Ecological Modelling 245 (2012) 41–54

Contents lists available at SciVerse ScienceDirect

Ecological Modelling

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

Modelling the skipjack tuna dynamics in the Indian Ocean with APECOSM-E: Part 1. Model formulation

Sibylle Dueri[a,*], Blaise Faugeras[b], Olivier Maury[a]

[a] Institut de Recherche pour le Développement (IRD), UMR EME 212 (IRD/Ifremer/Université Montpellier 2), Centre de Recherche Halieutique Méditerranéenne et Tropicale, Avenue Jean Monnet BP 171, 34203 Sète Cedex, France

[b] CNRS, Laboratoire J.A. Dieudonné (UMR 7351), Université de Nice Sophia-Antipolis, Faculté des Sciences, Parc Valrose, 06108 Nice Cedex 02, France

ARTICLE INFO

Article history:
Available online 21 March 2012

Keywords:
Tropical tuna
Pelagic fishery
Dynamic Energy Budget
Marine ecosystem model

ABSTRACT

APECOSM-E (Apex-Predator-Ecosystem-Model-Estimation) is a deterministic model that represents the 3D distribution and population dynamics of tropical tuna under the joint effect of environmental conditions and exploitation by fisheries. It is a simplified version of the top predator component of the APECOSM framework, based on a single partial differential equation. The model is structured in 3D space and fish size and considers size dependent reproduction, growth, predation, natural mortality and fishing mortality. Processes are time, space and size-dependent and linked to the environment through mechanistic bioenergetic or behavioral parameterizations. Physiological rates such as growth, reproduction and ageing mortality are derived from the Dynamic Energy Budget (DEB) theory, while horizontal movements and vertical distribution obey a mechanistically derived advection–diffusion formulation driven by habitat gradients and oceanic currents. The effect of fishing is accounted for through the use of fleet-specific size and depth selectivity functions and time-dependent catchability coefficients which relate observed fishing effort to catches and size-frequencies.

In this paper we present the mathematical formulations of the physiological and behavioral components of the model, and an application to the skipjack tuna population in the Indian Ocean. The model is run with a daily time step on a $1^\circ \times 1^\circ$ horizontal grid and considers 20 vertical layers, reaching a maximal depth of 500 m. Results show the effects of spatial and temporal variability of environmental conditions on tuna physiology in terms of growth, reproduction and survival. Moreover, our results suggest that observed trends in reported catches are connected to environmental conditions by means of recruitment dynamics. In addition, the model allows representing the horizontal and vertical distribution of skipjack tuna and assessing the effect of accessibility of the resource to fisheries. The ability of the model to represent the distribution of biomass in accordance with the pattern given by the observed fishing activity was evaluated by comparing the spatial distribution of the simulated biomass with the observed distribution of commercial purse seiners and bait boats catches in the Indian Ocean.

The likelihood based method used for estimating the model parameters as well as an analysis of its sensitivity to their values is provided in a companion paper (Dueri et al., 2012).

1. Introduction

Skipjack tuna (*Katsuwonus pelamis)* is a widely distributed, pelagic fish commonly found in tropical waters and commercially harvested by industrial and artisanal surface fisheries using purse seine, gillnet and bait boat. In the Indian Ocean skipjack represents almost half of the tropical tuna catches. The exploitation has increased rapidly after the introduction of industrial purse seining in the early 1980s and the concurrent raise of bait boat and gillnet catches. In 2006 the annual catch of skipjack in the Indian Ocean peaked at 620,000 t and since then, catches have not exceeded 450,000 t (Indian Ocean Tuna Commission, 2010). A possible explanation for this trend can be found in the recent development of the Somalian piracy, which induced a decline of the nominal effort along the usually well exploited Somalian coast (UNOSAT, 2009). Nevertheless, the simultaneous decrease of catches reported by the Maldivian fishery (Adam, 2010), one of the leading skipjack tuna fisheries in the Indian Ocean which is not subjected to pirates' attacks, may indicate that the population is overfished.

Skipjack tuna is considered to be a highly migratory species, which does not show clear spawning or feeding migration patterns (Stéquert and Ramcharrun, 1996) but rather exhibits home range movements within areas of good habitat. The spatial

DOI of original article: 10.1016/j.ecolmodel.2012.02.008.
* *Corresponding author.* Tel.: +33 0 499 57 32 53; fax: +33 0 499 57 32 95.
E-mail address: sibylle.dueri@ird.fr (S. Dueri).

0304-3800/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecolmodel.2012.02.007

distribution, movements and vulnerability to fishing of skipjack are affected by their habitat preferences, which are mostly determined by prey availability, temperature and oxygen conditions (Barkley et al., 1978; Brill, 1994; Brill and Lutcavage, 2001). As a consequence, the spatial distribution of fishing effort directed to skipjack exhibits seasonal and inter-annual patterns that can be related to environmental conditions (Mugo et al., 2010).

The current knowledge of the skipjack physiology states that the species is characterized by a fast growth and a high spawning potential, implying that the population is likely to have a high resilience to exploitation. However, the recently observed trend of the Indian Ocean skipjack catches questions the resilience of the population under present conditions and emphasizes the need for tools capable to evaluate the state of the population and its future evolution (Indian Ocean Tuna Commission, 2010). For this purpose, we propose the APECOSM-E model (Apex Predator Ecosystem Model-Estimation) a deterministic model that represents the spatio-temporal variability of the population under variable environmental and fishing conditions. Our approach integrates the main biological, behavioral and exploitation processes in a single mathematical framework, based on a partial differential equation that explicitly represents 3D movements, growth and mortality and their dependency on environmental conditions. By integrating these processes the model allows to assess the population dynamics and the sustainability of its exploitation.

The APECOSM-E model is a simplified version of the more general APECOSM framework (Maury, 2010), which represents the global flow of energy through the marine ecosystem considering different communities of epipelagic and mesopelagic organisms. APECOSM-E is derived from APECOSM, but is focused on a single species and its main objective is to integrate fisheries data for parameter estimation. It describes the physiology and behavior of individuals in a population with a very high level of detail and represents the state of the art of our knowledge about the physiology and behavior of skipjack tuna. In this paper we present an application of the model to the skipjack tuna population of the Indian Ocean and we use environmental variables to define the habitat and constrain the physiological rates of the species and their spatio-temporal variability. The main goal of the present application is to investigate the joint effects of environmental variability and fishing on the spatio-temporal dynamics of skipjack tunas in the Indian Ocean and improve our understanding of environmental effects on the physiology and behavior of this top-predator.

A likelihood method used for estimating the model parameters related to fisheries as well as an analysis of its sensitivity to their value is provided in a companion paper (Dueri et al., 2012).

2. The model

The dynamics of the skipjack tuna population described in the APECOSM-E model is driven by the environment and by fisheries exploitation. Environmental factors such as temperature, oxygen, food and currents determine the movements of tunas and affect their physiological rates (growth, reproduction and mortality). On the other hand, spatialized fishing effort data determine the fishing mortality and are used to simulate monthly catches and size frequencies. A schematic overview of the model components in terms of forcing, processes and outputs is provided (Fig. 1). Parameters descriptions are summarized in Table 1.

2.1. Implementation of the Dynamic Energy Budget approach

In the APECOSM-E model, the main physiological processes such as growth, reproduction and ageing mortality, are represented using a Dynamic Energy Budget (DEB) based approach. The DEB theory (Kooijman, 2000) relies on a mechanistic bioenergetic representation of the organism that describes the individual in terms of biomass and energy fluxes. In the standard DEB model the energy of an organism is stored in three pools: reserve, structure and maturity. Energy is introduced into the organism through the ingestion of food which is assimilated and stocked in the reserves compartment. A fixed fraction κ of the energy utilized from the reserve compartment is allocated to growth of structure and somatic maintenance while the remaining part $(1-\kappa)$ is allocated to maturity development and reproduction and maturity maintenance. Total biomass can be expressed as the sum of structural biomass, reserves biomass and biomass of the reproductive buffer.

The APECOSM-E model adds two assumptions to the DEB theory that allow considerable simplifications:

(1) the dynamics of the reserve pool is fast compared to the dynamics of structure (see Maury and Poggiale, submitted, for the mathematical details about this assumption). This implies that, at the time scale relevant for population dynamics, the reserve density $[E]$ is at or near equilibrium and equals the scaled functional response to food f_F times the maximum energy density in the reserve $[E_m]$; $[E]^* = f_F[E_m]$.
(2) reproduction is supposed to be continuous without stocking of energy in the reproductive buffer so that the influence of the reproductive buffer on total biomass and energy budget is neglected. Therefore the total weight W_{tot} of an organism can be approximated as the sum of the structural biomass and the reserves biomass:

$$W_{tot} \approx d_V V + f_F V \frac{[E_m]}{\psi} \tag{1}$$

where d_V is the density [g m^{-3}], V is the structural volume [m^3] (or the volume of structural biomass), f_F is the functional response to food [−], $[E_m]$ the maximum energy density of reserves [J m^{-3}] and ψ is the energy content of reserves [J kg^{-1}]. In the model, according to the DEB theory, the representation of growth, reproduction and ageing mortality is based on the structural volume, while the calculation of catches is based on total weight (Eq. (1)).

Following the standard DEB model assumption, we consider that skipjack is an isomorphic organism and keeps the same shape while growing. This allows to link structural volume to length using a shape coefficient. Structural volume is calculated as the cube of the volumetric length L, $V = L^3$, and L is related to the physical length L_w through the shape coefficient δ_M, $L = \delta_M L_w$. Therefore the structural volume can be written as

$$V = (\delta_M L_w)^3 \tag{2}$$

The allometric length-weight conversion for skipjack tuna in the Indian Ocean (Indian Ocean Tuna Commission, 2005) can be calculated using following empirical relationship:

$$W_{tot} = aL_w^b \tag{3}$$

where L_w is the physical length and the coefficients a and b are equal to 5.32×10^{-6} and 3.34 respectively. By substituting V and W_{tot} in Eq. (1) we obtain the value of the shape coefficient δ_M.

2.2. General model equation and boundary conditions

The tuna population is described through a biomass density function $p(x,y,z,V,t)$ [kg m^{-3} m^{-3}], where position $(x,y,z) \in \Omega$, a bounded domain representing the Indian Ocean in 3D, structural volume $V \in (V_b, V_{max})$ with V_b being the structural volume at birth and time $t \in (0,T)$.