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Research Paper

Long-term structural and functional changes driven by climate variability and fishery regimes in a sandy beach ecosystem

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ABSTRACT

Structural and functional changes in a sandy beach ecosystem in the southwestern Atlantic (Barra del Chuy, Uruguay) were assessed by contrasting four Ecopath trophic models and performing temporal dynamic simulations using Ecosim. Each model (1982, 1989, 1996 and 2012) represents a historical period of a clam fishery in which regulatory structure, management tools and resource status varied substantially. The results showed that this land-ocean interface experienced significant changes reflected at the population and ecosystem levels, owing to a combined effect of fishing and climate variability. Most system biomass (excluding phytoplankton and detritus) consisted of benthic invertebrates. Phytoplankton increased significantly over time, whereas the biomass of benthic macrofaunal components varied among the periods due to bottom-up processes, mass mortalities of the harvested clams and fishing intensity. Major fishing impacts on the targeted clam and mass mortalities occurred concurrently with low phytoplankton biomass, and clam recovery occurred in the absence of harvesting and increasing primary production. Ecosystem-level attributes (e.g., Total System Throughput, Ascendency) showed considerable temporal fluctuations, which were primarily related to changes in system productivity associated with a climatic shift from a cold phase to a warm phase and increasing onshore winds. An analysis of robustness and order showed an ecosystem state lacking the flexibility to adapt to new perturbations. Dynamic simulations showed the prominent bottom-up role of environmental variability on ecosystem function and structure. Temporal dynamics is conducted by changes in primary production forced mainly by temperature patterns. The concurrent role of climate variations and fishing explained the long-term dynamics of this ecosystem, suggesting that sandy beaches are fragile social-ecological systems whose services are increasingly threatened by long-lasting stressors.

1. Introduction

The proper function of marine ecosystems is essential to sustain the services that they provide (Balvanera et al., 2014). However, diverse human activities impose a complex blend of effects on ecosystems (Costanza, 1998). Management of human activities in marine environments has evolved to better account for anthropogenic impacts and natural variability toward sustainable ecosystem services. In this setting, the Ecosystem Approach (SCBD, 2004) has been developed as a planning procedure that integrates the management of human activities, considering the structure and function of the ecosystems. Usually, this approach requires practitioners to "identify and take action on influences that are critical to the health of ecosystems, thereby achieving sustainable use of ecosystem goods and services and maintenance of ecosystem integrity" (Borja et al., 2016). The ecosystem approach to fisheries (EAF) has been adopted to integrate the conservation of the structure, diversity and function of ecosystems and the fisheries management actions taken to satisfy societal demands for food and economic benefits (Garcia et al., 2003).

Fishery collapses may result from a combination of bottom-up (environmental) and top-down (fishing) effects, e.g., overfishing and recruitment failures caused by adverse environmental conditions (Larkin, 1996; Boudreau et al., 2015). Therefore, it is necessary to understand the species interactions along with the abiotic variables while recognizing the responses of fishers to changes in stock abundance. In particular, EAF requires an integrated system analysis that can differentiate between the human and natural

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factors underlying resource variability and ecosystem health. In this vein, climate variability strongly influences ocean productivity and these changes dramatically affect coastal marine ecosystems (Hoegh-Guldberg and Bruno, 2010). This is particularly noticeable in intertidal habitats that harbor valuable benthic small-scale fisheries (Defeo et al., 2016), where harvesting and environmental drivers acting together may alter demographic and life history traits of harvested species, and may propagate to higher-order ecological effects, such as disruptions of food-web linkages (Defeo et al., 2013).

Food web-based metrics are fundamental measures of ecosystem structure and function (Cury and Christensen, 2005; Libralato et al., 2014), which convey information about the dynamics, patterns and processes of fisheries management (ICES, 2014). Fisheries regulation, pollution reduction, pest control and other management activities benefit from information about food web components, which are also necessary for defining the environmental sustainability of marine ecosystems (Fath, 2015; EU Directive, 2008). Some food web indicators are potentially useful as proxies for decision criteria in EAF (Link, 2002; Shannon et al., 2014), including the mean trophic levels of the catches and the primary production required to sustain the fisheries (Pauly et al., 1998; Branch et al., 2010). Moreover, comparative modeling studies in which trophic representations of the same system are developed for different time periods (Shannon et al., 2014; Coll et al., 2009) allow comparisons of the changes in ecosystem structure and trophic relationships due to fishing, environmental perturbations, or combinations thereof (Corrales et al., 2015). In this way, modeling can provide scientifically based information on ecosystem health to regulatory and management systems, and constitute an essential input in data-poor situations, such as in the benthic small-scale fisheries referred above.

In Latin America, few studies have focused on analyzing the changes in food web structure in relation to resource management and environmental variations (Ortiz and Wolff, 2002; Neira et al., 2014). Barra del Chuy beach (BCB) is an exposed intertidal ecosystem on the Atlantic coast of Uruguay with a rich and abundant benthic community (Defeo et al., 1992). In this highly productive ecosystem, seabirds, fishes and gastropods are top predators (Lercari et al., 2010). The trophic function of this system, elucidated through stable isotopes, shows the combined importance of autochthonous phytoplankton and terrestrial organic matter infueling the food web (Bergamino et al., 2013). The yellow clam (*Mesodesma mactroides*) constitutes a major portion of the total community biomass at BCB; it has been harvested by indigenous people since prehistoric times (Villamarzo, 2010). During the past 50 years, this species has been subject to a small-scale fishery (Ortega et al., 2012), which has undergone contrasting phases of management, regulatory and resource status (Gianelli et al., 2015). Several studies have focused on understanding population fluctuations of the target species (the only one harvested in the study site), as linked to environmental variability and fishing effort (e.g., Defeo et al., 2016). However, comprehensive studies to elucidate changes occurring in ecosystem structure and function, and the interacting drivers of changes in these environments are still lacking.

We assessed temporal responses of the yellow clam population and ecosystem functioning and dynamics to concurrent changes in fishery management scenarios and primary production. The research strategy included the implementation of static trophic models representing four different historical periods to obtain ecological indicators employed to analyze structural and functional changes in the ecosystem. This description was complemented with dynamic simulations considering temporal changes in primary production, fishing effort and trophic effects. Thus, the main questions addressed were: 1) how did the ecosystem structure and function changed over 30 years? and 2) what were the main factors driving these changes?

2. Materials and methods

2.1. Study area

BCB is a dissipative sandy beach (mean grain size = 0.20 mm, sorting = 0.70 mm, slope = 3.53 cm m^{-1}, tide range = 0.5 m) (Lercari et al., 2010) 23 km long and 300 m wide (total area 7 km^2), located on the eastern coast of Uruguay in the southwestern Atlantic Ocean (SAO) (33°40′ S, 53°29′ W) (Fig. 1). Intertidal sandy beaches are peculiar ecosystems because of their small dimensions and ecological simplicity. The high productivity of this microtidal system sustains the highest diversity of macrobenthic communities among Uruguayan beaches (Lercari and Defeo, 2006, 2015).

2.2. Static food web modelling

For each period, a mass-balanced model was developed through Ecopath with Ecosim 6 (EwE6). The static trophic model (Ecopath) assumes mass balance, such that the production of a given ecological group is equal to the biomass lost to fishing or export, predation and natural mortality other than predation (Christensen and Walters, 2004). The model considers that all inputs are equal to the outputs for each species or group through a series of simultaneous lineal equations, which for each functional group is expressed as:

$$B_i \cdot \left({}^{P}\!/\!{}_{B}\right)_i \cdot EE_i - \sum_{i=1}^{n} B_j \cdot \left({}^{Q_j}\!/\!{}_{B_j}\right) \cdot DC_{ji} - EX_i = 0$$

where B is the biomass for group/species i. (P/B) is the production/biomass ratio. EE is the ecotrophic efficiency indicating the proportion of the production that is utilized in the system, values close to 1 mean a high utilization and values close to 0 represent a group having neither predation nor fishing in the system (Essington, 2007); DC_{ji} is the fraction of the prey (i) in the diet of the predator (j); Q_j/B_j is the consumption/biomass ratio for predator (j), and EXi is the export for prey i. Considering this equation for n groups, a system of lineal equations is developed where at least three of the four parameters of each group (B, P/B, Q/B and EE) must be known while the other one is estimated by the model.

To explore the consequences of fishing and environmental changes for the BCB trophic flows and the food web structure, we modeled four periods of contrasting conditions during the past 30 years (Table 1). The first model represented the first period of the fishery (1981–1986), in which centralized management (CM) and open access led to a sharp increase in catches. This phase was followed by a 2-year fishery closure and a reorganization of fishers into an informal co-management scheme (Co-M) (Defeo, 1998). This second period lasted 7 years (1987–1994). A third period (1994–2007) was characterized by mass mortalities (MM) that decimated clam populations across their entire distribution range, including BCB (Ortega et al., 2012). The yellow clam fishery was reopened in 2009 under an ecosystem approach to fisheries (EAF) and co-management as the institutionalized (Law N° 19175) mechanism for stakeholder participation (Gianelli et al., 2015). We followed the Ecopath with the Ecosim approach to perform an ecotrophic description for each period by computing both attributes for each trophic group and ecosystem level analysis (Christensen and Walters, 2004).

Regarding climatic variability in this region (Ortega et al., 2013), the first and second historical periods (CM and Co-M) were characterized by the influence of cold waters in the area, whereas warmer