



Natural variability of marine ecosystems inferred from a coupled climate to ecosystem simulation



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ABSTRACT

This modeling study analyzes the simulated natural variability of pelagic ecosystems in the North Atlantic and North Pacific. Our model system includes a global Earth System Model (IPSL-CM5A-LR), the biogeochemical model PISCES and the ecosystem model APECOSM that simulates upper trophic level organisms using a size-based approach and three interactive pelagic communities (epipelagic, migratory and mesopelagic). Analyzing an idealized (e.g., no anthropogenic forcing) 300-yr long pre-industrial simulation, we find that low and high frequency variability is dominant for the large and small organisms, respectively. Our model shows that the size-range exhibiting the largest variability at a given frequency, defined as the resonant range, also depends on the community. At a given frequency, the resonant range of the epipelagic community includes larger organisms than that of the migratory community and similarly, the latter includes larger organisms than the resonant range of the mesopelagic community. This study shows that the simulated temporal variability of marine pelagic organisms' abundance is not only influenced by natural climate fluctuations but also by the structure of the pelagic community. As a consequence, the size- and community-dependent response of marine ecosystems to climate variability could impact the sustainability of fisheries in a warming world.

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1. Introduction

Fisheries are of great importance in many regions, for food security as well as economic development. In 2012, the North Atlantic and the North Pacific Oceans respectively provided about 13% and 31% of global marine fish catches (Yearbook, 2012). Climate variations may impact ecosystems sustainability with consequences for fisheries as demonstrated in different regions of the world (Badjeck et al., 2010; Brander, 2010; Di Lorenzo and Ohman, 2013; Gröger et al., 2014; Perry et al., 2010). To better anticipate future fisheries management, it appears crucial to enhance our knowledge on the response of marine ecosystems to climate variability.

The variability of the marine environment, influenced by climate perturbations, is a key factor in driving the temporal variability of marine ecosystems (Alheit et al., 2014; Chavez et al., 2011; Gröger et al., 2014; Harris et al., 2014; Henson et al., 2009; Hollowed et al., 2001; Parsons and Lear, 2001). Over short time scales (years to decades), the natural variability of the climate system is known to induce

fluctuations in both environmental conditions and marine resources (Chavez et al., 2011; Di Lorenzo and Ohman, 2013; Gröger et al., 2014; Henson et al., 2009; Martinez et al., 2009; Sférian et al., 2014). Over multi-decadal to centennial time scales, in addition to natural variability, the impacts of anthropogenic climate change on marine environmental conditions (Rind et al., 1989; Salinger, 2005) are expected to affect marine ecosystems (Blanchard et al., 2012; Bopp et al., 2013; Dueri et al., 2012, 2014; Jones et al., 2014; Lefort et al., 2015). In their modeling study, Bell et al. (2013) showed that under the IPCC SRES A2 emissions scenario, climate change would modify the characteristics of the Pacific warm pool (temperature, stratification, spatial distribution), through changes in wind intensity and the strength of oceanic currents, with consequences on marine productivity levels and high trophic level organisms such as tuna.

The North Atlantic and the North Pacific regions undergo strong climate variability. In the North Atlantic, the NAO is the dominant mode of atmospheric variability. The NAO is characterized by a dipole linking a high-pressure zone over the Azores and a low-pressure zone over Iceland (Hurrell et al., 2001) and oscillates between positive and negative modes at a period shorter than 15 years (Gastineau et al., 2013; Hurrell et al., 2001). In the North Atlantic, the NAO represents

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about a third of the sea level pressure variance in winter (December–January–February), the season of the year when it is the strongest (Hurrell et al., 2001), and about 11% of the sea surface temperature (SST) variance (Harris et al., 2014). Another mode of variability in the North Atlantic is the Atlantic Multidecadal Oscillation (AMO), which explains about 15% of the SST variance (Harris et al., 2014). The AMO is related to the Atlantic Meridional Overturning Circulation (AMOC) variability (Zhang and Delworth, 2007) and oscillates between cold and warm phases at an un-evenly distributed period of 60–80 years. The AMO seems to influence the life-cycle of fishes in the temporal and spatial domains by affecting fish abundances and their migration patterns (Alheit et al., 2014). The North Pacific climate is impacted by the El Niño–Southern Oscillation (ENSO) mode which is located in the tropics but has worldwide impacts (19% of the non-seasonal variability of SST over all oceans) through modifications of wind patterns and near surface temperature (Deser et al., 2010). The North Pacific Ocean is also subject to the Pacific Decadal Oscillation (PDO) that is a long-lived El Niño-like pattern (with less weight in the tropical Pacific) with a periodicity of 20–30 years and explains about 25% of the SST variance (Deser et al., 2010; Mantua and Hare, 2002). The impact of these variability modes on marine ecosystems is difficult to characterize. Characterizing low-frequency modes indeed requires long time series of observations (at least twice the length of the event time-period). Long-term time series exist: for instance, Ravier (2001) gathered 54 time series longer than 20 years, with a few extending up to 400 years, of trap data on Bluefin tuna in the Atlantic Ocean and in the Mediterranean Sea. Based on these time series, she highlighted a 20-year period of variability of Bluefin tuna abundance. However, trap data or any data from fisheries are mostly limited to commercial species and to the harvested size ranges. For instance, Ravier (2001) and Ravier and Fromentin (2004) targeted mostly large specimens of Bluefin Tuna (>60 kg) and few juveniles (<35 kg) were included in their data. Consequently, the dataset misses some key links of the trophic chain variability.

In the natural environment, anthropogenic effects are superimposed on natural variability (Hsieh et al., 2006). Disentangling natural variability from anthropogenic contributions or secular trends in the observations is difficult, as climate change may alter natural climate variability. Gillett et al. (2003) showed that the increased trend of the North Atlantic Oscillation (NAO) index toward its positive phase may be connected to the increase of greenhouse gas concentration due to anthropogenic activities. Natural variability changes may also overcome those induced by anthropogenic climate change at global or regional scales (Henson et al., 2010; Séférian et al., 2014). In this context, it is critical to improve our understanding of the ecosystem response to natural modes of climate variability, in order not only to better understand the links between climate and ecosystems, but also to better detect the impact of anthropogenic climate change on marine systems. Mechanistic models considering the effect of the environmental variability in a holistic manner offer an interesting alternative tool to study the propagation of natural environmental variability in ecosystems. Using a size-structured ecosystem model, the Apex Predators Ecosystem Model (APECOSM), Maury et al. (2007b) showed that oscillations of primary production or temperature induce variations in high trophic level (HTL) biomass that depend on the frequency of the environmental perturbation. However, this study was restricted to the investigation of the effects of idealized variations of temperature or primary production on HTL. In addition, their model represented the size-spectrum of only one pelagic community disregarding their spatial variability.

In this study, we use a recent version of APECOSM (Maury, 2010; Maury et al., 2007a) that includes three interactive generic communities (epipelagic, migratory, and mesopelagic) and their global-scale 3-D distribution and movements (passive transport and active swimming). In addition, the model explicitly includes the effects of major environmental factors (food, temperature, light and oxygen) that determine

organism's habitat, swimming and metabolic rates. Through simulations with this state-of-the-art model, we analyze the response of three generic pelagic communities to a “realistic” representation of the variability of multiple environmental factors simulated by the IPSL Earth System Model.

2. Method

2.1. Models

This study exploits a 300-year long pre-industrial simulation using the coupled PISCES–APECOSM model. The PISCES model simulates marine biogeochemistry and lower trophic levels, including four plankton functional types (Aumont and Bopp, 2006) and APECOSM simulates the marine upper trophic levels through the representation of three size-structured generic marine pelagic communities (Maury et al., 2007b). The model configuration is the same as in Lefort et al. (2014), except that the simulated climate variability is not influenced by anthropogenic forcing.

2.1.1. The PISCES model

Production at the base of the trophic chain is calculated with the PISCES model. PISCES includes two phytoplankton types (nanophytoplankton and diatoms, respectively; NanoPHY and Diat), two zooplankton size-classes (micro- and meso-zooplankton, respectively; MicroZOO and MesoZOO) and two detritus compartments distinguished by their vertical sinking speed (small and large organic matter particles, respectively; SmallPOC and LargePOC), a dissolved organic carbon pool, and five nutrients (Fe, NO_3^- , NH_4^+ , Si, and PO_4^{3-}) (Aumont and Bopp, 2006). In PISCES, phytoplankton growth is a function of; temperature, a term of light limitation depending on the photosynthetic available radiation (PAR) and the mixed layer depth (MLD), and a term of nutrient limitation. In the following sections of the paper, the sum of all organic matter pools in the form of particles (living or dead biomass) is referred to as Low Trophic Level (LTL):

$$LTL = \text{NanoPHY} + \text{Diat} + \text{MicroZOO} + \text{MesoZOO} + \text{SmallPOC} + \text{LargePOC}.$$

2.1.2. The high trophic level model APECOSM

APECOSM represents the energy flow through the size-spectrum of marine organisms from 1 mm to 2 m. It simulates the food chain from small organisms at the base of the trophic chain up to high trophic level organisms at the top of the food chain. In the following sections, HTL designates all the organisms represented in APECOSM. Opportunistic predation, which depends on the size ratio between the prey and the predator, and organisms' growth, control the energy flux through the system (Maury, 2010; Maury et al., 2007b). Energy is only supplied by primary producers (LTL is the “source term” for APECOSM) and transferred to consumers through predation. All energy fluxes are explicit, predation is viewed as a loss of energy for preyed size classes and a gain of energy for predating size classes. The maximum amount of preyed energy is proportional to the body surface to meet the growth, reproduction and maintenance needs of the organism (Maury et al., 2007b). The allocation of energy for growth or reproduction is determined according to the Dynamical Energy Budget (DEB) theory (Kooijman, 2001). Part of the ingested energy is allocated to growth (and somatic maintenance which is not explicit in the model) and the rest of the energy is devoted to maturity maintenance and eggs production (as well as gonad development which is not explicit). The ingested energy is used in the same way by all the organisms, and mean physiological parameters are used to describe the energy fluxes through every consumer organism of the ecosystem. In APECOSM, all pelagic organisms of the open ocean are represented and divided into three Open Ocean Pelagic Communities (OOPCs): epipelagic, migratory and

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