Progress in Oceanography 146 (2016) 22–37

Contents lists available at ScienceDirect

Progress in Oceanography

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

Effects of lower trophic level biomass and water temperature on fish communities: A modelling study

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ARTICLE INFO

Article history:
Received 18 October 2015
Received in revised form 13 April 2016
Accepted 13 April 2016
Available online 12 May 2016

ABSTRACT

Physical and biogeochemical changes of the oceans have complex influences on fish communities. Variations of resource and temperature affect metabolic rates at the individual level, biomass fluxes at the species level, and trophic structure as well as diversity at the community level. We use a Dynamic Energy Budget-, trait-based model of the consumers' community size-spectrum to assess the effects of lower trophic level biomass and water temperature on communities at steady state. First, we look at the stressors separately in idealized simulations, varying one while the second remains constant. A multi-domain response is observed. Linked to the number of trophic levels sustained in the consumers' community, the regimes highlighted present similar properties when lower trophic level biomass is increased or temperature decreased. These trophic-length domains correspond to different efficiencies of the transfer of biomass from small to large individuals. They are characterized by different sensitivities of fish communities to environmental changes. Moreover, differences in the scaling of individuals' metabolism and prey assimilation with temperature lead to a shrinking of fish communities with warming. In a second step, we look at the impact of simultaneous variations of stressors along a mean latitudinal gradient of lower trophic level biomass and temperature. The model explains known observed features of global marine ecosystems such as the fact that larger species compose fish communities when latitude increases. The structure, diversity and metabolic properties of fish communities obtained with the model at different latitudes are interpreted in light of the different trophic-length domains characterized in the idealized experiments. From the equator to the poles, the structure of consumers' communities is predicted to be heterogeneous, with variable sensitivities to environmental changes.

1. Introduction

Climate driven physical and biogeochemical changes impact marine ecosystems properties in a number of ways (Bindoff et al., 2007; Doney et al., 2012). They affect individuals directly, modifying their access to resources through increased stratification (Sarmiento et al., 2004; Bopp et al., 2013) or their metabolism through temperature changes (Gillooly et al., 2001; Clarke and Fraser, 2004), acidification (Fabry et al., 2008) or de-oxygenation (Pörtner and Knust, 2007). These direct effects at the individual level propagate to the community level through alterations of the biomass transfer across trophic and organization levels. For example, climate change has been shown to induce a global body size shrinking (Daufresne et al., 2009; Sheridan and Bickford, 2011). It will also lead to changes in community level fish production (Blanchard et al., 2012; Lefort et al., 2015) or biodiversity (Cheung et al., 2009). These indirect responses modify the services provided by marine ecosystems. Fisheries are expected to be particularly affected and the consequences in terms of food security and economic profitability are major issues (Brander, 2007; Jennings and Brander, 2010). In this context, understanding the intricate response of fish communities to environmental changes is an urgent challenge (Rice and Garcia, 2011; Merino et al., 2012).

However, investigating and modelling environmental effects on fish communities is a difficult task, the environment acts directly on individuals and induces indirect species and community level emergent properties from individual interactions. Because of our limited knowledge, any attempt to model the response of fish communities to environmental changes usually implies pragmatic compromises depending on the focal levels and scales of organization. For example, some approaches fully account for individual life

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http://dx.doi.org/10.1016/j.pocean.2016.04.003
0079-6611/

history as well as intra- and inter-specific interactions on local scales with individuals based models (Grimm, 1999; Shin and Cury, 2001), while others only model target species and their evolution in a changing environment (Lehodey et al., 2008; Dueri et al., 2014). Yet other approaches focus on the species probability of occurrence as a function of given environmental variables with ecological niche models (Peterson, 2003; Cheung et al., 2009), others disregard species differences and only derive the ecosystem size-spectrum, namely the biomass distribution as a function of individuals' size (Maury et al., 2007; Blanchard et al., 2009, 2012; Woodworth-Jefcoats et al., 2013).

Body size plays a dominant role in fish communities. It structures individual's life history and trophic interactions. Recent studies use both body size and the trait species maximum (or maturity) size as structuring variables to integrate through organization levels and account for the influence of functional biodiversity on community dynamics. These trait-based size-spectrum models link individual's bioenergetics to the specific structure to the emergent response of communities (Andersen and Beyer, 2006; Hartvig et al., 2011; Maury and Poggiale, 2013). Similarly to physiologically structured populations models (Metz and Diekmann, 1986; De Roos and Persson, 2001, 2013) these approaches account for environmental signals impacts across organization levels.

In this paper, we use a trait-based size-spectrum model presented in Maury and Poggiale (2013) to investigate the impact of the environment on fish communities. We focus on the impact of two major factors affected by climate change; the lower trophic level biomass and water temperature. In the first section we summarize the model, especially how it links the individual's bioenergetics to the specific structure to community dynamics. The way environmental effects are introduced is also described. To analyze environmental impacts, indicators of the ecosystem state are derived. They characterize ecosystems in terms of structure, diversity and metabolism. The elicitation of the model's parameters is presented. In a second section we use this framework to analyze how the characteristics of fish communities are linked to the environment. The effects of lower trophic level biomass and temperature are first considered independently, before focusing on their combined impacts. Distinct trophic-length domains are observed over different lower trophic level biomass and temperature ranges. To bring realism into this idealized study, the structure of marine ecosystems is then investigated along a latitudinal gradient representative of mean temperature and mean lower trophic level biomass co-variations from South to North pole. Finally, the third section discusses the use of our mechanistic approach to explain features of global marine ecosystems. It agrees especially with the observation that larger species compose fish communities when latitude increases. The distinct trophic-length domains when changing lower trophic level biomass and temperature will lead to different sensitivities of fish communities to environment variations.

2. Method

2.1. Model

2.1.1. The trait-based community size-spectrum model

At the individual level, the model adopts a reduced formulation of the Dynamic Energy Budget theory (DEB, Kooijman, 2000, 2010) and represents the life history of fish individuals (Fig. 1). It dynamically prescribes the allocation of assimilated energy to growth in structural volume V (cm^3), respiration, maturation and reproduction during the life time of individuals. This life history is fully determined by: the quantity of food encountered which controls the satiation of individuals defined by a scaled Holling type II functional response (see $f_V^{V_m}$ Section 2.1.2); the body temperature T (°C), that increases or reduces metabolic rates (see T_{cor}, Section 2.2.2). In the DEB theory, most processes scale with the maximum structural volume V_m that a species reaches in a favourable environment. Therefore, the theory represents the life history of individuals belonging to an infinite number of fish species with a same set of generic parameters (see DEB parameters Table 2 and Section 2.4.2). It disregards other dimensions of species diversity since two individuals of different species with the same size V_m will be considered as functionally identical. But it models the main life history characteristics of the full range of fish species in an ecosystem keeping the model complexity tractable.

At species level, on a log–log scale the density of abundance $N_{V,t}^{V_m}$ (# cm^{-3} cm^{-3} m^{-3}) of fish individuals of a species of maximum size V_m can be represented as a function of their structural volume $V \in [V_b, V_m]$ with an abundance density spectrum (for V_b a birth volume). Each species characterized by $V_m \in [V_m^{min}, V_m^{max}]$, the range of specific traits of the community, can be represented with a distinct species spectrum (Fig. 1). These specific spectra are coupled to each other by predation. In aquatic ecosystems, predators are

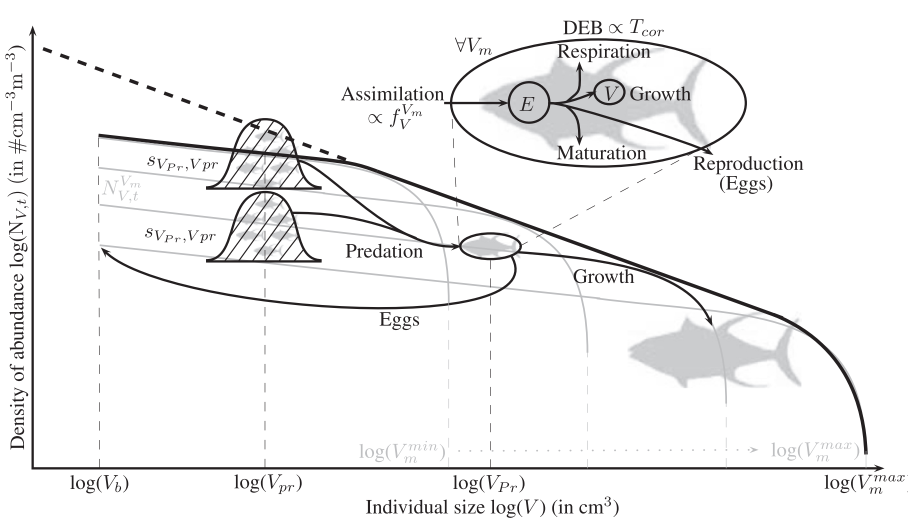

Fig. 1. Schematic representation of the fish community abundance density spectrum $N_{V,t}$ (black line) as a sum of species spectra $N_{V,t}^{V_m}$ (grey lines) emerging from the individual level DEB energy fluxes driven by size-selective predation (black arrows). Lower trophic level resource spectrum (dashed line).