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Vertical distribution of rocky subtidal assemblages along the exposed coast of north-central Chile

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ABSTRACT

Through a systematic study of a stretch of coast in north central Chile, the variety and vertical zonation patterns of the rocky subtidal communities are described, thereby revising apparent uniformity and lack of vertical zonation of the rocky subtidal of southeastern Pacific shores previously reported in the literature. Over the 600 km of coast studied, the following pattern of depth-zonation is described: an upper fringe (lower part of the sublittoral fringe) characterized by barren grounds dominated by calcareous encrusting algae and the sea urchin *Tetrapygus niger*; an intermediate fringe (upper Infralittoral sub-zone) characterized either by deep barren grounds similar to the former, or kelp beds of *Lessonia trabeculata*, or an assemblage of suspension feeding organisms, as the big barnacle *Austromegabalanus psittacus* and/or the tunicate *Pyura chilensis*; and a deep fringe (Circalittoral sub-zone) dominated by small encrusting or mobile invertebrates. This basic vertical zonation pattern of the shallow rocky subtidal communities seems to be common to most of the temperate coasts of the world. The analysis, first of the occurrence of the general zonation pattern and second of the species composition within the assemblages corresponding to each sub-zone, offers a useful framework for the assessment of the eventual impacts and changes within the shallow rocky subtidal habitat, for example within environmental monitoring programs.

1. Introduction

Impacts of human activity have reached all marine environments with intensified effects in the coastal zone (Halpern et al., 2008). The coast of Latin America is no exception. An estimation of the Threat Index for Latin American countries shows that the impacts are higher for the coasts of Brazil, northern Peru, and southern Ecuador (Chatwin and Rybock, 2007). The rest of the region has moderate index values. The main threats to biodiversity are fisheries, pollution, urban development, mine exploitation, oil industries, aquaculture, marine transport, invasive species, and climate change. However, it is unclear whether we have the necessary knowledge of marine communities to even detect such changes. Current knowledge of the diversity and structure of communities in this environment is insufficient to be able to detect effects of various human activities in the coastal marine system. In this context, Lubchenco et al. (1991) state the urgent need for the establishment of biological inventory programs, classifying types of habitat, associations of species and interactions with biotic and abiotic factors. More recently, Dayton (2003) has argued for the urgent need to generate basic information about the natural history of the local marine ecosystem, specifying "*Science and management demand that complex systems be simplified, but the art of appropriate simplification depends on a basic understanding of the important natural history: there are no shortcuts*". If we do not know the present communities, it will be difficult or even impossible to assess the degree of impact, or we will even not be able to detect any impact (Claudet and Fraschetti, 2010).

While a large body of literature exists for most coasts around the world with rocky and sandy intertidal communities and has shown the existence of universal patterns of zonation (for rocky intertidal areas see Stephenson and Stephenson (1972); for sandy beaches see MacLachlan and Jaramillo (1995); for tidal mud or sand flats, see Peterson (1991); for salt marches, see Pennings et al. (2005)), the knowledge of the shallow rocky subtidal is very fragmented (Borja et al., 2008). However, these ecosystems are valued in terms of products and services, although currently they suffer from strong human impact and are also vulnerable to climate change (Derrien-Courtel et al., 2013; Elahi et al., 2013). A first attempt to describe general patterns of structure and structuring processes was made by Witman and Dayton (2001). The existence and study of vertical zonation patterns in the intertidal zone has been a source of hypotheses that have aided in the comprehension of the structure and functioning of those habitats and the communities living there (Terlizzi and Schiel, 2009). The study of the zonation pattern facilitates, or in the future will facilitate, the

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detection and understanding of eventual changes in natural communities. As noted by Ellis (2003), the use of the widely recognized zonation patterns for the rocky intertidal makes monitoring programs more effective. For rocky subtidal habitats and communities, this type of knowledge is still scarce, and although the existence of zonation patterns is recognized (Chappuis et al., 2014; Hiscock, 1985; Pérès, 1982), their general use and applicability has not been carefully revised.

For Chile, most of the investigations conducted in the rocky subtidal zone have been devoted to communities dominated by kelp, easily accessed by diving, giving the impression of the existence of a relative uniform and homogeneous community structure. The revisions by Santelices (1989, 1991) only included descriptions of communities dominated by *Macrocystis pyrifera* (L.) C. Agardh on protected sites along the coast (Dayton et al., 1973; Dayton, 1985; Moreno and Jara, 1984; Moreno and Sutherland, 1982; Ojeda and Santelices, 1984; Santelices and Ojeda, 1984; Vásquez et al., 1984) and communities dominated by *Lessonia trabeculata* Villouta & Santelices on the exposed coast of north-central Chile (Núñez and Vásquez, 1987; Rodríguez and Ojeda, 1993; Santelices, 1990; Vásquez, 1992; Vásquez, 1993; Vásquez et al., 2006; Vega et al., 2005; Villouta and Santelices, 1984). However, this apparent uniformity of the rocky subtidal communities of southeastern Pacific shores is more likely representative of the lack of knowledge produced by concentration on some and little effort on other subtidal community types than a representative pattern. In fact, there have been no specific investigations of the occurrence and vertical distribution of rocky subtidal communities along the almost 5000 km of Pacific coast in Chile. In an extensive review of Chilean benthic nearshore ecosystems, Fernández et al. (2000) did not incorporate information on subtidal rocky bottoms and recognized that most of the work on experimental marine ecology in Chile has been in the intertidal zone. In addition to communities dominated by macroalgae, the occurrence of other types of communities, such as those dominated by the ascidian *Pyura chilensis* Molina described by Zamorano and Moreno (1975) in the subtidal zone of southern Chile and the description of barren grounds with high densities of the sea urchin *Tetrapygus niger* (Molina) in north-central Chile (Stotz et al., 1991), has been reported. Nevertheless, these types of communities have received little attention, and the published information on them is very scarce. Similarly, little is known about the distribution and abundance of encrusting species, such as barnacles and ascidians, which seem to characterize and probably sustain the secondary production in the rocky subtidal zone (Stotz and Pérez, 1992; Stotz et al., 2003). Some data were reported by Villouta and Santelices (1984). More recently, González et al. (2014) described different subtidal assemblages of rocky coastline dominated by suspension feeders and encrusting organisms replacing kelp forests in an area affected by sedimentation and turbidity generated by a discharge from mining.

The lack of information on subtidal environments is not exclusive to the southeastern Pacific coast, as knowledge of the shallow rocky subtidal zone is scarce almost around the world (Guinda et al., 2012). According to Hiscock (1985), researchers have been slow to recognize the great lack of knowledge regarding these communities. Witman and Dayton (2001) identified 40 publications in the Journals Ecology and Ecological Monographs regarding rocky subtidal ecology from 1960 to 1999 compared to 102 in the same time for rocky intertidal communities. In general, for rocky shores in temperate regions, emphasis has been placed on the intertidal zone and kelp beds in the subtidal zone, as shown by Nybakken (1988). One result is that the integration of information on littoral environments edited by Mathieson and Nienhuis (1991) is rich on data on intertidal communities but not on subtidal communities. Witman and Dayton's (2001) synthesis regarding this habitat constitutes an important contribution that will hopefully start a more systematic approach to the study, description and understanding of this habitat, including other communities besides kelp beds, with a more balanced treatment of representative communities.

Based on the information for British shores, Hiscock and Mitchell (1980) and Hiscock (1985) describe and define a vertical zonation pattern in the Sublittoral zone of the shallow rocky subtidal zone consisting of two sub zones, the Infralittoral sub-zone and Circalittoral sub-zone, each divided into an upper and a lower horizon. The sublittoral zone, the sub-zones and its divisions, proposed originally by Pérès and Molinier (1957), are defined by biological characteristics, analogous to the definitions used by Stephenson and Stephenson (1972) for the description of the intertidal zonation of rocky shores. According to Pérès (1982), the Infralittoral sub-zone is dominated and characterized by different associations of erect algae, which sometimes can be replaced by encrusting calcareous algae or suspension feeding organisms. In contrast, the Circalittoral sub-zone is always dominated by the presence of animals. While some authors have recognized the validity of the original classification of zonation, proposed by Pérès and Molinier (1957) (Cebrián and Ballesteros, 2004; Hiscock, 1985; Logan et al., 1983, 1984; Oigman-Pszczol et al., 2004), other studies do not use this nomenclature and instead describe a depth distribution of communities that coincides with this classification (e.g., Balata et al., 2006; Derrien-Courtel et al., 2013; Eriksson and Bergström, 2005; Foster et al., 1991; Himmelman and Laverge, 1985; Konar et al., 2009; Neushul, 1967; Perdersén and Snoeijs, 2001; Schiel and Hickford, 2001; Wallenstein et al., 2008; Wernberg and Connell, 2008; Wieters et al., 2014). For the southeastern Pacific coast, no complete dataset exists. According to published information, only the upper Infralittoral sub-zone, which is characterized by kelp beds, has been recognized for this coast. The lack of descriptions of other communities and subzones is probably more a consequence of the lack of study, rather than their real absence.

The current study describes the presence of a general pattern of community arrangements in the Chilean shallow rocky subtidal zone. Knowledge of this pattern will help to focus descriptions, make them comparable, and enable detection of changes with a qualitative approach, at least as a first alert. It also provides a basis for the formulation of hypotheses to study the functioning of this system and contributes to an evaluation strategy for the conservation and management of subtidal areas under a “seascape ecology” approach. The present paper contains a systematic study of the shallow rocky subtidal along ca. 600 km of Chilean coastline at different spatial scales to define basic community patterns, being the first of this type for the southeastern Pacific.

2. Materials and methods

2.1. Study sites

This study was conducted using the following two strategies: (a) an intensive qualitative and quantitative sampling on a 22 km stretch of coast, complemented (b) with a revision of the general pattern at a variety of sites along a ca. 600 km stretch of coast.

Intensive sampling was performed on the coast between Punta Lagunillas and La Herradura de Guayacán Bay, both sites located on the north-central coast of Chile (Fig. 1). This stretch of coast contains a wide variety and range of environments, including a protected bay (Bahía La Herradura) as well as very exposed rocky outcrops (Punta Lobos and Punta Lagunillas). Throughout the sector, the rocky bottom extends from the intertidal zone to approximately 20 m depth, with a sandy bottom characterizing the deeper subtidal. Only in the sector of Caleta Totoralillo is the rocky coast interrupted by a little sandy beach, which continues to the subtidal zone also characterized by a sandy bottom. The rocky bottom in general is diverse, some areas being of massive rock, others of boulders of different sizes or even a mixture of rocks and sand. The study area is located in a transition zone in the thermal conditions of the Chilean coast (Tapia et al., 2014), which is characterized by its diversity and productivity (Fernández et al., 2000; Thiel et al., 2007).

The second strategy included observing several points along the entire coast of the Atacama and Coquimbo Regions of Chile, between Caleta Pan de Azucar (northern limit of the Atacama Region) and Totoralillo Sur (southern limit of the Coquimbo Region) (Fig. 1). The northern and central part of this stretch of coast contains a series of