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

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A B S T R A C T

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° × 1° 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).

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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 Somali piracy, which induced a decline of the nominal effort along the usually well exploited Somali 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

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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 Lutjacavage, 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 APECSOM-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 APECSOM-E model is a simplified version of the more general APECSOM framework (Maury, 2010), which represents the global flow of energy through the marine ecosystem considering different communities of epipelagic and mesopelagic organisms. APECSOM-E is derived from APECSOM, 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 APECSOM-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 APECSOM-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 $x$ of the energy utilized from the reserve compartment is allocated to growth of structure and somatic maintenance while the remaining part $(1 - x)$ 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 APECSOM-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 $E_r$ is at or near equilibrium and equals the scaled functional response to food $f_T$ times the maximum energy density in the reserve $[E_r^* = f_T E_m^*].$

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:

$$W_{tot} \approx d_V V + f_T V E_m^* \psi$$

where $d_V$ is the density [g m$^{-3}$], $V$ is the structural volume [m$^3$] (or the volume of structural biomass), $f_T$ is the functional response to food $[-]$, $E_m^*$ is the maximum energy density of reserves [J m$^{-3}$] and $\psi$ 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 $L_v$, $V = L_v^3$, and is related to the physical length $L_w$ through the shape coefficient $\delta_M$, $L_v = \delta_M L_w$. Therefore the structural volume can be written as

$$V = (\delta_M L_w)^3$$

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

$$W_{tot} = a L_w^b$$

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

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$^{-3}$ s$^{-1}$], 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 $t \in (0,T)$. 


The biomass of fish with structural volume comprised between $V_1$ and $V_2$ at time $t$ in the domain $\Omega' \subset \Omega$ is given by the integral

$$\int_{\Omega'} \int_{V_1}^{V_2} p(x, y, z, V, t) \, dx dy dz dV$$

The change of the population density function $p$ as a function of time follows the mass balance equation below where $\nabla$ and $\text{div}$ are the usual differential operators. For technical reasons related to time-scale assumptions (see Section 2.6 for details) we distinguish horizontal movements from vertical movements.

$$\partial_t p = \text{div}(\nabla p - \nu p) + \partial_z (d_z \partial_z p - \nu_z p) - \partial_v (gp) - (m+f)p$$

The four terms on the right side of Eq. (5) represent: (1) horizontal advection and diffusion, (2) vertical advection and diffusion, (3) growth and (4) natural and fishing mortality. Advection and diffusion are represented by the horizontal velocity $v(x,y,z,V,t)$ [m s\(^{-1}\)], the vertical velocity $v_z(x,y,z,V,t)$ [m s\(^{-1}\)], the horizontal diffusion $d(x,y,z,V,t)$ [m\(^2\) s\(^{-1}\)] and the vertical diffusion $d_z(x,y,z,V,t)$ [m\(^2\) s\(^{-1}\)]. Here we assume that there is no cross-diffusion term in $z$. Growth is represented as an advection of the biomass density in the size dimension and is characterized by the growth rate $g(x,y,z,V,t)$ [m\(^3\) s\(^{-1}\)], while natural and fishing mortality rates are described by $m(x,y,z,V,t)$ [s\(^{-1}\)] and $f(x,y,z,V,t)$ [s\(^{-1}\)] respectively.

Initial and boundary conditions need to be prescribed to integrate Eq. (5). The initial population density distribution is given by:

$$p(x, y, z, V, 0) = p^0(x, y, z, V), \quad \forall(x, y, z, V) \in \Omega \times (V_0, V_{\text{max}})$$

The boundary conditions for the input of newborns into the systems $r(x,y,z,V,t)$ [g s\(^{-1}\)] is given by:

$$gp(x, y, z, V_b, t) = r(p), \quad \forall(x, y, z, t) \in \Omega \times (0, t_{\text{max}})$$

The mass conservation within the spatial domain is guaranteed by the following Neumann boundary condition:

$$\nabla p(x, y, z, V, t) \cdot \nu(x, y, z, V, t) = 0, \quad \forall \partial \Omega, \forall(V, t) \in (V_{\text{min}}, V_{\text{max}}) \times (0, t_{\text{max}})$$

where $\nu(x,y,z)$ is the unit normal vector pointing outside $\Omega$.

The parameterization of the coefficients $v, \nu_z, d_z, g, m, f$ and $r$ and their biological and ecological basis are provided in the section below.

### 2.3. Distribution of forage and selectivity

APECOSM-E considers size-structured forage distribution. This allows accounting for the size selection of preys by predators (in this case skipjack tuna). Size-structured forage concentration $\varepsilon(V)$ is extrapolated from the mesozooplankton distribution of the NEMO-PISCES simulations. The concentration of mesozooplankton biomass [kg m\(^{-3}\)] is set as the first size-class ($V_0$) of the prey distribution $\varepsilon(V_0)$; then for size classes between $[V_0, V_{\text{max}}]$ $\varepsilon(V)$ is calculated assuming that the decrease of forage biomass follows a power law with a scaling exponent equal to $-3$ with respect to length, in accordance with size-distributions obtained in the general APECOSM model (Maury et al., 2007):

$$\varepsilon(V) = a \cdot L^{-3} = a \left( \frac{V^{1/3}}{D_M} \right)^{-3}$$
Table 1
Parameter description and parameter used values in the APECSOM-E model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\kappa$</td>
<td>Fraction allocated to soma</td>
<td>0.8</td>
<td>–</td>
</tr>
<tr>
<td>$\delta_{\text{M}}$</td>
<td>Shape coefficient</td>
<td>0.25</td>
<td>–</td>
</tr>
<tr>
<td>$L_{\text{max}}$</td>
<td>Maximal length</td>
<td>1.1</td>
<td>m</td>
</tr>
<tr>
<td>$\rho_{\text{M}}$</td>
<td>Surface-area-specific assimilation rate</td>
<td>$22.5 \times 10^6 \times L_{\text{max}} \times \delta_{\text{M}}$</td>
<td>J m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$E_{\text{M}}$</td>
<td>Maximum energy density of reserves</td>
<td>$850 \times 10^6 \times L_{\text{max}} \times \delta_{\text{M}}$</td>
<td>J m$^{-3}$</td>
</tr>
<tr>
<td>$E_{\text{PC}}$</td>
<td>Volume-specific energetic growth cost</td>
<td>2800 $10^6$</td>
<td>J m$^{-3}$</td>
</tr>
<tr>
<td>$E_{\text{PM}}$</td>
<td>Volume-specific maintenance cost</td>
<td>$18 \times 10^6$</td>
<td>J m$^{-3}$ d$^{-1}$</td>
</tr>
<tr>
<td>$\psi$</td>
<td>Energy content of reserves</td>
<td>$38.8 \times 10^6$</td>
<td>J kg$^{-1}$</td>
</tr>
<tr>
<td>$\psi_{\text{str}}$</td>
<td>Energy content of structures</td>
<td>$3.86 \times 10^6$</td>
<td>J kg$^{-1}$</td>
</tr>
<tr>
<td>$l_{\text{mat}}$</td>
<td>Length at maturity</td>
<td>0.4</td>
<td>m</td>
</tr>
<tr>
<td>$k_{\text{K}}$</td>
<td>Fraction of reproduction energy fixed in eggs</td>
<td>0.95</td>
<td>–</td>
</tr>
<tr>
<td>$\phi$</td>
<td>Sex ratio</td>
<td>0.5</td>
<td>–</td>
</tr>
<tr>
<td>$h_{\alpha}$</td>
<td>Ageing acceleration</td>
<td>$5 \times 10^{-4}$</td>
<td>d$^{-2}$</td>
</tr>
<tr>
<td>$m_{\text{ps1}}$</td>
<td>Predation mortality coefficient 1</td>
<td>$9.7 \times 10^{-4}$</td>
<td>d$^{-1}$</td>
</tr>
<tr>
<td>$m_{\text{ps2}}$</td>
<td>Predation mortality coefficient 2</td>
<td>0.95</td>
<td>d$^{-1}$</td>
</tr>
<tr>
<td>$m_{\text{ps1}}$</td>
<td>Temperature mortality coefficient</td>
<td>−1.</td>
<td>d$^{-1}$</td>
</tr>
<tr>
<td>$T_{\text{ps}}$</td>
<td>Metabolic energy production/thermal capacity</td>
<td>0.2</td>
<td>°C s$^{-1}$</td>
</tr>
<tr>
<td>$k_{\text{f}}$</td>
<td>Thermic conductance/thermal capacity</td>
<td>0.12</td>
<td>m s$^{-1}$</td>
</tr>
<tr>
<td>$T_{\text{ps}}$</td>
<td>Arhenius temperature</td>
<td>5000</td>
<td>K</td>
</tr>
<tr>
<td>$T_{\text{f}}$</td>
<td>Lower boundary of tolerance range</td>
<td>299.15</td>
<td>K</td>
</tr>
<tr>
<td>$T_{\text{p}}$</td>
<td>Upper boundary of tolerance range</td>
<td>304.65</td>
<td>K</td>
</tr>
<tr>
<td>$T_{\text{ps}}$</td>
<td>Lower boundary Arhenius temperature</td>
<td>146000</td>
<td>K</td>
</tr>
<tr>
<td>$T_{\text{ps}}$</td>
<td>Upper boundary Arhenius temperature</td>
<td>380000</td>
<td>K</td>
</tr>
<tr>
<td>$T_{\text{f}}$</td>
<td>Reference temperature</td>
<td>298.65</td>
<td>K</td>
</tr>
<tr>
<td>$p_{\text{r}}$</td>
<td>Weighting factor temperature</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td>$k_{\text{c}}$</td>
<td>Half saturation constant for forage</td>
<td>$4 \times 10^{11}$</td>
<td>kg m$^{-3}$</td>
</tr>
<tr>
<td>$p_{\text{w}}$</td>
<td>Weighting factor forage</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td>$a_{\text{int}}$</td>
<td>Steepness of oxygen limitation curve</td>
<td>10$^3$</td>
<td>–</td>
</tr>
<tr>
<td>$a_{\text{int}}$</td>
<td>Half saturation constant for oxygen</td>
<td>0.00014</td>
<td>mol L$^{-1}$</td>
</tr>
<tr>
<td>$a_{\text{int}}$</td>
<td>Weighting factor oxygen</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td>$a_{\text{eff}}$</td>
<td>Maximal attraction factor for Maldives</td>
<td>0.35</td>
<td>–</td>
</tr>
<tr>
<td>$r_{\text{ps}}$</td>
<td>Maximal horizontal speed</td>
<td>1</td>
<td>m s$^{-1}$</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Concentration factor coefficient</td>
<td>1000</td>
<td>–</td>
</tr>
<tr>
<td>$b$</td>
<td>Maximal vertical speed</td>
<td>1</td>
<td>m s$^{-1}$</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Behavioral diffusivity, vertical</td>
<td>0.15</td>
<td>m$^2$ s$^{-1}$</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Physical diffusivity, vertical</td>
<td>$10^{-3}$</td>
<td>m$^2$ s$^{-1}$</td>
</tr>
<tr>
<td>$p_{\text{ps1}}$</td>
<td>Catchability PS1</td>
<td>0.015</td>
<td>–</td>
</tr>
<tr>
<td>$p_{\text{ps2}}$</td>
<td>Catchability PS2</td>
<td>0.015</td>
<td>–</td>
</tr>
<tr>
<td>$p_{\text{ps3}}$</td>
<td>Catchability PS3</td>
<td>0.025</td>
<td>–</td>
</tr>
<tr>
<td>$p_{\text{ps}}$</td>
<td>Catchability BB</td>
<td>0.005</td>
<td>–</td>
</tr>
<tr>
<td>$a_{\text{int}}$</td>
<td>Increased efficiency due to technological development, PS1</td>
<td>0.200</td>
<td>–</td>
</tr>
<tr>
<td>$a_{\text{int}}$</td>
<td>Increased efficiency due to technological development, PS2</td>
<td>0.020</td>
<td>–</td>
</tr>
<tr>
<td>$a_{\text{int}}$</td>
<td>Increased efficiency due to technological development, PS3</td>
<td>0.200</td>
<td>–</td>
</tr>
<tr>
<td>$a_{\text{int}}$</td>
<td>Increased efficiency due to technological development, BB</td>
<td>0.100</td>
<td>–</td>
</tr>
<tr>
<td>$l_{\text{ps1}}$</td>
<td>Length selectivity, PS1</td>
<td>0.5</td>
<td>m</td>
</tr>
<tr>
<td>$l_{\text{ps2}}$</td>
<td>Length selectivity, PS2</td>
<td>0.5</td>
<td>m</td>
</tr>
<tr>
<td>$l_{\text{ps3}}$</td>
<td>Length selectivity, PS3</td>
<td>0.5</td>
<td>m</td>
</tr>
<tr>
<td>$l_{\text{ps}}$</td>
<td>Length selectivity, BB</td>
<td>0.45</td>
<td>m</td>
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<tr>
<td>$k_{\text{ps}}$</td>
<td>Steepness length selectivity, PS</td>
<td>45</td>
<td>–</td>
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<td>$k_{\text{ps}}$</td>
<td>Steepness length selectivity, BB</td>
<td>45</td>
<td>–</td>
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<tr>
<td>$x_{\text{ps}}$</td>
<td>Depth selectivity, PS</td>
<td>100</td>
<td>m</td>
</tr>
<tr>
<td>$x_{\text{ps}}$</td>
<td>Depth selectivity, BB</td>
<td>20</td>
<td>m</td>
</tr>
<tr>
<td>$k_{\text{ps}}$</td>
<td>Steepness depth selectivity, PS</td>
<td>0.3</td>
<td>–</td>
</tr>
<tr>
<td>$k_{\text{ps}}$</td>
<td>Steepness depth selectivity, BB</td>
<td>0.3</td>
<td>–</td>
</tr>
</tbody>
</table>

where $a = e^{(V_0)/L_0 - 3}$.

The function $F(x,y,z,v,t)$ describes the biomass of forage “ingestible” by predators of size $v$. It is calculated by integrating the biomass of prey of size $u$, $e(x,y,z,u,t)$ multiplied by the size-dependent selectivity function $s(v,u)$ (Fig. 2) of a predator of size $v$ on a prey of size $u$, over the size classes of the prey.

$$F(x, y, z, v, t) = \int_{V_{\text{min}}}^{V_{\text{max}}} s(v,u) e(x, y, z, u, t) du$$

(10)

The selectivity function is calculated as the product of two sigmoid functions. It considers that predation occurs if the ratio of predator length over prey length is neither too small (prey too large to be ingested) nor too large (prey too small to be located and kept in the mouth). A detailed description of the selectivity function $s$ is provided in Maury et al. (2007).

2.4. Growth, reproduction and mortality

In the DEB approach, physiological rates depend upon food availability and temperature (Kooijman, 2000) and the following sections describe the relation used in the model for this purpose.

2.4.1. Functional response for temperature

Physiological rates depend on body temperature and tuna are endothermic organisms, able to retain heat and maintain body temperature above that of ambient temperature (Block and Stevens, 2001). The APECSOM-E model uses a mechanistic size-dependent description of the body temperature as a function of external temperature (Maury, 2005).

$$T_b(x, y, z, v, t) = \frac{V^{1/3}}{\delta_{MS}} T_0 + T_b(x, y, z, t)$$

(11)
where \( k_T \) represents thermic conductance over thermal capacity and \( T_0 \) is metabolic energy production over thermal capacity. The values of \( k_T \) and \( T_0 \) for skipjack were estimated using data reported in Brill et al. (1994). This equation implies that, at a given external temperature, the steady state body temperature of a fish increases linearly with its length. As a result, to reach the same body temperature, a large fish will have to stay in cooler water than a small one.

The effects of body temperature on physiological rates can be represented as a product of several Arrhenius functions (Kooijman, 2000):

\[
\dot{f}_r(T_b) = a_r(T_b) \dot{r}(T_b)
\]

where \( a_r \) describes the changes of any physiological rate with temperature:

\[
a_r(T_b) = \exp \left( \frac{T_a - T_b}{T_1} \right)
\]

and \( \dot{r} \) describes the reduction of any physiological rates at low temperature due to congelation of phospholipidic cell membranes and subsequent inhibition of cellular metabolism and at high temperatures due to the loss of quaternary structure of protein catalytic enzymes and the subsequent inactivation of metabolic reactions:

\[
r(T_b) = \left( 1 + \exp \left( \frac{T_a - T_b}{T_1} \right) \right) + \exp \left( \frac{T_a - T_b}{T_1} \right)^{-1}
\]

The final physiological response to temperature is normalized and reads

\[
f(T_b) = \frac{\dot{f}_r(T_b)}{\dot{f}_{r,\text{max}}}
\]

The value of the Arrhenius temperature \( T_a \) was set in agreement with previous studies (Maury et al., 2007; Van der Veen et al., 2003) while the reference temperature \( T_1 \), the temperature at the lower and upper boundaries \( T_a \) and \( T_1 \) and the Arrhenius temperature for the rate of decrease at the upper and lower boundaries \( T_{\text{ub}} \) and \( T_{\text{al}} \) were determined according to reported habitat preferences of tropical tuna in the Indian Ocean, which are constrained between 20 and 32 °C (Stéquert and Marsac, 1989).

\[\text{Fig. 2.} \ \text{Size selectivity function of predators on preys.}\]

\[\text{Fig. 3.} \ \text{Size and depth selectivity of purse seine and bait boat.}\]

2.4.2. Functional response to food density

Physiological rates of tunas are affected by food intake, which in turn depends on the food availability. According to the DEB theory, APECOSM-E expresses this dependence with a Holling type 2 function:

\[
f_r = \frac{F}{k_F + \dot{F}}
\]

where \( k_F \) is the half saturation constant and \( \dot{F} \) is the biomass of accessible preys. The variable \( F \) accounts for the effect of density-dependence, so that when preys have to be shared between many predators, they become less accessible per capita. Since the rigorous computation of the abundance of predators sharing common preys (Maury et al., 2007) is computationally extremely demanding, we had to introduce an approximation. The biomass of accessible preys is therefore obtained by dividing the “ingestible” forage (Eq. (10)) at a given spatial location by the number of skipjack in the first size class \( V_1 \) at the same place.

\[
\dot{F}(v) = \int_{V_{\text{min}}}^{V_{\text{max}}} s(u, v) \frac{\kappa(u)}{\int_{V_1}^{V} (p(V)/dV)} \, dV
\]

2.4.3. Growth

Assuming that the reserve compartment is at equilibrium (cf. Section 2.1) and that heating costs are negligible in the energy budget, we can express the growth rate as follows (Kooijman, 2000)

\[
g = \frac{dV}{dt} = f_r \left[ \frac{k_F [p_{\text{Am}}]^V (2/3) - [p_M] V^+}{k_F [E_m] + [E_C]} \right] ^+
\]

where \([p_{\text{Am}}]\) is the surface-area specific assimilation rate \([\text{J} \text{m}^{-2} \text{s}^{-1}]\), \([p_M]\) is the volume-specific maintenance cost \([\text{J} \text{m}^{-3} \text{s}^{-1}]\) and \([E_C]\) is the volume-specific energetic growth cost \([\text{J} \text{m}^{-3}]\) and \([V^+]\) is the function defined by

\[
\begin{aligned}
[x]^+ &= \begin{cases} x & \text{if } x < 0 \\ x & \text{if } x \geq 0 \end{cases} \\
\end{aligned}
\]

The numerical values of \([p_{\text{Am}}]\), \([p_M]\) and \([E_C]\) were derived from Kooijman (2010) and their values are given in Table 1.
Following Kooijman (2000), under constant food availability conditions, the DEB growth equation is equivalent to the von Bertalanffy equation \( L(t) = L_\infty - L_\infty e^{-rt} \), where \( L_\infty \) is the maximal length and \( r_B \) is the von Bertalanffy growth rate. As a consequence, \( r_B \) can be expressed as a function of DEB parameters:

\[
  r_B = \frac{1}{2} \frac{[p_m]}{k_f [E_m] + [E_C]} \tag{19}
\]

The von Bertalanffy growth rate estimated for skipjack tuna in the Indian Ocean \( (r_B = 0.288, \text{Indian Ocean Tuna Commission, 2008}) \) is therefore used to calculate the maximum energy density of reserves \([E_m]\), under the assumption that food and temperature conditions are constant and close to optimum \((f_T = 0.8 \text{ and } f_r = 0.85)\).

### 2.4.4. New born input

According to the standard DEB scheme, \((1 - \kappa)\) of the energy mobilized from the reserve pool is allocated to reproduction and maturity maintenance. Reproduction rate is expressed using the same energetic parameters as growth plus two additional parameters: the mean proportion of females in the mature population \( \phi \) and the fraction of the energy in the gonads which is turned into eggs \( k_E \). In our study \( \phi \) is set at 0.5, which matches empirical observations regarding skipjack population of the Indian Ocean (Grande et al., 2010), while \( k_E \) is set at 0.95 (Kooijman, 2000). In accordance with the DEB theory the total reproductive flux of the population \( r(p) \) \( [\text{g s}^{-1}] \) is calculated as:

\[
r(p) = f_T \int_{V_{\text{str}}}^{V_{\text{max}}} \left( p \left[ \frac{f_T}{[E_m]} + k_f [E_m] \right] [E_C] \dot{v}(V) \right)^{-1/3} dV \tag{20}
\]

where \( \dot{v} \) is the energy conductance equal to \( [p_m]/[E_m] \) \( [\text{ms}^{-1}] \) and \( V_{\text{str}} \) is the structural volume at maturity. Grande et al. (2010) have estimated that 50% of the Indian Ocean skipjack females reach maturity at a length of 37.81 cm, while the additional results of Stéquert and Ramcharrun (1996) indicate slightly higher values of 41–42 cm. We therefore choose a mean length of sexual maturity at 40 cm. Moreover, we assume that reproduction occurs whenever the temperature is above 24 °C (Cayré and Farrugio, 1986).

The reproductive flux of the spawning population is used to calculate the size dependent population fecundity \( [\text{g oocytes per kg of female per day}] \):

\[
  F_{\text{ec}}(V) = \frac{r(p(V))}{\dot{v}(V)} \tag{21}
\]

where \( r(p(V)) \) is the size dependent reproductive flux \([\text{g s}^{-1} \text{m}^{-3}]\) and the batch fecundity \( ([\text{oocytes per kg of female per spawning event}] )

\[
  BF = \frac{F_{\text{ec}}(V) \times f_f}{w_{\text{oocyte}}} \tag{22}
\]

where \( f_f \) is the spawning frequency and \( w_{\text{oocyte}} \) is the weight of an egg. A mean weight of 0.6 mg/oocytes is calculated by combing the mean dry weight, 0.042 mg/oocytes (Margulies et al., 2007) and the mean water content of tuna eggs, 93% (Ortega and Mourente, 2010).

### 2.4.5. Mortality

#### 2.4.5.1. Natural mortality

The total natural mortality is represented as the sum of ageing, predation, starvation and temperature mortalities, i.e. \( m = m_{\text{aging}} + m_{\text{pred}} + m_{\text{starv}} + m_{\text{temp}} \).

The DEB theory relates ageing mortality to the amount of cellular damages that increase at a rate proportional to the respiration rate not associated to assimilation (Kooijman, 2000). As a consequence, a low metabolic rate corresponds to a longer life span. For the sake of simplicity we use the formula proposed by Maury and Poggiale (submitted) who calculate the mean size dependent ageing mortality rate by replacing the food functional response by its mean value \( \bar{f}_T \). This leads to an explicit size-dependent expression of the ageing mortality based on DEB parameters only:

\[
  m_{\text{aging}} = \frac{h_a}{V_t} \left\{ \frac{a_1}{V_t} - \frac{1}{c} \left( \frac{3 a_2 d e_2 c t v + \frac{1}{3} d^3 e_3 c t v}{1} \right) \right\} \tag{23}
\]

With

\[
  \begin{align*}
    a &= \kappa [p_{Am}] f_T / [P_M] \\
    b &= V_b^{(1/3)} \\
    c &= \frac{-[p_M]}{3(\kappa f_T [E_m] + [E_C])} \\
    d &= a - b \\
    V_t &= \frac{\left( \kappa [p_{Am}] f_T - \kappa [p_{Am}] f_T [V_b^{(1/3)}] \right) / [P_M]}{\left( \kappa [p_{Am}] f_T - [p_m] [V_b^{(1/3)}] \right) / [P_M]} \\
    &\times \left( \kappa [p_{Am}] f_T - [p_m] [V_b^{(1/3)}] \right) / [P_M] \\
    &\times \ln \left( \frac{\kappa [p_{Am}] f_T - [p_m] [V_b^{(1/3)}]}{\kappa [p_{Am}] f_T - [p_m] [V_b^{(1/3)}]} \right)
  \end{align*}
\]

where \( V_t \) is the time to reach size \( V \) with a mean food density of \( \bar{f}_T \), \( V_b \) is the volume at birth and \( h_a \) \( [\text{s}^{-2}] \) is the ageing acceleration.

Size dependent predation mortality is described by a power law relation with two mortality coefficients \( m_{\text{pred}} \) and \( m_{\text{starv}} \) that define the strength and the steepness of the function. Its value is maximal for small organisms (e.g. larvae) and decreases for larger organisms:

\[
  m_{\text{pred}} = m_{\text{p1}} \left( \frac{V_b^{(1/3)}}{\delta M} \right)^{-m_{\text{p2}}} \tag{24}
\]

The DEB theory states that the assimilated energy is used first for the maintenance of the organism before being allocated to growth and reproduction. If food availability is too low, the growth and reproduction ceases, and all the available energy is allocated to maintenance. When maintenance costs are not covered, the organism health declines and this threatens its survival. Therefore a starvation process is introduced. As in Maury et al. (2007) starvation mortality \( m_{\text{starv}} \) is expressed as the energy which would be needed for maintenance but cannot be provided by the assimilation of food:

\[
  m_{\text{starv}} = \frac{1}{[f_T [E_m] + d]} \left\{ [E_C] \left[ \frac{[p_m] - \kappa [p_{Am}] f_T V^{(1/3)}}{[E_C] + k_f [E_m]} \right] \right\}^{+} \tag{25}
\]

Finally, we include a mortality term for organisms subject to temperatures too cold or too warm for their survival. This term is linked to the variable \( r_T \) of the Arrhenius relationship (see Eq. (14)) that describes the reduction of physiological rates at low and high
temperatures. The temperature mortality is computed only when physiological rates are lower than a given threshold.

\[ m_{\text{temp}} = m_{T1} \log(m_T) \quad \text{if} \ m_T = 0.1 \]  \hspace{1cm} (26)

where \( m_T = \frac{I}{I_{\text{max}}} \) and \( m_{T1} \) is a negative parameter.

### 2.4.5.2. Fishing mortality

Fishing mortality is calculated using observed \( 1 \times 1 \) monthly fishing effort for four different fleets: French purse seiners “PS1”, Spanish purse seiners “PS2”, “World” purse seiners “PS3” grouping the fishing data of Mauritius, Seychelles, and NEI-other and Maldivian bait boats “BB”. These fleets represent the main skipjack fisheries of the Indian Ocean providing a time series of fishing data with a spatial resolution of \( 1 \times 1 \).

Fishing mortality of fleet \( k \) is calculated as the product of the observed fishing effort \( e_k \) by the catchability \( p_k \) at \( T_0 \) multiplied by an exponential function representing the increase in fishing efficiency at a rate \( a_k \) due to technological development in time, and two selectivity functions, one for size and the other for depth.

\[ f_k(i, z, V, t) = e_k(i, t)p_k \exp(a_k(t) \frac{1}{1+\exp(-k_1(V^{1/3}/\delta_M) - l_i)}) \times \frac{1}{1+\exp(-k_2(z-z_i))} \]  \hspace{1cm} (27)

For the purse seiners the fishing effort is expressed as the amount of time the fishermen spend at fishing while for bait boat it is expressed as the amount of time spent at sea. Technological development is a continuous process and includes the increase of the size and performance of the fishing vessels, the enhancement of the fishing gears, the progressive use of new electronic devices such as bird radar and other remote sensing tools and the deployment of more and more sophisticated fish aggregating devices (FADS) (Valdemarsen, 2001). The gear specific length and depth selectivity are represented using sigmoid functions where \( k_1 \) and \( k_2 \) are the length and depth leading to 50% selection while \( k_1 \) and \( k_2 \) characterize the steepness of the sigmoid curves (Fig. 3).

### 2.5. Habitat and movements

Water temperature, dissolved oxygen concentration and forage availability are the main factors affecting the physiological and behavioral responses of tuna to the environment. In the model, tunas are attracted to areas where the environmental conditions are favorable to their growth, reproduction and survival. For that purpose, structural environmental factors are translated into a synthetic functional habitat variable by means of functional responses that characterize the habitat suitability. The spatial heterogeneity of the modeled functional habitat creates gradients that steer the movements of tunas.

#### 2.5.1. Habitat suitability index

The model calculates the 3D habitat suitability index \( h \) by considering 3 factors: temperature, food and oxygen conditions. For each factor a functional response varying between 0 (highly unfavorable) and 1 (highly favorable) quantifies environmental suitability with respect to that factor (Fig. 4). The habitat suitability index is then expressed as the product of weighted functional responses to temperature \( f_T \), food \( f_F \) and oxygen \( f_O \), with \( p_T, p_F, p_O \) being the respective weighting factor.

\[ h(x, y, z, V, t) = f_T(x, y, z, V, t)p_Tf_F(x, y, z, V, t)p_Ff_O(x, y, z, V, t)p_O \]  \hspace{1cm} (28)

The functional responses describing the habitat suitability in terms of temperature and food availability are consistent with the ones that represent the change in physiological rates (Eqs. (15) and (16)). The functional response for oxygen is presented in the next section.

#### 2.5.2. Functional response for oxygen

The functional response to oxygen \( f_O(x, y, z, V, t) \) is represented using a sigmoidal curve:

\[ f_O = \frac{1}{1 + \exp(\theta_0(O - O_0))} \]  \hspace{1cm} (29)

where \( \theta_0 \) is the steepness of the curve and \( O_0 \) is the half saturation coefficient for oxygen limitation. The value of the steepness and half saturation coefficient have been determined according to previous studies which estimated that skipjack tuna need oxygen concentrations above 2 ml/L to survive (Gooing et al., 1981; Sharp, 1978) and usually prefer environments with oxygen levels higher than 3.0–3.5 ml/L (Barclay et al., 1978; Brill, 1994).

#### 2.5.3. Maldivian Island attraction

The enhancement of primary production and associated aggregations of zooplankton, micronekton and fish arising in conjunction with ocean currents impinging on abrupt topographies is a known phenomenon and the mechanisms that drive this bio-physical process have been described by Genin (2004). The Maldives are a typical example of this enhanced productivity: the presence of narrow channels between the double chain of atolls and the mixing of the stratified equatorial water pumps nutrient rich subsurface water to the surface (Anderson et al., 2011). This so-called island mass effect (IME) has been observed in different channels of the Maldives Islands using chlorophyll-a field data of the Moderate Resolution Imaging Spectrometer (MODIS) (Sasamal, 2006).

Given the importance of the Maldivian fisheries in terms of tuna catches, it is essential to represent the IME in the model in order to explain the high productivity of this area; however the small-scale hydrodynamic and biogeochemical processes responsible for an increased productivity around the Maldives are missing in our model based the fact that the environmental forcing comes from an oceanographic simulation with a resolution of 0.5° (cf. 26), which is too coarse to capture the processes responsible for the enrichment. Therefore it was necessary to introduce an attraction factor \( \beta \) that increases the habitat quality around the Maldives. \( \beta \) can vary between 0 and \( a_{\text{mdv}}(y_{\text{mdv}} \leq 1) \) and is modeled using a two dimensional \((x,y)\) Gaussian function centered on the islands.

\[ \beta = a_{\text{mdv}} \cdot e^{-\frac{(x-x_{\text{mdv}})^2}{2\sigma_x^2} - \frac{(y-y_{\text{mdv}})^2}{2\sigma_y^2}} \]  \hspace{1cm} (30)

where \( x_{\text{mdv}} \) and \( y_{\text{mdv}} \) are the coordinates of the center of the attraction basin which is located at 4.5°N and 74.5°E. To account for the north-south extent of the Maldives archipelago, the standard deviation of the Gaussian attraction function was set to 4° along the latitude and 2° along the longitude axis.

The Maldivian islands attraction is not supposed to be added to the normal habitat driven movements but to replace them so that the resulting habitat function \( \hat{h} \) still varies between [0,1]:

\[ \hat{h}(x, y, z, t, V) = (1 - \beta) \cdot h(x, y, z, t, V) + \beta \]  \hspace{1cm} (31)

#### 2.5.4. Horizontal and vertical movements

Horizontal advection and diffusion have both a physical component due to passive transport by marine currents and a biological component due to active movement of fish. In APECSM-M E the biological advection depends on the habitat gradient: the velocity and direction of tuna movement are locally affected by temperature, oxygen, forage fields and the Maldivian island attraction. Advection is oriented in the direction of the habitat gradient and the balance between advection and diffusion depends on the gradient intensity. While strong gradients impose strong advection and weak diffusion, weak gradients induce weak advection and strong diffusion. Moreover, active swimming of the fish is assumed to decrease when habitat quality increases so that both advection and diffusion...
Fig. 4. Functional responses for temperature, food density and oxygen conditions.

decrease simultaneously. This implies that the better the habitat, the lower the interest in heading toward better habitats.

Accordingly, horizontal movement in APECOSM-E are expressed using the mechanistically derived advection–diffusion equation presented in Faugeras and Maury (2007) which allows to conserve the total size and habitat dependent distance traveled per time by a fish when advection and diffusion change. The horizontal advection vector is presented as the sum of biological advection due to swimming (left term) and physical advection due to marine currents (right term):

$$
\nu = v_{\text{max}} \frac{V^{(1/3)}_0}{\sigma_m} (1 - h) \frac{I_1(\alpha \|V_h\|)}{I_0(\alpha \|V_h\|)} \left( \cos \theta_{Vh} \sin \theta_{Vh} \right) + v_{\text{phy}}
$$

(32)

where \( v_{\text{max}} \) is the maximal speed that a 1 m fish can reach, \( \alpha \) is the concentration factor, \( \|V_h\| \) is the norm of the habitat gradient, \( I_1 \) is the modified Bessel function at order 0 and 1, \( \theta_{Vh} \) is the angle of the gradient and \( v_{\text{phy}} \) is the physical velocity determined by the current forcing field.

The horizontal diffusion matrix is given by a physical diffusion term \( (D_{\text{min}}) \) that is added to the behavioral term:

$$
d = D_{\text{min}} \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} + \frac{\tau}{2} \left( \begin{array}{cc} v_{\text{max}} \frac{V^{(1/3)}_0}{\sigma_m} (1 - h) & \frac{I_1(\alpha \|V_h\|)}{I_0(\alpha \|V_h\|)} \\ \frac{I_1(\alpha \|V_h\|)}{I_0(\alpha \|V_h\|)} & \frac{I_1(\alpha \|V_h\|)}{I_0(\alpha \|V_h\|)} \end{array} \right) \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}
$$

(33)

where \( \tau \) is a small mean time during which the velocity vector of an individual is constant. Vertical advection relies only on active movements such as bounce-dive foraging behavior (Schaef er et al., 2009) while passive vertical transport due to vertical marine currents is neglected. In the model the vertical advection velocity decreases with habitat quality and is proportional to the maximal vertical speed \( b \), the size of the organism and the vertical gradient of the habitat function:

$$
\nu_z = b(1 - h) \left( \frac{V}{V_{\text{max}}} \right)^{1/3} \sigma_z h
$$

(34)

The vertical diffusion \( d_z \) has two components: a behavioral and a physical one.

$$
d_z = ah \left( \frac{V}{V_{\text{max}}} \right)^{2/3} + d_z^\phi
$$

(35)

The first term describes the size-dependent diffusion emerging from random foraging vertical movements. It depends on the behavioral diffusivity coefficient \( a \) (m² s⁻¹), the size of the organisms and increases linearly with the habitat index \( h \) meaning that the tuna spend more time randomly looking for food when the habitat is good. The second term of the equation is a physical vertical diffusivity term \( d_z^\phi \) (m² s⁻¹) that accounts for purely physical vertical mixing which is especially important for small organisms.

2.6. Numerical integration and forcing

In order to speed up the calculation and reduce the memory needs, we simplify Eq. (5) using time-scale assumptions. Assuming that the vertical movements are fast processes compared to horizontal movements, mortalities and newborns input, vertical movements can be partially decoupled from the other processes and integrated analytically. This avoids a costly numerical solving of the full 3D + size system and reduced the numerical procedure to a lighter 2D + size problem. The mathematical details of this simplification are provided in the Annex.

The numerical integration of APECOSM-E uses a \( 1 \times 1 \) horizontal grid covering the Indian Ocean (20°–130° East, 40° South to 30° North). There are 20 vertical layers from 0 to 500 m, with a 10 m interval in the first 150 m. This vertical grid allows having a good resolution of the water column between 0 and 150 m, which owing to temperature and oxygen conditions corresponds to the depth usually occupied by skipjack. Organisms considered in the model range between 1 mm and 1 m length. In order to accurately and effectively account for growth and predation of organism having very different sizes, we define 83 size classes using a logarithmic scale (see Maury et al., 2007 for details). Therefore the size interval is very small for small organisms and becomes progressively larger. This allows reducing the number of size classes and ensures that all processes are considered at the proper resolution.

The non-dispersive MUSCL (monotonic upstream centered scheme for conservation laws) is used for integrating the spatial advection terms (Van Leer, 1977), while for diffusion we use a three-point finite difference scheme explicit in time. A first order upwind finite difference scheme is used to integrate the growth term of Eq. (5). All integrals are evaluated using first order centered approximations.

Simulations are run with a daily time step for the time period 1958–2001, with the industrial fishery exploitation starting in
1984. The first 10–15 years of simulation are considered to be a spin-up phase of the model. The environmental conditions that determine the tuna habitat are provided by 3D temperature, oxygen, mesozooplankton and marine current fields generated by the NEMO-PISCES model (Aumont and Bopp, 2006), a coupled physical–biogeochemical model that is run for the global ocean. NEMO-PISCES was run at a 0.5° resolution using the ERA40 reanalysis, a re-analysis of the global atmosphere and surface conditions from 1957 to 2002 performed by the European Centre for Medium-Range Weather Forecast (ECMWF). This environmental forcing is read by the APECOSM-E model every 10 simulated days.

The effect of fishing activities is introduced by means of observed effort data obtained from the Indian Ocean Tuna Commission in the standardized form available on the CLIOTOP website (http://vmmdst-proto.mpl.ird.fr/MDST/). Fishing efforts is spatially aggregated on a 1° × 1° grid and on a monthly basis for the four fleets considered. They are used to simulate catches and size frequencies.

3. Results and discussion

3.1. Spatio-temporal variability of growth and reproductive flux

Skipjack tuna are highly mobile species and during their life span they encounter a wide range of environmental conditions that affect their physiological rates. While all metabolic rates are regulated by temperature according to Eq. (12), the energy allocated to growth and reproduction depends upon the food assimilation rate, which is proportional to ingestion and which in turn is determined by the food availability. The model allows to explicitly account for this spatial variability of food and temperature conditions and to represent the range of predicted growth and reproduction rates anywhere in the Indian Ocean, from food and temperature fields.

Following Longhurst (1998), the Indian Ocean can be subdivided into seven biogeochemical provinces with homogeneous conditions for temperature and productivity (Fig. 5): Northwestern Arabian Upwelling (ARAB), Australia-Indonesia Coastal (AUSW), Eastern Africa Coastal (EAFR), Eastern India Coastal (INDE), Western

Fig. 5. Longhurst provinces in the Indian Ocean.

Fig. 6. Yearly average of Von Bertalanffy growth function (left) and daily fecundity (oocytes per kg biomass and day) (right) for the Longhurst provinces of the Indian Ocean.
India Coastal (INDW), Indian South Subtropical Gyre (ISSG), Indian Monsoon Gyres (MONS). Here, we use this subdivision to quantify the spatial variability of the mean yearly growth rates and fecundity as a function of size at the basin scale (Fig. 6).

The results point out that the provinces of the southern hemisphere (ISSG, EAFR, AUSW) are characterized by a slower growth rate and a lower fecundity, as a consequence of the lower temperature and generally lower food availability in those areas. On the contrary, the MONS and the INDW province appear to be the ones with the most suitable conditions for growth and reproduction of the population. Moreover, the comparison of the growth rates between provinces implies an important variability of the size-at-age of tunas exposed to different environmental conditions. It is important to account for this variability since environmental conditions change in time and space following seasonal cycles and tunas might be exposed to more or less favorable conditions during their migration and their physiological development might be therefore affected. By representing explicitly the spatio-temporal variations of physiological rates and their dependency on environmental conditions, the model provides a valuable tool to investigate the complex interactions between population and environment and explains the wide range of observed growth rates and the dispersion of sizes at age.

The comparison of the predicted and observed reproduction and growth rates allows us to evaluate the model’s performance. The comparison is based on the MONS province, which covers a large portion of the area exploited by industrial surface fisheries and where most of the data were collected. The mean observed batch fecundity of skipjack having a size between 40 and 60 cm ranges from 40 to 150 oocytes per g of biomass (Grande et al., 2010; Stéquert and Ramcharrun, 1996). These values are in the order of magnitude of the predicted batch fecundity (Eq. (22)), which is in the range of 10–70 oocytes per g biomass for fishes of comparable size and considering a spawning frequency of 2 days. Growth rates predicted by the model for the MONS province are also in good agreement with the IOTC growth curve (Fig. 6).

3.2. Population dynamics, environmental variability and fisheries

The monthly fishing mortality applied to the stock was calculated from the ratio catches/exploitable biomass, using values of simulated catches and defining the exploitable biomass as the biomass >30 cm. The fishing mortality was then compared to the size-dependent natural mortality due to predation and ageing (Eqs. (23) and (24)) (Fig. 7). At the beginning of industrial fisheries, computed fishing mortalities were in the range of 0.003–0.005 month$^{-1}$ and they have increased to 0.005–0.02 month$^{-1}$ between 1996 and 2001. In comparison, total natural mortality of skipjack tuna ranges...
Fig. 10. Computed vertically integrated exploitable skipjack population vs observed catches (circles) in the Indian Ocean: April 1993 (top), February 1998 (center), April 1998 (bottom).
between 0.085 and 0.125 month$^{-1}$ for the fish sizes between 30 cm and 80 cm, corresponding to the exploited sizes. The model thus suggests that fishing mortality added approximately 20% of mortality to the natural mortality in the period between 1996 and 2001. Since catches have further increased in recent years this percentage has presumably risen.

The yearly recruitment, defined as the number of surviving fish entering the fishery, was calculated as the number of fishes reaching the exploitable size of 30 cm. The computed temporal dynamics of the yearly recruitment for the Indian Ocean is marked by four periods with increased recruitment: 1988, 1993, 1996 and 1999–2000 (Fig. 8). If we compare these peaks with the mean annual temperature in the top 100 m of the water column of the 3 biogeographical provinces that cover most of the areas exploited by industrial fisheries in the Indian Ocean (MONS, ARAB, and INDW), we observe that the years with increased recruitment occur in general with a delay of one year with respect to the periods with higher temperature. The warmer periods accelerate the growth of larvae and juveniles and allow them to escape more quickly the small size domain where the predation mortality is the highest, thus improving survival and enhancing recruitment. This illustrates well how the dynamics of the population depends on the environment. In the model the recruitment is linked to the environmental factors by the bioenergetic representation of growth, reproduction and survival. Furthermore, we explore the relation between the predicted recruitment trends and the yearly total observed catches of the four fleets considered in the model. The temporal dynamics of reported catches shows three years of increased productivity that occur in 1989, 1995 and 1999, between 0 and 2 years after the recruitment peaks. The model suggests a strong link between environmental factors, recruitment and observed trends in fisheries. However, it has to be noted that other factors influence the temporal dynamics of catches such as the accessibility to the resource, which is also affected by the environment and by the technological development of fisheries.

In order to assess the impacts of exploitation on the population we compare simulations with and without the effects of fisheries. For this purpose, the model was run for the period 1958–2001 with the observed fishing effort of purse seine and bait boat fisheries starting after 1984. The starting year 1984 corresponds to the year when a simultaneous and important rise in both, industrial and artisanal fisheries begun in the Indian Ocean, leading to an increasing level of catches. The results indicate that the exploitation of the resource by industrial fisheries induced a marked decrease of both exploitable and spawning biomasses (Fig. 9). Compared to the simulation without the effect of fisheries, exploitation induces a reduction of 30% in spawning biomass and of 25% in exploitable biomass. Moreover the model indicates that the decrease of the population is not steady: periods of nearly stable biomass alternate with periods of steeper decrease. An important decrease is observed between 1991 and 1999 and is followed by a stable period. This stability is presumably induced by an increase of the recruitment during the years 1999–2000 due to environmental factors (the 1998 El Niño year, see next section), which have partially compensated the loss of biomass due to fishing mortality.

### 3.3. Spatial dynamics of the skipjack population compared to catches

The ability of the model to represent the spatial dynamics of the skipjack biomass under variable environmental conditions was also explored. Considering that the distribution of observed catches must be linked to the distribution of the resource, we compared the horizontal distribution of the accessible exploitable biomass (size > 30 cm, depth < 50 m) to the spatial distribution of observed catches (Fig. 10). In general, most of the skipjack catches are localized in the central-western part of the Indian Ocean and the main fishery areas are spread between the Somali upwelling, the Mozambique Channel and the Maldivian Islands. Comparing the vertically integrated exploitable biomass to the catches distribution shows that the model is able to represent the main features of the horizontal distribution of the biomass at different periods of the year and under different environmental condition.

An examination of the vertical distribution of the simulated biomass (Fig. 11) shows that the biomass is not always located near the surface, where it is more accessible to fishers, but that habitat conditions can attract the skipjack biomass in deeper waters, usually between 50 m and 100 m depth. This limits the ability of the surface fleets to detect and catch the resource and implies that skipjack tunas might be present in certain zones but not fished.

The conjunction of a dipole mode (IODM) and a strong El Niño–Southern Oscillation (ENSO) event in 1997–1998 lead to important environmental anomalies in the Indian Ocean which had important consequences on fishing activities (Marsac and Le Blanc, 1998;...
Ménard et al., 2007). The abnormal easterly wind stress along the equator caused the reversal of the E–W thermocline slope. The inversion of the normal thermocline E–W slope depth increased the catchability of tropical tuna for purse seine gears in the east and decreased it in the West where they are normally fished. This lead to massive and very unusual movement of the fishing fleets to the eastern area while the usual fishing grounds in the western part of the ocean were deserted by fishers. This exceptional event was well captured by the model as important changes in both the horizontal and vertical distribution of skipjack are clearly visible in the simulation in 1998 (Figs. 10 and 11). The simulations indicate that a substantial part of the biomass was still present in the western basin but since skipjack habitat was deeper than usual, the resource likely remained in deeper waters (50–100 m) thus less detectable and accessible to surface fishers. On the contrary, biomass was closer to the surface in the central and eastern parts of the basin, therefore increasing the catchability in these sectors.

4. Conclusion

The comparison of the model and the data has reinforced the model and has highlighted the importance of the joint effect of environmental factors and exploitation by fisheries for the assessment of population dynamics. The model allowed integrating the spatio-temporal variability of temperature, dissolved oxygen and food conditions and evaluating their effect on the population. It has shown how environmental factors produce differences in growth and reproduction at the basin scale and how this can affect the size-at-age of skipjack tuna. Moreover the model allowed computing the temporal dynamics of mortality and recruitment and therefore provides a means to bridge the gap between environmental variability and observed temporal dynamics of total catch. This kind of analysis is essential to increase our understanding of the ecosystem's dynamics, since it allows a better interpretation of the data.

The model was also able to represent the environmentally driven spatial variability of the skipjack tuna population in the Indian Ocean and a good overlap of the simulated spatial distribution of biomass with observed fishing data distribution was observed, even during the extreme ENSO event that occurred in 1997–1998. Results have highlighted the influence of the environmental conditions on the horizontal and vertical distribution of skipjack tuna, and their effect on the accessibility of the resource to fishers.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2012.02.007.

References


Ortega, A., Mourente, G., 2010. Comparison of the lipid profiles from wild caught eel and unfished larvae of two scombroid fish: northern bluefin tuna (Thunnus thynnus L., 1758) and Atlantic bonito (Sarda sarda Bloch, 1793). Fish Physiology and Biochemistry 36, 461–471.


