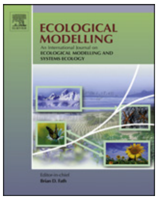
Ecological Modelling 250 (2013) 307–318

Contents lists available at SciVerse ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Network properties and keystoneness assessment in different intertidal communities dominated by two ecosystem engineer species (SE Pacific coast): A comparative analysis

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ARTICLE INFO

Article history:
Received 7 July 2012
Received in revised form 13 October 2012
Accepted 19 October 2012
Available online 20 December 2012

Keywords:
Lessonia nigrescens
Pyura praeputialis
Ecopath
Ecosim
Loop Analysis model keystone indices

ABSTRACT

Multispecies quantitative and qualitative models of the kelp *Lessonia nigrescens* and the tunicate *Pyura praeputialis* were constructed for intertidal areas of northern Chile (SE Pacific). Information on biomass, P/B ratios, catches, food spectrum, consumption and dynamics of commercial and non-commercial species was obtained and examined using *Ecopath* with *Ecosim* and *Loop Analysis* theoretical frameworks. The biomass of *L. nigrescens* and *P. praeputialis* constituted the most important compartments, exceeding 97% of the total biomass in each model system. Based on Pp/R, the system of *P. praeputialis* appeared to be the most developed. However, according to Pp/B, A/C, A_i/C_i, and redundancy, the *L. nigrescens* system was the most developed and, in turn, the least resistant to disturbances. The results obtained using *mixed trophic impacts* (*MTI*), *Ecosim* simulations, and *system recovery time* (*SRT*) showed different response patterns. The tunicate species propagated higher effects on the remaining species, whereas the kelp species presented the longest *SRT* (as a resilience measure). The model keystone species indices suggested that each model system contained a core of ecologically related species. In the *L. nigrescens* system, core was made up of the filter feeders *Semimytilus algosus*, barnacles, and small epifauna herbivores (SEH) and the predators *Concholepas concholepas* and *Heliaster helianthus*. In the *P. praeputialis* system, the core consisted of phyoplankton, zooplankton, other filter feeders and the predators *C. concholepas*, *H. helianthus*, other starfish, and large epifauna. The outcomes obtained in the current work did not indicate that the alien tunicate *P. praeputialis* was a better or superior bio-engineer when compared to the system constructed by the kelp *L. nigrescens*. Rather, each species was relevant and relied on different ecological mechanisms.

1. Introduction

The search for unique species or groups of related species whose main purpose is to sustain – in part – the properties and dynamics of communities and ecosystems has been one of the most researched areas in ecology (Wilson, 1987; Dufrene and Legendre, 1987; Padani and Csányi, 2010). These investigations reported: (1) the contribution of the ecological system, in which species or functional groups with greater biomass play a fundamental role in the structure and dynamics of the ecosystems and their emergent properties (Ulanowicz, 1986, 1997); (2) thanks to the development of experimental ecology at the end of the 1960s, certain less abundant species were also found to play an important role in the structure, dynamics, and functioning of communities and ecosystems, leading to the concept of *keystone species* (Paine, 1969) and its later applications (Paine, 1992; Wootton, 1994; Power et al., 1996; Berlow, 1999); (3) another 30 years later, the new concept of *bio-engineer* (Lawton, 1994) or *ecosystem engineer species* (Jones et al., 1994, 1997) was defined and applied to those species that create, modify, and/or increment the heterogeneity of the habitat, thereby allowing the maintenance of high species richness locally and regionally (Takeshi and Romero, 1995; Cerda and Castilla, 2001; Thiel and Ulrich, 2002; Roff et al., 2003); and (4) parallel to the research lines described above, Lewontin (1983) and Levins and Lewontin (1985) proposed a process that would explain the properties of certain species, that is, those dynamic and permanent

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http://dx.doi.org/10.1016/j.ecolmodel.2012.10.014

organisms that, through their metabolism and different activities, select, define, partially create, and destroy their own niches. This led to the proposal of the concept of *niche construction*, which has not yet been widely accepted within contemporary evolutionary theory (Lewontin, 1983; Odling-Smee, 1988; Odling-Smee et al., 1996; Laland et al., 1996, 2001).

Intertidal communities have received much attention from ecologists around the planet. In the case of the SE Pacific coast, numerous investigations have been done in all areas of biology, with notable studies of the kelp communities dominated by the native brown algae *Lessonia nigrescens* (Vasquez and Santelices, 1984) and later works done in San Jorge Bay (Antofagasta) with communities dominated by the alien tunicate *Pyura praeputialis* (Cerda and Castilla, 2001). In both communities, the importance of these organisms as *bio-engineers* or *ecosystem engineer species* (Lawton, 1994; Jones et al., 1994, 1997) or *niche constructers* (after Odling-Smee et al., 1996) has been described and evaluated. Both species offer specific conditions of protection for numerous other invertebrate species, particularly for their juvenile stages (Vasquez and Santelices, 1984; Cerda and Castilla, 2001; Castilla et al., 2004).

Cerda and Castilla (2001) relied exclusively on estimators of species diversity and richness when proposing that *P. praeputialis* constructs a more complex and diverse ecological community than does *L. nigrescens*. Although this study is an interesting exploration intending to discriminate the importance of one species or another in their respective communities, it is limited, as it fails to include the interspecific relationships based on network analysis and does not allow estimates of the emergent properties related to the state of growth and development of such systems. These properties include: *ascendency*, *redundancy*, *ascendency/capacity* ratio, *system recovery time* (as a measure of resilience), propagation of higher order effects, and quantitative and qualitative model keystoneness in both ecological systems.

Multispecies modelling offers a way to deal with some of the difficulties in the experimental identification of relevant species. It also allows the estimation of the ecosystem macrodescriptors. The application of network theory has proven to be a useful tool for evaluating and describing system properties, dynamics, and the overall health of ecosystems (Costanza and Mageau, 1999), as well as for predicting the propagation of direct and indirect effects on system recovery times in response to disturbances (e.g. Monaco and Ulanowicz, 1997; Ortiz and Wolff, 2002a,b; Arias-González et al., 2004; Pinnegar and Polunin, 2004; Patrício and Marques, 2006; Ortiz, 2008a,b, 2010). Besides, quantitative trophic models have permitted estimates of the strength of the interactions between model species or functional groups by identifying the presence of topological keystone species that occupy key positions in trophic interaction networks (Jordán et al., 1999; Jordán and Scheuring, 2004). Likewise, keystoneness can also be identified using qualitative loop models in which the topological key position of a species is a consequence of changes in its self-dynamics (density-dependent or density-independent of growth rates), modifying the balance (prevalence) of positive and negative feedbacks and, therefore, the local stability of the network.

Therefore, in the current work, we have attempted to construct quantitative and qualitative models of intertidal benthic ecological subsystems dominated by *L. nigrescens* and *P. praeputialis*. The quantitative trophic model was built using *Ecopath* with *Ecosim* software package v.5.1 (Polovina, 1984; Christensen and Pauly, 1992; Walters et al., 1997; Christensen and Walters, 2004) and the qualitative version was based on *Loop Analysis* (Levins, 1998). These models were used to estimate the macrodescriptors of each subsystem and try to determine: (1) the biomass distribution and biomass flow structure in each system type; (2) the principal benthic predators in each system; (3) the possibility for recognizing and quantifying redundancy, i.e. if several species played similar trophic roles (Lawton, 1994) in the systems; (4) which species or functional groups were most likely to be affected by different disturbance scenarios; (5) the resistance to disturbances and resilience time of each ecological subsystem as a response to disturbances; and (6) the model keystone species.

2. Materials and methods

2.1. Habitat characteristics

L. nigrescens beds and *P. praeputialis* matrices

In general terms, the beds of *L. nigrescens* constitute a band between the intertidal and the subtidal over rocky shelves and large boulders, normally exposed to the waves and the wind, which blows predominantly from the south-west (for more details, see Vasquez and Santelices, 1984; Vasquez et al., 1998). Aggregations of *P. praeputialis* develop in the normally protected intertidal sectors of Antofagasta Bay, characterized by flat, rocky shelves with a coastal slope of less than 20°. The vertical amplitude of *P. praeputialis* beds in the intertidal fluctuates between 1 and 7 m (for more details, see Cerda and Castilla, 2001). It is important to note that aggregations of *P. preaputualis* are restricted only along Antofagasta Bay, limited on the north and south of their distribution by the macroalgae, *L. nigrescens* (Fig. 1).

2.2. Selection of model compartments and data sources

The species and functional groups selected for the construction of the quantitative and qualitative trophic models were based on studies describing communities dominated by *L. nigrescens* (Vasquez and Santelices, 1984; Vasquez et al., 1998) and *P. praeputialis* (Cerda and Castilla, 2001). The biomass (*B*), catches (*Ca*), turnover rates (*P/B*), consumption rates (*Q/B*), and food items for the variables selected were obtained from the literature. Appendix A1 shows the source data for each of the compartments selected for both ecological subsystems. Although most of the model compartments represent individual species, it was necessary to consider functional groups, which included different species. In order to make the following comparison of the macrodescriptors that emerged from the network analysis more robust, these were constructed with the same number of compartments ($n = 20$), sharing most of them except the macroalgae *L. nigrescens*, the tunicate *P. praeputialis*, the sea urchin *Loxechinus albus*, and the functional group small epifauna carnivore (SEC). The remaining compartments included the sea urchin *Tetrapigus niger*, the mytilid *Semimytilus algosus*, the muricidea *Concholepas concholepas*, the seastar *Heliaster helianthus*, and the limpets *Fissurella* spp. The following functional groups were established: the macroalgae compartment, including plants belonging to the Chlorophyta (*Ulva* sp., *Enteromorpha* sp., and *Chaetomorpha* sp.), Rhodophyta (*Chondrus* sp., *Corallina* sp., and *Gelidium* sp.), and other Phaeophyta (*Glossophora* sp., *Colpomenia* sp., and *Endarachne* sp.); the mesograzers, including different gastropod herbivores (*Tegula* spp., *Scurria scurra*, *Crepipatella dilatata*, *Chiton* spp., among others); the other filter feeders (*Petrolisthes tuberculatus*, *P. violaceous*, *Allopetrolisthes puntatus*, and *Pachycheles grosimanus*); the barnacles (*Austromegabalanus psittacus*, *Balanus flosculus*, and *Chthamalus scabrosus*); the worms belonging to the classes Polychaeta and Nemertina; the Cnidaria (*Phymactis clematis* and *Anthothoe chilensis*); the bivalves (*Brachidontes granulata* and *Aulacomya ater*); other starfish (*Patiria chilensis* and *Stichaster striatus*); small epifauna herbivores (SEH), consisting of *S. scurra*, *S. araucana*, *Tegula atra*, *Acanthopleura echinata*, *Chaetopleura peruviana*; small epifauna carnivores (SEC), which contain the snails *Thais* spp.; and the large epifauna (LE), made up of specimens from the class Crustacea