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Spatial and mass balanced trophic models of La Rinconada Marine Reserve (SE Pacific coast), a protected benthic ecosystem: Management strategy assessment

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ABSTRACT

Steady-state, dynamic, and spatial models were constructed for the benthic system of La Rinconada Marine Reserve off northern Chile (SE Pacific coast). We examined data on biomass, P/B ratios, catches, food spectrum, consumption, and the dynamics of commercial and non-commercial populations using three theoretical frameworks: Ecopath, Ecosim, and Ecospace. The biomass of the scallop *Argopecten purpuratus* and the clam *Tagelus dombeii* were the most relevant compartments of the studied ecosystem. Among the carnivores, the functional crab group *Cancer* spp. was the most relevant. The Rhodophyta was the dominant macroalga compartment of the system. The results obtained using mixed trophic impacts (MTI) showed that the predatory snail *Thais chocolata* propagated higher magnitudes of direct and indirect effects on the other species or functional groups. The sea star *Luidia magallanica* and Rhodophyta had the least effects on the remaining compartments. According to the Ecosim estimates (increasing mortality by fishing), the scallop *A. purpuratus* had the highest impact on the other compartments. The Ecospace model showed similar qualitative and quantitative effects for changes in biomass under three different exploitation scenarios (by subsystems and globally). Nevertheless, the greatest changes were provoked by using the top-down control and the vulnerabilities estimated by Ecosim. System recovery times were highest with increased mortality of the asteroid *L. magallanica* and the carnivorous snail *T. chocolata*, suggesting that the sea star could be considered to be a top predator with a top-down control. The F_{MSY} estimated for the scallop *A. purpuratus* was close to the F_i originally entered in Ecopath, limiting the design and execution of an exploitation plan within ecologically sustainable boundaries. The situation was different ($F_{MSY} \ll F_i$) for the other commercial species, making possible multi-species exploitation programs. The Ecospace trophic-spatially explicit model shows a similar pattern of direct and indirect effects generated when exerting exploitation separately by subsystems. Therefore, habitat rotation of fisheries is not justified.

1. Introduction

To date, five areas are protected from open fishery intervention along the Chilean coast (SE Pacific) (SUBPESCA, 2008). One of these, La Rinconada Marine Reserve in Antofagasta Bay (Mejillones Peninsula), has the main natural shoal of the scallop *Argopecten purpuratus* (Lamarck, 1819), an important national fishery resource. The creation of La Rinconada Marine Reserve has had diverse consequences including, but not limited to, the following: (1) The protection of the scallop has benefited other species of commercial interest such as the bivalves *Aulacomya ater* (Molina, 1782) and *Tagelus dombeii* (Lamarck, 1818) and the carnivorous snail *T. chocolata* (Duclos, 1832). (2) Moreover, the closing of extractive activities within the reserve sparked the interest of several artisanal fishing organizations eager to design and execute exploitation programs for the diverse hydrobiological resources found within the reserve. (Although La Rinconada Marine Reserve is protected from open fisheries, the fishermen proposed extraction for research, which can be permitted.) (3) Unfortunately, an illegal fishery has reduced the abundance of scallops and notably modified their size structure (Avendaño and Cantillanez, 1996).

Despite knowledge on the oceanographic conditions of the La Rinconada Marine Reserve ecosystem (Escribano et al., 1995), its primary productivity (Rodriguez et al., 1991), and different aspects of the *A. purpuratus* population dynamics (Avendaño and Le Penenc, 1998; Avendaño et al., 2001, 2007; Avendaño and Cantillanez, 2005; Cantillañez et al., 2005), the different expectations of the parties interested in the productive use of the reserve could not be

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addressed adequately. The design, implementation, and execution of sustainable, multi-species management requires integrated biological and ecological information on the most important species and/or functional groups living in the benthic ecosystem of La Rinconada Marine Reserve.

For some years, the scientific community has been highly interested in evaluating, quantifying, and predicting the changes that fisheries cause in ecosystem properties (Frid et al., 1999; Hall, 1999a,b; Hawkins, 2004). This has even led to a change in the way scientific studies are carried out, shifting the focus towards the different types of ecological inter-relationships that occur in communities and ecosystems, and away from the observation and analysis of isolated populations (Francis et al., 2007; Scotti et al., 2007). In this sense, multi-species models complement the classical reductionist-population abstractions and can be used to evaluate: (1) the properties, dynamics, and global health of an ecosystem (Costanza and Mageau, 1999); (2) the propagation of higher-order effects within the complex subsystems (Levins, 1974, 1998; Hawkins, 2004); and (3) the system recovery time in response to human disturbances (Walters et al., 1997; Christensen and Walters, 2004). The ecological network theory of Ulanowicz (1986, 1997) and the Ecopath with Ecosim software package (Polovina, 1984; Christensen and Pauly, 1992; Walters et al., 1997; Christensen and Walters, 2004) have become necessary – although not exclusive – tools for evaluating the aspects laid out above. However, the use of these tools requires connecting the different ecosystem components (species and/or functional groups) through flows of energy and matter (e.g. Jørgensen, 1992, 2000; Wolff, 1994; Gaedke, 1995; Monaco and Ulanowicz, 1997; Ortiz and Wolff, 2002a,b, 2008; Arias-González et al., 2004; Pinneger and Polunin, 2004; Patrício and Marques, 2006; Ortiz, 2008a).

The multi-species trophic models based on the theoretical body of Ecopath II (Christensen and Pauly, 1992) and Ecosim (Walters et al., 1997) have become quite popular, especially for studies interested in both describing the trophic chains and predicting the effects resulting from different exploitation scenarios in marine ecosystems (Pikitch et al., 2004). In spite of this, neither of these two theoretical bodies incorporates the spatial heterogeneity responsible for the patchy distribution of the populations in the communities (Levins, 1970). Thus, stationary and dynamic trophic models should be conceptualized within geographic areas having different types of habitats or subsystems (Hall and Raffaelli, 1993). In benthic marine ecosystems, different habitats can be defined through physical and biological factors such as types of substrate, currents, vegetation, depth, recruitment, and ecological interactions (Shima et al., 2008); habitats can also be created by human activities (e.g. fisheries, eutrophication, pollution, etc.) (Thrush and Dayton, 2002; Robinson and Frid, 2003).

Spatially explicit models have been developed since the 1980s. These consider the dynamics of isolated populations or include, at most, predator–prey and parasite-host type interactions and intra or inter-specific competition (e.g. Burrows and Hawkins, 1998; Hanski, 2008). Nonetheless, few attempts have been made to build spatially explicit models based on trophic interactions at the ecosystem level. This could be due, in part, to the large amount of information and differential equations required for the classic population models (Levins, 1998). In order to overcome this limitation, Walters et al. (1997, 1999) developed a theoretical framework called Ecospace that allows the construction of spatial models based on trophic models initially balanced using Ecopath II and dynamically simulated through Ecosim. Ecospace spatial models require information about rates of movement; trophic interactions controlled by bottom-up, mixed, or top-down mechanisms; habitat preferences for each compartment; and the spatial distribution of the fishing effort. Ecospace was recently used to assess the changes caused by enacting spatial closures and restricting fishing efforts in Marine Protected Areas of the North Atlantic (Walters et al., 1999; Beattie et al., 2002; Zeller and Reinert, 2004). However, few spatially explicit Ecospace models have been built for the eastern South Pacific coast. To date, the only such work that has been published is a study describing the trophic interactions in a benthic community of the Tongoy Bay ecosystem (central-northern Chile) (Ortiz and Wolff, 2002c) and assessing the higher-order effects of different exploitation scenarios on each habitat. It is difficult to carry out replicable experiments for evaluating sustainability and the propagation of direct and indirect effects at the community or ecosystem level in response to fishing activities. Therefore, the present article aims to create a multi-species trophic model that includes the spatial heterogeneity (different habitats) of the benthic system in La Rinconada Marine Reserve. The spatial dynamic model is based on a quantitative trophic model previously balanced using Ecopath II software (Christensen and Pauly, 1992) and treated dynamically using Ecosim and Ecospace software (Walters et al., 1997, 1999). The mass-balance and dynamic models will be used to support evaluations of the following ecological aspects: (1) biomass distribution and spatial changes due to the eventual application of different fishery exploitation scenarios (fishing effort) over commercial species; (2) the species or functional groups most likely to be affected by different management scenarios and the sustainability of different potential management strategies; (3) resistance to disturbances and resilience time in response to different resource exploitation strategies (harvest pressure); and (4) the fishing mortality that represents the maximum sustainable yield (F_{MSY}) for the most valuable and important species in the system. All the simulations were executed using the following vulnerabilities: bottom-up ($v = 1.0$), mixed ($v = 2.0$), top-down ($v = 6.0$), and v's estimated by Ecosim.

2. Materials and methods

2.1. Description of the benthic habitat

The benthic system of La Rinconada Marine Reserve (23°28′S–70°30′W) in Antofagasta Bay (Mejillones Peninsula, Chile) was chosen for this study (Fig. 1). Oceanographically, this part of the bay is influenced by three different currents/water masses: subantarctic water (SAW), subtropical water (STW), and equatorial subsurface water (ESSW) (Escribano et al., 1995). The benthos is dominated by sand and gravel. Two ecological subsystems hosting different aggregates of species can be clearly identified between 8 and 15 m depth (Fig. 1). It is important to mention that an important upwelling centre near Mejillones Peninsula supplies nutrients to the coastal ecosystem (Escribano et al., 2004). Surface water temperatures range between 16 °C in winter and 20 °C in summer (Escribano et al., 2004).

2.2. Mass-balance and dynamic modelling

Ecospace describes the dynamics of biomass (B) and consumption (Q) (Eqs. (1)–(3)) over spatial and temporal dimensions, that is, as they vary within the spatial coordinates x and y and over time. Ecospace is an extension of the steady-state and dynamic models previously obtained with Ecopath II (Polovina, 1984; Christensen and Pauly, 1992) and Ecosim software (Walters et al., 1997), respectively, and is based on the following mathematical expression:

$$B_i\left(\frac{P}{B}\right)_i EE_i - \sum_{j=1}^{n} B_j\left(\frac{Q}{B}\right)_j DC_{ji} - Y_i - BA_i - E_i = 0 \quad (1)$$

where B_i and B_j are the biomasses of prey i and predator j; P/B_i is the productivity (production/biomass ratio), which is equivalent to total mortality (Z) (Allen, 1971); EE_i is ecotrophic efficiency, that