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A spatial ecosystem and populations dynamics model (SEAPODYM) – Modeling of tuna and tuna-like populations

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ABSTRACT

An enhanced version of the spatial ecosystem and population dynamics model SEAPODYM is presented to describe spatial dynamics of tuna and tuna-like species in the Pacific Ocean at monthly resolution over 1° grid-boxes. The simulations are driven by a bio-physical environment predicted from a coupled ocean physical–biogeochemical model. This new version of SEAPODYM includes expanded definitions of habitat indices, movements, and natural mortality based on empirical evidences. A thermal habitat of tuna species is derived from an individual heat budget model. The feeding habitat is computed according to the accessibility of tuna predator cohorts to different vertically migrating and non-migrating micronekton (mid-trophic) functional groups. The spawning habitat is based on temperature and the coincidence of spawning fish with presence or absence of predators and food for larvae. The successful larval recruitment is linked to spawning stock biomass. Larvae drift with currents, while immature and adult tuna can move of their own volition, in addition to being advected by currents. A food requirement index is computed to adjust locally the natural mortality of cohorts based on food demand and accessibility to available forage components. Together these mechanisms induce bottom-up and top-down effects, and intra- (i.e. between cohorts) and inter-species interactions. The model is now fully operational for running multi-species, multi-fisheries simulations, and the structure of the model allows a validation from multiple data sources. An application with two tuna species showing different biological characteristics, skipjack (*Katsuwonus pelamis*) and bigeye (*Thunnus obesus*), is presented to illustrate the capacity of the model to capture many important features of spatial dynamics of these two different tuna species in the Pacific Ocean. The actual validation is presented in a companion paper describing the approach to have a rigorous mathematical parameter optimization [Senina, I., Sibert, J., Lehodey, P., 2008. Parameter estimation for basin-scale ecosystem-linked population models of large pelagic predators: application to skipjack tuna. Progress in Oceanography]. Once this evaluation and parameterization is complete, it may be possible to use the model for management of tuna stocks in the context of climate and ecosystem variability, and to investigate potential changes due to anthropogenic activities including global warming and fisheries pressures and management scenarios.

1. Introduction

The last two decades have shown a fundamental change at the international level to address marine exploitation issues from an ecosystem perspective. However, ecosystem models adapted to an ecosystem-based management approach are at an early stage of development, and all the basic stock assessment works done by Regional Fisheries Organisations (RFOs) are still based on a species by species analytical stock assessment using population dynamics models, statistically fitted to fishing data. Ecosystem-based approach implies the integration of spatio-temporal and multi-population dynamics of at least, exploited and protected species. It requires also the consideration of interactions between populations and their physical and biological environment. These end-to-end ecosystem models should finally include a representation of the spatially-distributed effect of fisheries on the modeled population(s) to investigate impacts due to both fishing and environmental changes.

One advantage of this approach compared to the standard one currently used for stock assessment is that environmentally-constrained, spatially-explicit models allow investigation of the mechanisms that lead to observed fluctuations through the detailed spatio-temporal prediction of all age-classes. In addition, once the model parameterization is achieved for a given species, the model can be used to produce hindcast and forecast simulations to explore long-term scale variability or impacts of global warming. Taking advantage of the large fishing datasets for these

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exploited species, the parameterization can be largely facilitated using data assimilation methodologies.

Briefly, models including movement and behavior of animals can be described either from a Lagrangian or Eulerian approach. While Lagrangian models focus on individual movements, the Eulerian approach considers the flux in time of density or number of individuals on a point in space. Individual-Based Models (IBMs) are typical examples of Lagrangian approach (see e.g., the model Nemuro.Fish in Megrey et al. (2007)). They can describe movement, physiology and behavior of individuals from deterministic and very detailed mechanisms, but at a high computational cost making it difficult to consider multi-species and multi-fisheries applications at Ocean basin-scale. The Eulerian approach includes the class of models based on diffusion and advection–diffusion-reaction (ADR) equations (e.g., Sibert et al., 1999). They rely on less detailed behavioral or energetic assumptions and less parameters than IBMs and appear more suited to describe population dynamics at large spatial and temporal scales. In these models the equations are numerically solved using a network of regularly spaced grid points and a discrete time step (for instance, 1° square × month). Using continuous functions, these models are also ideal for implementing parameter optimization techniques (Sibert et al., 1999; Senina et al., 2008).

The spatial ecosystem and population dynamics model (SEAPODYM) is an implementation of an ADR formulation that focuses on tuna spatial population dynamics. Since its early development in 1995, SEAPODYM has been continuously enhanced to provide a general framework allowing integration of the biological and ecological knowledge of tuna species, and potentially other oceanic top-predator species, within a comprehensive description of the pelagic ecosystem (Bertignac et al., 1998; Lehodey et al., 1998; Lehodey, 2001; Lehodey et al., 2003). It includes a forage (prey) sub-model describing the transfer of energy of stored biomass through functional groups of mid-trophic levels and an age-structured population sub-model of tuna predator species and their multi-fisheries. The dynamics of forage and predators are driven by environmental forcing (temperature, currents, oxygen, and primary production) that can be predicted from coupled physical–biogeochemical models.

Pursuing this development, we present here an update of the modeling approach including substantial improvements in the representation of the mid-trophic level functional groups (Lehodey, 2004) and more realistic definitions of habitats, movements, and mortality functions. Flexibility of the updated model will be illustrated with an application to two tuna species in the Pacific Ocean, skipjack and bigeye which have very different biological characteristics.

Skipjack (*Katsuwonus pelamis*) is a fast growing species, with a short lifespan (4–5 years for most of the individuals; Langley et al., 2005). They mature at an early age (9–10 months), and have relatively high natural mortality rates (Langley et al., 2005). Bigeye (*Thunnus obesus*) has longer lifespan (>10 years), older age at maturity (after 2 years), and lower natural mortality rates than skipjack (Hampton et al., 1998). They have both high fecundity and exhibit year-round spawning, though seasonal peaks are observed for bigeye. Juveniles of bigeye (*Thunnus obesus*) are frequently found together with skipjack in the surface layer, especially around drifting logs that aggregate many epipelagic species. As they become older and larger, bigeye tuna explore deeper (>600 m) layers than skipjack; the latter are usually confined to the upper mixed-layer, though occasionally able to dive below 200 m. Tuna can thermoregulate using a specialized counterflow heat exchange system (the *rete mirabile*). This system is particularly well-developed in bigeye tuna, allowing the species to have extended temperature range and hence a larger latitudinal and vertical habitat temperature. Adult bigeye tuna are thus exploited by the sub-surface longline fishery throughout the tropical and sub-tropical oceans. As other tuna species, skipjack and bigeye have highly opportunistic feeding behavior resulting in a very large spectrum of micronektonic prey species from a few millimeters (e.g., euphausids and amphipods) to several centimeters (shrimps, squids and fish, including their own juveniles) in size. Their diets reflect their ability to capture prey at different depths and periods of the day (i.e., daytime, nighttime, and twilight hours). Thus differences in vertical behavior can be identified through detailed stomach contents analyses; e.g., adult bigeye tuna accessing deeper micronekton species (Brill et al., 2005).

While the present paper focuses on the description of new developments in the model and illustration of its capacity to capture important features of spatial dynamics of different tuna species in the Pacific Ocean, the actual validation is presented in a companion paper describing the approach to have a rigorous mathematical parameter optimization (Senina et al., 2008).

2. Modeling approach

The model domain covers the Pacific Ocean at a spatial resolution of 1° and a one-month time resolution for the period 1948–2005. Forcing fields of these simulations (temperature, currents, dissolved oxygen concentration, primary production) are provided by a coupled biogeochemical–physical ocean model that reproduces ecosystem dynamics and biogeochemical fields at seasonal to interannual time scales ((Murtugudde et al., 1996; Christian et al., 2002; Wang et al., 2005). Temperature, current, and oxygen variables are averaged in three vertical layers: epipelagic (0–100 m), mesopelagic (100–400 m) and bathypelagic (400–1000 m). They are also used to predict the biomass distributions of the six functional mid-trophic groups (Lehodey, 2004) that are potential prey of young and adult tuna and predator of their larvae.

The model simulates tuna age-structured populations with one length and one weight coefficient by cohort obtained from independent studies (see previous references and Appendix). At each time step, survival relationships describe ageing processes for the cohorts while advection–diffusion-reaction equations describe migrations, recruitment and mortality. Different life stages are considered: larvae, juveniles and (immature and mature) adults. The age structure is defined with one monthly age class for larvae, two monthly age-classes for juveniles, and then quarterly age-classes for immature (from second quarter of age to age at first maturity) and mature adults (after age at first maturity). The last age class is a "plus class" where all oldest individuals are accumulated. All temporal dynamics are computed at the time step of the simulation, i.e., one-month in the present case. Note that for simplicity, we will omit the notations of species, space and time in the following model description.

2.1. Fish thermal habitat (Φ_a)

In Holland and Brill's heat budget model of tuna (Holland et al., 1992; Brill, 1994), the difference between body temperature and ambient water temperature is shown to be linked to the whole-body heat-transfer coefficient, the rate of temperature change due to internal heat production, the ambient water temperature and the body temperature (T_b). Maury (2005) provided a more general equation of the size-dependent tuna body temperature dynamics, showing that at steady state, body temperature increases linearly with size. Similarly, it can be shown that the thermal inertia (the gradual change of the heat flux under a rapid change of the temperature gradient), is inversely proportional to the fish weight.

At the scale of a population, we consider that the thermal habitat of a given cohort (defined by an average size) can be repre-