Ecological Modelling 274 (2014) 41–49

Contents lists available at ScienceDirect

Ecological Modelling

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

Analysing changes in the southern Humboldt ecosystem for the period 1970–2004 by means of dynamic food web modelling

Sergio Neira [a,b,*], Coleen Moloney [c,f], Villy Christensen [d], Philippe Cury [e], Lynne Shannon [c,f], Hugo Arancibia [a]

[a] Departamento de Oceanografía, Universidad de Concepción, Chile
[b] Programa COPAS Sur Austral, Universidad de Concepción, Chile
[c] Zoology Department, University of Cape Town, South Africa
[d] Fisheries Centre, University of British Columbia, Vancouver, BC, Canada
[e] UMR EME-212, CRH-Centre de Recherche Halieutique Méditerranéenne et Tropicale, IRD– IFREMER and Université Montpellier II, Sète, France
[f] Marine Research Institute, University of Cape Town, South Africa

ARTICLE INFO

Article history:
Received 28 November 2012
Received in revised form
27 September 2013
Accepted 29 September 2013
Available online 25 December 2013

Keywords:
Ecopath with Ecosim
Fishing patterns
Physical forcing
Regime shifts
Southern Humboldt
Trophic controls

ABSTRACT

A 22-group Ecopath model representing the southern Humboldt (SH) upwelling system in the year 1970 is constructed. The model is projected forward in time and fitted to available time series of relative biomass, catch and fishing mortality for the main fishery resources. The time series cover the period 1970 to 2004 and the fitting is conducted using the Ecopath with Ecosim (EwE) software version 5.1. The aim is to explore the relative importance of internal (trophic control) and external (fishing, physical variability) forcing on the dynamics of commercial stocks and the Southern Chilean food web. Wide decadal oscillations are observed in the biomass of commercial stocks during the analyzed period. Fishing mortality explains 21% of the variability in the time series, whereas vulnerability (v) parameters estimated using EwE explain an additional 20%. When a function affecting primary production (PP) is calculated by Ecosim to minimize the sum of squares of the time series, a further 28% of variability is explained. The best fit is obtained by using the fishing mortality time series and by searching for the best combination of v parameters and the PP function simultaneously, accounting for 69% of total variability in the time series. The PP function obtained from the best fit significantly correlates with independent time series of an upwelling index (UI; rho = 0.47, $p < 0.05$) and sea surface temperature (SST; rho = −0.45, $p < 0.05$), representing environmental conditions in the study area during the same period of time. These results suggest that the SH ecosystem experienced at least two different environmentally distinct periods in the last three decades: (i) from 1970 to 1985 a relatively warm period with low levels of upwelling and PP, and (ii) from 1985 to 2004 a relatively cold period with increased upwelling and PP. This environmental variability can explain some of the changes in the food webs. Fishing (catch rate) and the environment (bottom-up anomaly in PP) appear to have affected the SH both at the stock and at the food web level between 1970 and 2004. The vulnerability setting indicates that the effects of external forcing factors may have been mediated by trophic controls operating in the food web.

1. Introduction

Fishing is a partly managed human activity that often represents a major threat to marine ecosystems (Jackson et al., 2001; Halpern et al., 2008). Technology applied to shipping, navigation, stock detection, and fishing devices (Valdermarsen, 2001) transformed human abilities, so humans could become efficient and dangerous predators, able to capture almost anything that is abundant and/or valuable in the sea (Pauly et al., 2002). This behaviour has disrupted many ecosystems through changes in marine food webs and destruction of physical habitat (Jennings and Kaiser, 1998; Pauly et al., 1998; Daan et al., 2005). Although worldwide decreases in fish stocks are strongly correlated with the start of the industrial fishing era (Hutchings, 2000; Myers and Worm, 2003; Christensen et al., 2003), physical factors are widely recognized to play an important role in fish population dynamics (Cushing, 1982). Marine populations showed fluctuations even before the start of

* Corresponding author at: Cabina 10, Departamento de Oceanografía, Universidad de Concepción, P.O. Box 160-C, Concepción, Chile/Zoology Department, University of Cape Town, Rondebosch, 7701, South Africa. Tel.: +56 41 2661329; fax: +56 41 2225400.
E-mail address: seneira@udec.cl (S. Neira).

0304-3800/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.ecolmodel.2013.09.022

fishing, revealing a strong link between their dynamics and environmental variability (Shackleton, 1987; Schwartzlose et al., 1999). Marine ecosystems also undergo large-scale, decadal fluctuations and regime shifts, which seem to be driven by climate forcing (Hare and Mantua, 2000; Stenseth et al., 2002; Chavez et al., 2003; Steel, 2004), but some have been also related to overfishing (Cury and Shannon, 2004; Lees et al., 2006; Daskalov et al., 2007).

In some marine ecosystems predation mortality is the main source of total mortality (Bax, 1991, 1998) and fishery removal of predatory species has revealed putative trophic cascades (top-down control) in the ocean (Stenek, 1998; Dulvy et al., 2004; Frank et al., 2005; Daskalov et al., 2007). On the other hand, wasp-waist control exerted by small pelagic fish (*sensu* Cury et al., 2000) seems to be a characteristic feature in upwelling ecosystems (Cury et al., 2005). This suggests that in such ecosystems, marine populations are often also regulated by the behaviour of predators, total consumption and prey availability. Therefore, the effects of fishing and physical forcing on living groups and food web structure can strongly depend on who eats whom, and more significantly on who controls whom (Shannon et al., 2000; Hunt and McKinnell, 2006).

Upwelling ecosystems are productive areas of the world's oceans where fishing, environmental shifts and trophic controls are key processes (Schwartzlose et al., 1999; Chavez et al., 2003; Cury et al., 2005; Fréon et al., 2009). However, the relative importance of each factor on food web dynamics is poorly understood and quantified. In particular, the southern section of the Humboldt system – off central Chile – is one of the least studied upwelling systems of the world (Morales and Lange, 2004). Although species replacement, trophic controls and fishery-induced changes at the ecosystem level are likely to affect the whole ecosystem (Yáñez et al., 1992; Neira et al., 2004; Arancibia and Neira, 2005; Alheit and Ñiquen, 2004), single-species approaches dominate fisheries management in Chile.

The global call for an ecosystem approach to fisheries (FAO, 2003) implies the adoption of a wider and holistic view in management, necessitating consideration of multi-species and climate effects. Ecopath with Ecosim (EwE; Walters et al., 1997; Christensen and Walters, 2004) is a family of models that has been applied to many different regions around the world (see www.ecopath.org), allowing global and local assessments of aquatic food webs and ecosystem effects of fishing (e.g., Pauly and Christensen, 1995; Pauly et al., 1998, 2002; Christensen et al., 2003; Neira and Arancibia, 2004; Neira et al., 2004). The dynamic Ecosim model allows users to fit food web models to observed data and, in the process, evaluate the relative effects of fishing, trophic relationships and bottom-up forcing on observed dynamics (Christensen and Walters, 2004; Christensen et al., 2005).

Shannon et al. (2008) used three EwE models representing the Benguela Current and the northern (Peru) and southern (central Chile) subsections of the Humboldt Current, with the aims of comparing internal and external forcing in these three ecosystems, with focus on environmental forcing in different trophic levels. The fitting process revealed that changes in the sum of squares were sensitive to, among others, trophic relationships involving common sardine and anchovy as predators and prey (Shannon et al., 2008). Unfortunately, these authors did not analyzed further the dynamics of other functional groups that are of economic or ecological value in the Southern Humboldt. However, the above authors indicated that food web dynamics in the Southern Humboldt may be different from the other upwelling systems due to unique features.

Comparing marine ecosystems using inter-calibrated models is important in understanding ecosystem effects of fishing and the environment worldwide. This endeavour requires relatively detailed understanding of the different ecosystems and models. Previous publications describing the EwE model of the Southern Humboldt are not readily available (Neira, 2008) and/or not present all details regarding model parameterization and findings (Shannon et al., 2008). Thus, we consider important to fully introduce the dynamic simulation for the southern Humboldt in order to allow future comparisons of marine ecosystems affected by environmental variation and fishing. Therefore, in this paper we further investigate the southern Humboldt system introducing an Ecopath model representing the upwelling system off central Chile in 1970 that is constructed and projected forward in time using the Ecosim routines. The model simulations are fit to available time series of biomass, landings and fishing mortality for the main commercial fish stocks. Our aim is to analyze the relative importance of fishing mortality, predator–prey interactions (through prey vulnerability) and bottom-up forces (through changes in primary productivity) on observed stocks and food web dynamics.

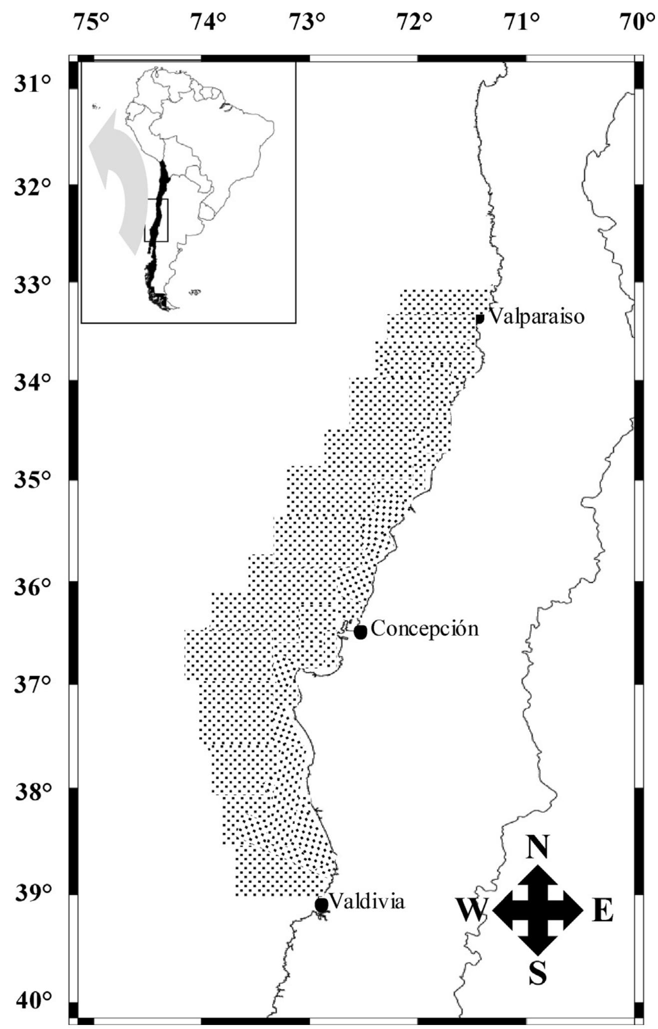

Fig. 1. Map of the study area, the upwelling system off central Chile (33°–39° S).

2. Methods

The study area corresponds to the southern section of the Humboldt (SH) system off central Chile, from 33° S to 39° S and from the coast to 30 nautical miles offshore, covering a total area of 50 000 km^2 (Fig. 1). The geographic, oceanographic, ecological and fishing features of this sub-system have been described in Camus (2001), Strub et al. (1998), Daneri et al. (2000), Escribano et al. (2003) and Neira et al. (2004). The area consists of a narrow