007. Effects of *Chiton granosus* (Frembly 1827) and other molluscan grazers on algal succession in wave exposed mid-intertidal rocky shores of central Chile. *Journal of Experimental Marine Biology and Ecology*. 349, 84-98.
- Alamo V, Valdivieso V 1997. Lista sistemática de moluscos marinos del Perú. Instituto del Mar del Perú. 183 pp.
- Allan S, Ramírez C, Vásquez JA 2008. Effects of dredging on subtidal macrobenthic community structure in Mejillones Bay, Chile. *International Journal of Environment and Health*. 2, 64-81.
- Armonies W 1994. Drifting meio-macrofauna invertebrates on tidal flats in Königshafen: a review. *Helgolander Meeresun*. 48, 299-320.
- Arntz WE 1981. Zonation and dynamics of macrobenthos biomass in an area stressed by oxygen deficiency. In: Barrett GW, Rosenberg R (Eds.), *Stress effects on Natural Ecosystems*. John Wiley & Sons Ltd., Chichester, pp. 215-225.
- Arntz WE 1986. The two faces of El Niño 1982-83. *Meeresforschung*. 31, 1-46.
- Arntz W, Rumohr H 1982. An experimental study of macrobenthic colonization and succession, and the importance of seasonal variations in temperate latitudes. *Journal of Experimental Marine Biology and Ecology*. 64, 17-45.
- Arntz WE, Rumohr H 1986. Fluctuations of benthic macrofauna during succession and in an established community. *Meeresforschung*. 31, 97-114.
- Arntz WE, Arancibia H 1989. Fluctuaciones en el ecosistema bentodemersal del Pacífico Suroriental y el del norte de Europa: una comparación. Comisión Permanente del Pacífico Sur (CPPS), *Revista Pacífico Sur (Número Especial)*, 35-48.
- Arntz WE, Fahrbach E 1996. El Niño Experimento Climático de la Naturaleza. Causas Físicas y Efectos Biológicos. Fondo de Cultura Económica, México. 311 pp.
- Arntz W, Gallardo V, Gutiérrez D, Isla E, Levin L, Mendo J, Neira C, Rowe GT, Tarazona J, Wolff M. 2006. El Niño and similar perturbation effects on the benthos of the Humboldt, California and Benguela current upwelling ecosystems. *Advances in Geosciences*. 6, 243-265.
- Avendaño M, Cantillán M 1997. Necesidad de crear una reserva marina de ostiones en el banco de la Rinconada (Antofagasta-II Region, Chile). *Estudios Oceanológicos* 16, 109-113.

---

<sup>▲</sup> This list of references compiles all citation in the text and the respective publications.

## References

---

- Barber RT, Smith RL 1981. Coastal Upwelling Ecosystems. In: Longhurst AR (ed), Analysis of Marine Ecosystems. Academic Press. pp. 31-68.
- Barnes H, Klepal W 1972. Phototaxis in stage I nauplius larvae of two cirripedes. Journal of Experimental Marine Biology and Ecology. 10, 267-273.
- Baynes TW 1999. Factors structuring a subtidal encrusting community in the southern Gulf of California. Bulletin of Marine Science. 64, 419-450.
- Berger JA 1990. Macrofauna recolonization of subtidal sediments. Experimental studies on defaunated sediment contaminated with crude oil in two Norwegian fjords with unequal eutrophication status. I. Community responses. Marine Ecology Progress Series 66, 103-115.
- Berlow EL 1997. From canalization and contingency: historical effects in a successional rocky intertidal community. Ecological Monographs 64, 435-460.
- Berlow EL, Navarrete SA 1997. Spatial and temporal variation in rocky intertidal community organization: lessons from repeating field experiments. Journal of Experimental Marine Biology and Ecology. 214, 195-229.
- Bernatis JL, Gerstenberger SL., McGaw IJ 2007. Behavioural responses of the dungeness crab, *Cancer magister* during feeding and digestion in hypoxic conditions. Marine Biology. 150, 941-951.
- Bieler R 1995. Vermetids gastropods from Sao Miguel, Azores: Comparative anatomy, systematic position and biogeographic affiliation. Acoreana Supplement. 173-192.
- Bieler R 1996. Mörch's worm snail taxa (Caenogastropoda:Vermetidae, Siliquariidae, Turritellidae). American Malacological Bulletin 13(1/2), 23-35.
- Bourget E, De Guise J, Daigle G 1994. Scales of substratum heterogeneity, structural complexity, and the early establishment of a marine epibenthic community. Journal of Experimental Marine Biology and Ecology. 181, 31-51.
- Bowden DA, Clarke A, Peck LS, Barnes DKA 2006. Antarctic sessile marine benthos: colonisation and growth on artificial substrata over three years. Marine Ecology Progress Series. 316, 1-16.
- Brattström H, Johanssen A 1983. Ecological and regional zoogeography of the marine benthic fauna of Chile. Sarsia. 68, 289-339.
- Bullard SG, Whitlatch RB, Osman RW 2004. Checking the landing zone: Do invertebrate larvae avoid settling near superior spatial competitors? Marine Ecology Progress Series. 280, 239-247.

## References

---

- Burnaford JL 2004. Habitat modification and refuge from sublethal stress drive a marine plant-herbivore association. *Ecology*. 85, 2837-2849.
- Calvo M, Templado J, Penchaszadeh PE 1998. Reproductive biology of the gregarious Mediterranean gastropod *Dendropoma petraeum*. *Journal of the Marine Biology Association of the United Kingdom* 78, 525-549.
- Camus P 1994. Recruitment of the intertidal kelp *Lessonia nigrescens* Bory in northern Chile: successional constraints and opportunities. *Journal of Experimental Marine Biology and Ecology*. 184, 171-181.
- Camus P 2001. Marine biogeography of continental Chile. *Revista Chilena de Historia Natural*. 74, 587-617.
- Camus P 2008. Understanding biological impacts of ENSO on the eastern Pacific: an evolving scenario. *International Journal of Environment and Health*. 2, 5-19.
- Carrasco FD 1997. Sublittoral macrobenthic fauna off Punta Coloso, Antofagasta, northern Chile: high persistence of the polychaete assemblage. *Bulletin of Marine Science*. 60, 443-459.
- Carrasco FD, Moreno RA 2006. Long-term dynamics (1990 to 2004) of the polychaete fauna from the sublittoral soft-bottoms off Punta Coloso (Antofagasta), northern Chile. *Scientia Marina*. 70, 169-178.
- Castilla JC 1979. Características bióticas del Pacífico Sur-Oriental, con especial referencia al sector chileno. *Revista de la Comisión Permanente del Pacífico Sur*. 10, 167-182.
- Castilla JC, Lagos NA, Guíñez R, Largier J 2002. Embayments and nearshore retention of plankton: the Antofagasta Bay and other examples. In: Castilla JC, Largier J (eds) *The Oceanography and Ecology of the Near Shore and Bays in Chile*. Proceedings of the International Symposium on Linkages and Dynamics of Coastal Systems: Open Coasts and Embayments, Ediciones Universidad Católica de Chile, Santiago, pp 179–203
- Castilla JC, Uribe M, Bahamonde N, Clarke M, Desqueyroux-Faúndez R, Kong I, Moyano H, Rozbaczylo N, Santelices B, Valdovinos C, Zavala P 2005. Down under the south eastern Pacific: marine non-indigenous species in Chile. *Biological Invasions*. 7, 213-232.
- Chaparro OR, Bahamondes-Rojas I, Vergara AM, Rivera AA 1998. Histological characteristics of the foot and locomotory activity of *Crepidula dilatata* Lamarck (Gastropoda: Calyptraeidae) in relation to sex changes. *Journal of Experimental Marine Biology and Ecology*. 223, 77-91.

## References

---

- Chaparro OR, Segura CJ, Navarro RJ, Thompson RJ 2004. The effect of food supply on feeding strategy in sessile female gastropods *Crepidula fecunda*. *Marine Biology*. 144, 79-87.
- Chapman MG 2002. Early colonization of shallow subtidal boulders in two habitats. *Journal of Experimental Marine Biology and Ecology*. 275, 95-116.
- Chapman MG 2007. Colonization of novel habitat: test of generality of patterns in a diverse invertebrate assemblage. *Journal of Experimental Marine Biology and Ecology*. 348, 97-110.
- Cifuentes M, Kamlah C, Thiel M, Lenzd M, Wahl M 2007. Effects of temporal variability of disturbance on the succession in marine fouling communities in northern-central Chile. *Journal of Experimental Marine Biology and Ecology*. 352, 280-294.
- Cisterna JA, Saldías GS, Cáceres CW. 2008. Hypoxia effect on foraging behaviour of *Cancer setosus* (Molina, 1782) (Crustacea: Decapoda) feeding on *Mytilus chilensis* (Hupé, 1854). *Revista de Biología Marina y Oceanografía* 43, 419-423.
- Clarke KR 1993. Non-parametric multivariate analices of changes in community structure. *Australian Journal of Ecology*. 18, 117-143.
- Clarke KR, Gorley RN 2006. PRIMER v6: User Manual/Tutorial, PRIMER-E: Plymouth.
- Conlan KE, Kvitek RG 2005. Recolonization of soft-sediment ice scours on an exposed Arctic coast. *Marine Ecology Progress Series*. 286, 21-42.
- Connell JH 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology*. 93, 11-45.
- Connell JH 1997 Disturbance and recovery of coral assemblages. *Coral Reefs*, 16 Suppl., S101-S113.
- Connell JH, Slatyer RO 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*. 111, 1119-1144.
- Connell SD 2005. Assembly and maintenance of subtidal habitat heterogeneity: synergistic effects of light penetration and sedimentation. *Marine Ecology Progress Serires*. 289, 53-61.
- Coyer JA, Ambrose RF, Engle JM, Carrol JC 1993. Interactions between corals and algae on a temperate zone rocky reef: mediation by sea urchins. *Journal of Experimental Marine Biology and Ecology*. 167: 21-37.
- Cummings VJ, Pridmore RD, Thrush SF, Hewitt JE 1995. Post-settlement movement by intertidal benthic invertebrates: do common New Zealand species drift in the water column? *New Zealand Journal of Marine and Freshwater Research*. 29, 59-67.

## References

---

- Danovaro R, Fraschetti S 2002 Meiofaunal vertical zonation on hard-bottoms: comparison with soft-bottom meiofauna. *Marine Ecology Progress Series*. 230, 159-169.
- Day RW, Osman RW 1981 Predation by *Patiria miniata* (Asteroidea) on Bryozoans: prey diversity may depend on the mechanism of succession. *Oecologia*, 51, 300-309.
- Dayton P 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in rocky intertidal community. *Ecological Monographs*. 41, 351-389.
- Dayton P 2003. The importance of the natural science to conservation. *American Naturalist*. 162, 1-13.
- Dean TA, Hurd LE 1980. Development in an estuarine fouling community: the influence of early colonist on later arrivals. *Oecologia*. 46, 295-301.
- Desqueyroux R, Moyano H 1987. Zoogeografía de demospongias chilenas. *Boletín de la Sociedad de Biología de Concepción, Chile*. 58, 39-66.
- De Vries TJ 1987. A review of geological evidence for ancient El Niño activity in Peru. *Journal of Geophysical Research*. 92, 14471-14479.
- Dexter SC, Lucas KE 1985. The study of biofilm formation under water by photoacoustic spectroscopy. *Journal of Colloid and Interface Science*. 104, 15-27.
- Díaz A, Ortlieb L 1993. El fenómeno "El Niño" y los moluscos de la costa Peruana. *Bulletin de l'Institut Française de études andines*. 22, 159-177.
- Díaz-Castaneda V, Richard A, Frontier S 1989. Preliminary results on colonization, recovery and succession in a polluted area of the southern North Sea (Dunkerque's harbour, France). *Scientia Marina*. 53, 705 -716.
- Duggins OD, Eckman JE, Sewell AT 1999. Ecology of understory kelp environments. II. Effects of kelps on recruitment of benthic invertebrates. *Journal of Experimental Marine Biology and Ecology*. 143, 27-45.
- Escribano R 1998. Population dynamics of *Calanus chilensis* from northern Chile. *Fisheries and Oceanography*. 7, 245-251.
- Escribano R, Hidalgo P 2000. Spatial distribution of copepods in the north of the Humboldt Current region off Chile during coastal upwelling. *Journal of the Marine Biological Association of the United Kingdom*. 80, 283-290.
- Escribano R, Hidalgo P 2001. Wind-driven circulation in Bahía de Antofagasta, northern Chile (23°S). *Revista de Biología Marina y Oceanografía*. 36, 43-60.

## References

---

- Escribano R, Marín V, Hidalgo P, Olivares G 2002. Physical-biological interactions in the pelagic ecosystem of the nearshore zone of the northern Humboldt Current System. In: Castilla JC, Largier J (eds), *The Oceanography and Ecology of the Nearshore Bays in Chile*. Proceedings of the International Symposium on Linkages and Dynamics of Coastal Systems: Open Coast and Embayments. Ediciones Universidad Católica de Chile. Santiago, pp. 145-175.
- Escribano R, Daneri G, Farias L, Gallardo VA, Gonzalez HE, Gutiérrez D, Lange CB, Morales CE, Pizarro O, Ulloa O 2004. Biological and chemical consequences of the 1997-1998 El Niño in the Chilean coastal upwelling system: a synthesis. *Deep Sea Research II* 51 (20-21), 2389-2411.
- Fernández M, Jaramillo E, Marquet PA, Moreno CA, Navarrete SA., Ojeda FP, Valdovinos CR, Vásquez JA 2000. Diversity, dynamics and biogeography of Chilean benthic nearshore ecosystems: an overview and guidelines for conservation. *Revista Chilena de Historia Natural*. 73, 797–830.
- Foster MS, Nigg EW, Kiguchi LM, Hardin DD, Pearse JS 2003. Temporal variation and succession in an algal-dominated high intertidal assemblage. *Journal of Experimental Marine Biology and Ecology*. 289, 15-39.
- Freites L, Himmelman J, Lodeiros CJ 2000. Impact of predation by gastropods and crabs recruiting onto culture enclosures on the survival of the scallop *Euvola ziczac* (L.) in suspended culture. *Journal of Experimental Marine Biology and Ecology*. 224, 297-303.
- Gallagher ED, Gardner GB, Jumars PA 1990. Competition among the pioneers in a seasonal soft-bottom benthic succession: field experiments and analysis of the Gilpin-Ayala competition model. *Oecologia*. 83, 427-442.
- Gallardo C 1977. Two modes of development in the morphospecies *Crepidula dilatata* (Gastropoda: Calyptridae) from Southern Chile. *Marine Biology*. 39, 241-251.
- Glasby TM 1999a. Effects of shading on subtidal epibiotic assemblages. *Journal of Experimental Marine Biology and Ecology*. 234, 275-290.
- Glasby TM 1999b. Interactive effects of shading and proximity to the seafloor on the development of subtidal epibiotic assemblages. *Marine Ecology Progress Series*. 190, 113-124.
- Glasby TM 2000. Surface composition and orientation interact to affect subtidal epibiota. *Journal of Experimental Marine Biology and Ecology*. 248, 177-190.

## References

---

- Glasby TM, Connell SD 2001. Orientation and position of substrata have large effects on epibiotic assemblages. *Marine Ecology Progress Series*. 214, 127-135.
- Grantham BA, Eckert G, Shanks AL 2003. Dispersal potential of marine invertebrates in diverse habitats. *Ecological Applications*, 13 (Supplement 1), S108-S116.
- Grimm V, Wissel C 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*. 109, 323-334.
- Guerra-García JM, Corzo J, García-Gomez JC 2003. Short-term benthic recolonization after dredging in the harbour of Ceuta, North Africa. *Pubblicazioni Della Stazione Zoologica Di Napoli I Marine Ecology*. 24, 217-229.
- Guerra-García JM, García-Gomez JC 2006. Recolonization of defaunated sediments: Fine versus gross sand and dredging versus experimental trays. *Estuarine Coastal and Shelf Science*. 68, 328-342.
- Gutiérrez D, Gallardo VA, Mayor S, Neira C, Vásquez C, Sellanes J, Rivas M, Soto A, Carrasco F, Baltazar M 2000. Effects of dissolved oxygen and fresh organic matter on the bioturbation potential of macrofauna in sublittoral sediments off Central Chile during the 1997/1998 El Niño. *Marine Ecology Progress Series*. 202, 81-99.
- Gutt J, Starmans A 2001. Quantification of iceberg impact and benthic recolonisation patterns in the Weddel Sea (Antarctica). *Polar Biology*. 24, 615-619.
- Guzmán N, Saá S, Ortlieb L 1998. Descriptive catalogue of nearshore molluscs (Gastropoda and Pelecypoda) from Antofagasta area, 23°S (Chile). *Estudios Oceanológicos*. 17, 17-86.
- Guzmán N, Díaz A, Ortlieb L, Clarke M 2001. TAMAs, ocurrencia episódica de moluscos tropicales en el norte de Chile y el evento El Niño. In: Tarazona J, Arntz WE, Castillo de Maruenda E (eds) *El Niño en America Latina: Impactos Biológicos y Sociales*. Consejo Nacional de Ciencia y Tecnología, Lima, Perú, pp 385-393.
- Hadfield MG, Kay EA, Gillette MU, Lloyd MC 1972. The Vermetidae (Mollusca: Gastropoda) of the Hawaiian Islands. *Marine Biology*. 12, 81-98.
- Hill MF, Witman JD, Caswell H 2004. Markov chain analysis of succession in rocky subtidal community. *American Naturalist*. 164, 47-61.
- Himmelman JH, Cardinal A, Bourget E 1983. Community development following removal of urchins, *Strongylocentrotus droebachiensis*, from the rocky subtidal zone of the St. Lawrence Estuary, Eastern Canada. *Oecologia*. 59, 27-39.

## References

---

- Irving AD, Connell SD 2002. Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: algal versus invertebrate dominated assemblages. *Marine Ecology Progress Series*. 245, 83-91.
- Jackson JBC 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *American Naturalist*. 111, 743-767.
- Jesse S, Stotz W 2002. Spatio-temporal distribution patterns of the crab assemblage in the shallow subtidal of the north Chilean pacific coast. *Crustaceana*. 75, 1161-1200.
- Keen AM 1961. A proposed reclassification of the gastropod family Vermetidae. *Bulletin of British Museum (Natural History) Zoology* 7(3), 181-213.
- Keen AM 1971. *Sea shells of tropical West America*. Stanford University Press., Stanford (California), 1064 pp.
- Keough M 1983. Patterns of recruitment of sessile invertebrates in two subtidal habitats. *Journal of Experimental Marine Biology and Ecology*. 66, 213-245.
- Knowlton N, Jackson JBC 2001. The ecology of coral reefs. In: Bertness MD, Gaines SD, Hay ME (eds.) *Marine Community Ecology*. Sinauer Associates Inc, Sunderland, Massachusetts, pp 395-422.
- Konar B 2007. Recolonization of a high latitude hard-bottom nearshore community. *Polar Biology*. 30, 663-667.
- Kröger K, Gardner JPA, Rowden AA, Wear RG 2006. Recovery of a subtidal soft-sediment macroinvertebrate assemblage following experimentally induced effects of a harmful algal bloom. *Marine Ecology Progress Series*. 326, 85-98.
- Lagos NA, Tapia FJ, Navarrete SA, Castilla JC 2007. Spatial synchrony in the recruitment of intertidal invertebrates along the coast of central Chile. *Marine Ecology Progress Series*. 350, 29-39.
- Lagos NA, Castilla JC, Broitman BR 2008. Spatial environmental correlations of intertidal recruitment: a test using barnacles in northern Chile. *Ecological Monographs*. 78, 245-261.
- Lancellotti DA, Vásquez J A 2000. Zoogeography of benthic macroinvertebrates of the Chilean coast: contribution for marine conservation. *Revista Chilena de Historia Natural*. 73, 99-129.
- Laudien J, Brey T, Arntz WE 2001. Reproduction and recruitment patterns of the surf clam *Donax serra* (Bivalvia, Donacidae) on two Namibian sandy beaches. *South African Journal of Marine Science* 23, 53-60.

## References

---

- Laudien J, Herrmann M, Arntz WE 2007a. Soft bottom species richness and diversity as a function of depth and iceberg scour in Arctic glacial Kongsfjorden (Svalbard). *Polar Biology*. 30, 1035-1046.
- Laudien J, Rojo M, Oliva M, Arntz W, Thatje S 2007b. Sublittoral soft-bottom communities and diversity of Mejillones Bay in northern Chile (Humboldt Current upwelling system). *Helgoland Marine Research*. 61, 103-116.
- Lenihan HS, Micheli F 2001. Soft-sediment communities. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine Community Ecology*. Sinauer Associates Inc, Sunderland, Massachusetts, pp 253-287.
- Leon IL, Stotz W 2004. Diet and prey selection dynamics of *Cancer polyodon* in three different habitat types in Tongoy Bay, Chile. *Journal of the Marine Biological Association of the United Kingdom*. 84, 751-756.
- Lu L, Wu RSS 2000. An experimental study on recolonization and succession of marine macrobenthos in defaunated sediment. *Marine Biology*. 136, 291-302.
- Lu L, Wu RSS 2007. Seasonal effects on recolonization of macrobenthos in defaunated sediment: a series of field experiments. *Journal of Experimental Marine Biology and Ecology*. 351, 199-210.
- MacAllen R, Davenport J, Bredendieck K, Dunne D 2009. Seasonal structuring of a benthic community exposed to regular hypoxic events. *Journal of Experimental Marine Biology and Ecology*. 368, 67-74.
- Margalef R 1968. *Perspectives in ecological theory*. University of Chicago Press, Chicago, 111 pp.
- Marín V, Olivares G 1999. Estacionalidad de la productividad primaria en Bahía Mejillones del sur: una aproximación proceso-funcional. *Revista Chilena de Historia Natural*. 72, 629-641.
- Marín VH, Escribano R, Delgado LE, Olivares G, Hidalgo P 2001. Nearshore circulation in a coastal upwelling site off the northern Humboldt Current system. *Continental Shelf Research*. 21, 1317-1329.
- Marincovich L 1973. Intertidal mollusks of Iquique, Chile. *Natural History Museum Los Angeles County Science Bulletin*. 16, 1-49
- Marinelli RL, Woodin SA 2002. Experimental evidence for linkages between infaunal recruitment, disturbance, and sediment surface chemistry. *Limnology and Oceanography*. 47, 221-229.

## References

---

- Martínez EA, Cárdenas L, Pinto R. 2003. Recovery and genetic diversity of the intertidal kelp *Lessonia nigrescens* (Phaeophyceae) 20 years after El Niño 1982/83. *Journal of Phycology*. 39, 504-508.
- Matsumura K, Hill JM, Thomason PO, Thomason JC, Clare AS 2000. Discrimination at settlement in barnacles: laboratory and field experiments on settlement behaviour in responses to settlement-inducing protein complexes. *Biofouling*. 16, 181-190.
- Meneses I 1993. Vertical distribution of coralline algae in the rocky intertidal of northern Chile. *Hydrobiologia*. 260/261, 121-129.
- Melville AJ, Connell SD 2001. Experimental effects of kelp canopies on subtidal coralline algae. *Austral Ecology*. 26, 102-108.
- Miller RJ, Etter R 2008. Shading facilitates sessile invertebrate dominance in the rocky subtidal Gulf of Maine. *Ecology*. 89, 452-462.
- Moreno RA, Sepúlveda RD, Badano EI, Thatje S, Rozbaczylo N, Carrasco FD 2008. Subtidal macrozoobenthos communities from northern Chile during and post El Niño 1997-1998. *Helgoland Marine Research*. 62(Suppl.1), 45-55.
- Morgan SG 2001. The larval ecology of marine communities. In: Bertness MD, Gaines SD, Hay ME (eds.) *Marine Community Ecology*. Sinauer Associates Inc, Sunderland, Massachusetts, pp 159-182.
- Morin P 1999. *Community ecology*. Blackwell Science, Inc. Massachusetts, USA.
- Moseman SM, Levin L, Currin C, Forder C 2004. Colonization, succession, and nutrition of macrobenthic assemblages in a restored wetland at Tijuana Estuary, California. *Estuarine Coastal Shelf Science*. 60, 755-770.
- Moy CM, Seltzer GO, Rodbell DT, Anderson DM 2002. Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. *Nature* 420, 162-165.
- Narváez DA, Navarrete SA, Largier J, Vargas CA 2006. Onshore advection of warm water, larval invertebrate settlement, and relaxation of upwelling off central Chile. *Marine Ecology Progress Series*. 309, 159-173.
- Navarrete SA, Broitman B, Wieters EA, Finke GR, Venegas RM, Sotomayor A 2002. Recruitment of intertidal invertebrates in the southeast Pacific: interannual variability and the 1997-1998 El Niño. *Limnology and Oceanography*. 47, 791-802.

## References

---

- Navarrete SA, Castilla JC 2003. Experimental determination of predation intensity in an intertidal predator guild: dominant versus subordinate prey. *Oikos*. 100, 251-262.
- Navarrete SA, Wieters EA, Broitman B, Castilla JC 2005. Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top-down control. *Proceedings of the National Academy of Sciences of United States of America*. 120, 18046-18051.
- Navarrete SA, Parragué M, Wieters EA 2008. Local and meso-scale patterns of recruitment and abundance of two intertidal species that compete for refuges. *Marine Biology*. 155, 223-232.
- Navarro JM, Chaparro OR 2002. Grazing-filtration as feeding mechanisms in motile specimens of *Crepidula fecunda* (Gastropoda: Calyptraeidae). *Journal of Experimental Marine Biology and Ecology*. 270, 111-122.
- Nielsen KJ, Navarrete SA 2004. Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. *Ecology Letters*. 7, 31-41.
- Nilsson HC, Rosenberg R 2000. Succession in marine benthic habitats and fauna in response to oxygen deficiency: analysed by sediment profile-imaging and by grab samples. *Marine Ecology Progress Series*. 197, 139-149.
- Norkko A, Rosenberg R, Thrush SF, Whitlatch RB 2006. Scale and intensity dependent disturbance determines the magnitude of opportunistic response. *Journal of Experimental Marine Biology and Ecology*. 330, 195-207.
- Ólafsson EB 1988. Inhibition of larval settlement to a soft bottom benthic community by drifting algal mats: an experimental test. *Marine Biology*. 97, 571-574.
- Ortlieb L, Escribano R, Follegati R, Zuniga O, Kong I, Rodriguez L, Valdes J, Guzmán N, Iratchet P 2000. Recording of ocean-climate changes during the last 2,000 years in a hypoxic marine environment off northern Chile (23°S). *Revista Chilena de Historia Natural*. 73, 221-242.
- Osman RW 1977. The establishment and development of a marine epifaunal community. *Ecological Monographs*. 47, 37-63.
- Osman RW 1978. The influence of seasonality and stability on the species equilibrium. *Ecology*. 59, 383-399.
- Osman RW, Whitlatch RB, Malatesta RJ 1992. Potential role of micro-predators in determining recruitment into a marine community. *Marine Ecology Progress Series*. 83, 35-43.

## References

---

- Osman RW, Whitlatch RB 1995a. The influence of resident adults on larval settlement: experiments with four species of ascidians. *Journal of Experimental Marine Biology and Ecology*. 190, 199-220.
- Osman RW, Whitlatch RB 1995b. The influence of resident adults on recruitment: a comparison to settlement. *Journal of Experimental Marine Biology and Ecology*. 190, 169-198.
- Osman RW, Whitlatch RB 1998. Local control of recruitment in an epifaunal community and the consequences to colonization processes. *Hydrobiologia*, 375/376, 113-123.
- Osman RW, Whitlatch RB 2004. The control of the development of a marine benthic community by predation on recruits. *Journal of Experimental Marine Biology and Ecology*. 311, 117-145.
- Ortiz M 2003. Qualitative modelling of the kelp forest of *Lessonia nigrescens* Bory (Laminariales: Phaeophyta) in eulittoral marine ecosystems of the south-east Pacific: an approach to management plan assessment. *Aquaculture*. 220, 423-436.
- Pacheco A, Laudien J 2008. *Dendropoma mejillonensis* sp. nov. new species of vermetid (Mollusca, Caenogastropoda) from northern Chile. *The Veliger*. 50(3), 219-224.
- Pagès F, González HE, Ramón M, Sobarzo M, Gili JM 2001. Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by *Bassia bassensis* (Siphonophora: Calycophorae). *Marine Ecology Progress Series*. 210, 13-24.
- Paine RT 1974. Intertidal community structure; experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*. 15, 93-120.
- Paine RT, Suchanek TH 1983. Convergence of ecological process between independently evolved competitive dominants: a tunicate-mussel comparison. *Evolution*. 37, 821-831.
- Palma M, Quiroga E, Gallardo VA, Arntz W, Gerdes D, Schneider W, Hebbeln D 2005. Macrobenthic animal assemblages of the continental margin off Chile (22° to 42°S). *Journal of the Marine Biological Association of the United Kingdom*. 85, 233-245.
- Paredes C, Cardoso F, Tarazona J 2004. Distribución temporal de moluscos y crustáceos tropicales en la Provincia Peruana y su relación con los eventos El Niño. *Revista Peruana de Biología* 11, 213-218.
- Pearson TH, Rosenberg R 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: An Annual Review*. 16, 229-311.

## References

---

- Pechenik JA 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology Progress Series*, 177, 269-297.
- Pechenik JA, Scheltema RS, Eyster LS 1984. Growth stasis and limited shell calcification in larvae of *Cymatium parthenopeum* during trans-atlantic transport. *Science*. 224, 1097-1099.
- Perron FE, Heslinga GA, Fagolimus JO 1985. The gastropod *Cymatium muricinum*, a predator on juvenile tridacnid clams. *Aquaculture*. 48, 211-221.
- Petraitis PS, Latham RE 1999. The importance of scale in testing the origins of alternative community states. *Ecology*. 80, 429- 442.
- Petraitis PS, Dudgeon SR 2004. Detection of alternative stable states in marine communities. *Journal of Experimental Marine Biology and Ecology*. 300, 343-371.
- Petraitis PS, Dudgeon SR 2005. Divergent succession and implications for alternative states on rocky intertidal shores. *Journal of Experimental Marine Biology and Ecology*. 326, 14-26.
- Piñones A, Castilla JC, Guíñez R, Largier JL 2007. Nearshore surface temperatures in Antofagasta Bay (Chile) and adjacent upwelling centers. *Ciencias Marinas* 33, 37-48.
- Platt WJ, Connell JH 2003. Natural disturbances and directional replacement of species. *Ecological Monographs*. 73, 507-522.
- Quinn G, Keough M 2002. *Experimental design and data analysis for biologists*. Cambridge University Press.
- Quiroga E, Soto R, Rozbaczylo N 1999. The spionid polychaetes (Polychaeta: Spionidae) and its importance in the community structure: an study case in the bay of Iquique northern Chile (20°11'S; 70°10'W). *Gayana*. 63, 1-16.
- Raimondi P, Morse A 2000. The consequences of complex larval behaviour in a coral. *Ecology*. 81, 3193-3211.
- Ramírez J 1987. *Moluscos de Chile. II. Mesogastropoda*. Santiago de Chile Imprenta Museo Nacional de Historia Natural: Chile. 172 pp.
- Ramírez ME, Osorio C 2000. Patrones de distribución de macroalgas y macroinvertebrados intermareales de la isla Robinson Crusoe, archipiélago de Juan Fernández, Chile. *Investigaciones Marinas Valparaíso*. 28, 1-13.
- Rawlings T, Collins T, Bieler R 2001. A major mitochondrial gene rearrangement among closely related species. *Molecular Biology and Evolution*. 18,1604-1609.

## References

---

- Rehder HA 1980. The marine mollusks of Easter Island (Isla de Pascua) and Sala y Gómez. Smithsonian Contributions to Zoology N°- 289.
- Reise K 2002. Sediment mediated species interactions in coastal waters. *Journal of Sea Research*. 48, 127-141.
- Rhoads DC, Germano J 1986. Interpreting long-term changes in benthic community structure: a new protocol. *Hydrobiologia*. 142, 291-308.
- Richter C, Wunsch M, Rasheed M, Kötter I, Badran MI 2001. Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. *Nature*. 413, 726-730.
- Roleda MY, Wiencke C, Hanelt D, Bischof K 2007. Sensitivity of the early life stages of macroalgae from the northern hemisphere to ultraviolet radiation. *Photochemistry Photobiology*. 83: 851-862.
- Rodríguez SR, Ojeda P, Inestrosa NC 1993. Settlement of benthic marine invertebrates. *Marine Ecology Progress Series*. 97, 193-207.
- Rojo M, Laudien J 2005. Granulometric composition of a soft sediment habitat in Mejillones Bay (northern Chile), PANGAEA, DOI:10.1594/PANGAEA.308893.
- Rosenberg R 2001. Marine benthic faunal successional stages and related sedimentary activity. *Scientia Marina*. 65 suppl. 2, 107-119.
- Rosenberg R, Agrenius S, Hellman B, Nilsson HC, Norling K 2002. Recovery of marine benthic habitats and fauna in a Swedish fjord following improved oxygen conditions. *Marine Ecology Progress Series*. 234, 43-53.
- Roughgarden J, Gaines S, Possingham H 1988. Recruitment dynamics in complex life cycles. *Science*. 241, 1460-1466.
- Rozbaczylo N 1980. Clave para el reconocimiento de familias de anélidos poliquetos del mar Chileno. *Studies on Neotropical Fauna and Environment*. 15, 167-196.
- Santos SL, Bloom SA 1980. Stability in an annually defaunated estuarine soft-bottom community. *Oecologia*. 46, 290-294.
- Santos SL, Bloom SA 1983. Evaluation of succession in an estuarine macrobenthic soft bottom community near Tampa, Florida. *Internationale Revue der Gesamten Hydrobiologie*. 68, 617-632.
- Santos SL, Simon JL 1980a. Response of soft-bottom benthos to annual catastrophic disturbance in south Florida estuary. *Marine Ecology Progress Series*. 3, 347-355.

## References

---

- Santos SL, Simon JL 1980b. Marine soft-bottom community establishment following annual defaunation: larval or adult recruitment? *Marine Ecology Progress Series*. 2, 235-241.
- Scheffer M, Carpenter S 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution*. 18, 648-656.
- Schiaparelli S, Métivies B 2000. On the identity of "*Vermetus*" *roussai* Vaillant 1871 (Mollusca, Caenogastropoda, Vermetidae), with description of the new species. *Zoosystema*. 22, 677-687.
- Schiaparelli S, Guidetti P, Cattaneo-Vietti R 2003. Can mineralogical features affect the distribution patterns of sessile gastropods? The Vermetidae case in the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*. 83, 1267-1268.
- Sebens KP 1982. Competition for space: growth rate, reproductive output, escape size. *American Naturalist*. 120, 189-197.
- Sebens KP 1986. Spatial relationships among encrusting marine organisms in the New England subtidal zone. *Ecological Monographs*. 56, 73-96.
- Sellanes J, Quiroga E, Neira C, Gutiérrez D 2007. Changes of macrobenthos composition under different ENSO cycle conditions on the continental shelf off central Chile. *Continental Shelf Research*. 27, 1002-1016.
- Siddon CE, Witman JD 2004. Behavioral indirect interactions: multiple predator effects and prey switching in the rocky subtidal. *Ecology*. 85, 2938-2945.
- Sielfeld W 2002. Subphylum Cephalochordata. *Guías de Identificación y Biodiversidad Fauna Chilena*. Apuntes de Zoología, Universidad Arturo Prat, Iquique, Chile. 4 pp.
- Skoglund C 2002. Panamic province molluscan literature. Additions and changes from 1971 through 2001. III Gastropoda. *The Festivus*. 33(Suppl), 1-286.
- Sommer U, Meusel B, Stielau C 1999. An experimental analysis of the importance of body-size in the seastar-mussel predator-prey relationship. *Acta Oecologica*. 20, 81-86.
- Sousa WP 1980. The responses of a community to disturbance: the importance of successional age and species' life histories. *Oecologia* 45, 72-81.
- Sousa WP 2001. Natural disturbance and the dynamics of marine benthic communities. In: Bertness MD, Gaines SD, Hay ME (eds.) *Marine Community Ecology*. Sinauer Associates Inc, Sunderland, Massachusetts, pp 85-130.

## References

---

- Sugden H, Panusch R, Lenz M, Wahl M, Thomason J 2007. Temporal variability of disturbances: is this important for diversity and structure of marine fouling assemblages? *Marine Ecology*. 28, 368-376.
- Sutherland JP 1974. Multiple stable points in natural communities. *American Naturalist*. 108, 859-873.
- Sutherland JP 1981. The fouling community at Beaufort, North Carolina: a study of stability. *American Naturalist*. 118, 499-519.
- Sutherland JP, Karlson RH 1977. Development and stability of the fouling community at Beaufort, North Carolina. *Ecological Monographs*. 47, 425-446.
- Tarazona J, Salzwedel H, Arntz W 1988a. Positive effects of "El Niño" on macrozoobenthos inhabiting hypoxic areas of the Peruvian upwelling system. *Oecologia*. 76, 184-190.
- Tarazona J, Salzwedel H, Arntz W 1988b. Oscillations of macrozoobenthos in shallow waters of the Peruvian central coast induced by El Niño 1988b. *Journal of Marine Research*. 46, 593-611.
- Tarazona J, Arntz W, Canahuire E 1996. Impact of two "El Niño" events of different intensity on the hypoxic soft bottom macrobenthos off central Peruvian coast. *PSZNI Marine Ecology*. 17, 425-446.
- Tarazona J, Arntz W 2001. The Peruvian coastal upwelling system. In: Seeliger U, Kjerfve B (eds.) *Coastal Marine Ecosystems of Latin America, Ecological Studies, Vol. 144*. Springer-Verlag, Berlin Heidelberg. pp. 229-244.
- Teixidó N, Garrabou J, Arntz WE 2002. Spatial pattern quantification of Antarctic benthic communities using landscape indices. *Marine Ecology Progress Series*. 242, 1-14.
- Teixidó N, Garrabou J, Gutt J, Arntz WE 2007. Iceberg disturbance and successional spatial patterns: the case of the shelf antarctic benthic communities. *Ecosystems*. 10, 142-157.
- Thatje S, Heilmayer O, Laudien J 2008. Climate variability and El Niño Southern Oscillation: implications for natural coastal resources and management. *Helgoland Marine Research*. 62(Suppl 1), 5-14.
- Thiel M, Ullrich N 2002. Hard rock versus soft bottom: the fauna associated with intertidal mussels beds on hard bottoms along the coast of Chile, and considerations on the functional role of mussels beds. *Helgoland Marine Research*. 56, 21-30.
- Thiel M, Haye P 2006. The ecology of rafting in the marine environment III. Biogeographical and evolutionary consequences. *Oceanography and Marine Biology: An Annual Review*. 44, 323-429.

## References

---

- Thiel M, Macaya EC, Acuña E, Arntz WE, Bastías H, Brokordt K, Camus P, Castilla JC, Castro LR, Cortés M, Dumont CP, Escribano R, Fernandez M, Gajardo JA, Gaymer CF, Gomez I, González AE, González HE, Haye PA, Illanes JE, Iriarte JL, Lancellotti DA, Luna-Jorquera G, Luxoro C, Manriquez PH, Marín V, Muñoz P, Navarrete SA., Pérez E, Poulin E, Sellanes J, Sepúlveda HH, Stotz W, Tala F, Thomas A, Vargas CA, Vasquez JA, Vega JMA 2007. The Humboldt Current system of northern and central Chile oceanographic processes, ecological interactions and socioeconomic feedback. *Oceanography and Marine Biology: An Annual Review*. 45, 195-344.
- Thistle D 1981. Natural physical disturbances and communities of marine soft bottoms. *Marine Ecology Progress Series*. 6, 223-228.
- Todd CD 1998. Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? *Hydrobiologia*, 375/376, 1-21.
- Tokeshi M, Romero L 1995. Filling a gap: dynamics of space occupancy on a mussel-dominated subtropical rocky shore. *Marine Ecology Progress Series*. 119, 167-176.
- Tomicic JJ 1985. Efectos del fenómeno El Niño 1982–83 en las comunidades de la Península de Mejillones. *Investigaciones Pesqueras (Chile)*. 32, 209-213.
- Underwood AJ, Keough MJ 2001. Supply-side ecology: the nature and consequences of variations in recruitment of intertidal organisms. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine Community Ecology*. Sinauer Associates Inc, Sunderland, Massachusetts, p 183-200.
- Underwood AJ, Chapman MG 2006. Early development of subtidal macrofaunal assemblages: relationships to period and timing of colonization. *Journal of Experimental Marine Biology and Ecology*. 330, 221-233.
- Urban HJ 2000. Culture potential of the pearl oyster (*Pinctada imbricata*) from the Caribbean: II. Spat collection, and growth and mortality in culture systems. *Aquaculture*. 189, 375–388.
- Valdivia N, Heidemann A, Thiel M, Molis M, Wahl M 2005. Effects of disturbance on the diversity of hard-bottom macrobenthic communities on the coast of Chile. *Marine Ecology Progress Series*. 299, 45–54.
- Valdovinos C 1999. Biodiversidad de moluscos chilenos: base de datos taxonómica y distribucional. *Gayana* 63, 111-164.
- Van Blaricom G 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. *Ecological Monographs*. 52, 283-305.

## References

---

- Vance RR 1988. Ecological succession and the climax community on a marine subtidal rock wall. *Marine Ecology Progress Series*. 48, 125-136.
- Van Colen C, Montserrat F, Vincx M, Herman PMJ, Ysebaert T, Degraer S 2008. Macrobenthic recovery from hypoxia in a estuarine tidal mud flat. *Marine Ecology Progress Series*. 372, 31-42.
- Vargas CA, Manríquez PH, Navarrete SA 2006. Feeding by larvae of intertidal invertebrates: assesing their position in pelagic food webs. *Ecology*. 87, 444-457.
- Vásquez JA 1995. Ecological effects of brown seaweed harvesting. *Botanica Marina*. 38, 251-257.
- Vásquez JA, Santelices B 1990. Ecological effects of harvesting *Lessonia* (Laminariales, Phaeophyta) in central Chile. *Hydrobiologia*. 204/205:41-77.
- Vásquez JA, Vega JMA 2004. Ecosistemas marinos costeros del Parque Nacional Bosque Fray Jorge. In: Squeo FA, Gutiérrez JR, Hernández LR (eds.), *Historia Natural del Parque Nacional Bosque Fray Jorge*. Ediciones Universidad de La Serena: La Serena, Chile. pp. 235-252.
- Vásquez JA, Vega JMA, Buschman A 2006. Long term variability in the structure of kelp communities in northern Chile and the 1997–98 ENSO. *Journal of Applied Phycology*. 18, 505-519.
- Veit-Köhler G, Laudien J, Knott J, Velez J, Sahade R 2008. Meiobenthic colonisation of soft sediments in arctic glacial Kongsfjorden (Svalbard). *Journal of Experimental Marine Biology and Ecology*. 363, 58-65.
- Vega JMA, Vásquez JA, Buschmann A 2005. Population biology of the subtidal kelps *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales, Phaeophyceae) in an upwelling ecosystem of northern Chile: Interannual variability and El Niño 1997–98. *Revista Chilena de Historia Natural*. 78, 33-50.
- Villegas MJ, Laudien J, Sielfeld W, Arntz WE 2008. *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales; Phaeophyceae) kelp habitats structures and associated macrobenthic community off northern Chile. *Helgoland Marine Research*. 62(Suppl 1), 33-43.
- Wahl M 2001. Small scale variability of benthic assemblages: biogenic neighbourhood effects. *Journal of Experimental Marine Biology and Ecology*. 258, 221-233.
- Walker SJ, Schlacher TA, Schlacher-Hoenlinger MA 2007. Spatial heterogeneity of epibenthos on artificial reefs: fouling communities in the early stages of colonization on an East Australian shipwreck. *Marine Ecology*. 28, 435-445.

## References

---

- Warwick RM 1988. Analysis of community attributes of the macrobenthos of Frierfjord/Langesundfjord at taxonomic levels higher than species. *Marine Ecology Progress Series* 46, 167-170.
- Watson DI, Barnes DKA 2004. Quantifying assemblage distinctness with time: an example using temperate epibenthos. *Journal of Experimental Marine Biology and Ecology*. 312, 367-383.
- Witman JD, Dayton PK 2001. Rocky subtidal communities. In: Bertness MD, Gaines SD, Hay ME (eds.) *Marine Community Ecology*. Sinauer Associates Inc, Sunderland, Massachusetts, p 339-366.
- Wiieters EA, Kaplan DM, Navarrete SA, Sotomayor A, Largier J, Nielsen, KJ, Véliz F 2003. Alongshore and temporal variability in chlorophyll a concentration in Chilean nearshore waters. *Marine Ecology Progress Series*. 249, 95-105.
- Wolff WJ, Sandee AJJ, de Wolff L 1977. The development of a benthic ecosystem. *Hydrobiologia*. 52, 107-115.
- Wolff M, Wosnitza-Mendo C, Mendo J 2003. The Humboldt Current – trends in exploitation, protection and research. In: Hempel G, Sherman K (eds.) *Large Marine Ecosystems of the World*. Elsevier publisher, p 279-309.
- Woodin SA 1991. Recruitment of infauna: positive or negative cues? *American Zoologist*. 31, 797-807.
- Wu RSS, Shin PKS 1997. Sediment characteristics and colonization of soft-bottom benthos: a field manipulation experiment. *Marine Biology* 128, 475-487.
- Yakovis EL, Artemieva AV, Fokin MV, Grishankov AV, Shunatova NN 2005. Patches of barnacles and ascidians in soft bottoms: associated motile fauna in relation to the surrounding assemblage. *Journal of Experimental Marine Biology and Ecology*. 327, 210-224.
- Yakovis LE, Artemieva AV, Shunatova NN, Varfolomeeva MA 2008. Multiple foundation species shape benthic habitats islands. *Oecologia*. 155, 785-795.
- Yund PO, Gaines SD, Bertness MD 1991. Cylindrical tube traps for larval sampling. *Limnology and Oceanography*. 36, 1167-1177.
- Zajac RN, Whitlatch RB 1982a. Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonization. *Marine Ecology Progress Series*. 10, 1-14.
- Zajac RN, Whitlatch RB 1982b. Responses of estuarine infauna to disturbance. II. Spatial and temporal variation of succession. *Marine Ecology Progress Series*. 10, 15-27.

## References

---

- Zajac RN, Whitlatch RB 1991. Demographic aspects of marine, soft sediments patch dynamics. *American Zoologist*. 31, 808-820.
- Zajac RN, Whitlatch RB, Thrush SF 1998. Recolonization and succession in soft-sediment infaunal communities: the spatial scale of controlling factors. *Hydrobiologia*. 375/376, 227-240.
- Zajac RN, Whitlatch RB 2001. Response of macrobenthic communities to restoration efforts in a New England estuary. *Estuaries*. 24, 167-183.
- Zajac RN, Whitlatch RB 2003. Community and population-level of responses to disturbance in a sandflat community. *Journal of Experimental Marine Biology and Ecology* 294, 101-125.
- Zühlke R, Reise K 1994. Response of macrofauna to drifting tidal sediments Helgoländer Meeresuntersuchungen. 48, 277-289.
- Zuñiga O 2002. Crustáceos, Guía de biodiversidad N°2, Vol 1 Macrofauna y algas marinas, Universidad de Antofagasta, Centro regional de estudios y educación ambiental, Chile. 71pp.