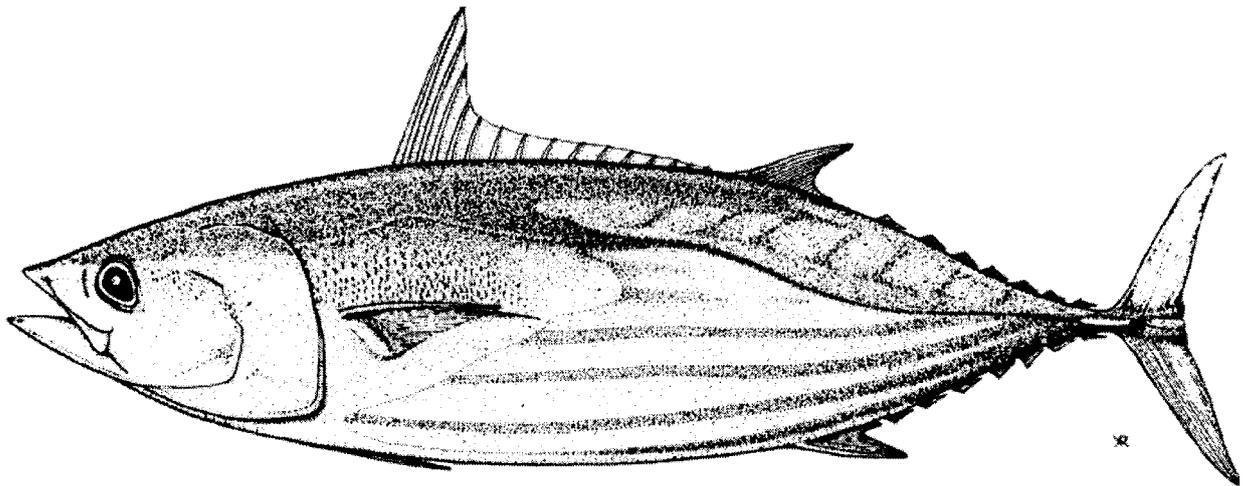SCTB13 Working Paper

RG-2

Update on the Spatial Environmental Population Dynamics Model: SEPODYM

Patrick Lehodey

Oceanic Fisheries Programme
Secretariat of the Pacific Community
Noumea, New Caledonia

Foreword: This working paper is a summary of a more detailed paper presented at the "Beyond El Niño conference", San Diego March 23-26,2000 and currently in review.

Introduction

Evidence has accumulated in the last two decades that both environmental variability and spatial heterogeneity have to be considered in fisheries management. This is particularly true for tuna fisheries since tuna are widely distributed, migratory species and are particularly sensitive to their oceanic environment. To take into account such issues, the Oceanic Fisheries Programme of the Secretariat of the Pacific Community has developed a spatial, multi-gear, multi-species population dynamics simulation model for tropical tuna in the Pacific Ocean. Since this model includes environmental and spatial effects, it was called Spatial Environmental Population Dynamics Model (SEPODYM).

In the first stage, two sub-models were developed and run separately (off-line), one for the tuna forage (Lehodey et al. 1998), and the second for tuna populations and fisheries based on them(Bertignac et al. 1998). Environmental variables are used in the models for delimiting the spawning area of tuna, reproducing the transport of larvae and juveniles, and simulating the tuna forage necessary for the definition of a habitat index. This index is used to constrain the movement of tuna. The development of a simple sub-model for simulating tuna forage was made necessary because direct observations of the forage organisms, relying on sparse samplings, are largely insufficient to reproduce their spatio-temporal distribution. The simplest modelling approach was sought and led to a model requiring a simple parameterization and providing great flexibility. A recent advance in the development of this spatial modelling has been to couple both sub-models. The coupling takes into account the effect of tuna population density on the forage density since the local mortality of forage is made proportional to the local density of tuna. Therefore, an increasing density of tuna increases the forage mortality, and if there is no additional supply of forage, decreases the habitat index value. Since the movement of tuna is based on the gradient of the index, tuna will start to leave the zone when forage will be not sufficiently abundant to support the local tuna population density.

By introducing such environmental determinism in a population dynamic model, it becomes clear that the interpretation of results is strongly dependent on the environmental variability. Therefore, the mechanisms of ENSO, the main source of environmental variability in the equatorial Pacific Ocean, and their biological consequences in the pelagic food web need to be investigated (cf. SCBT13 WP RG-1 and WP SKJ-3), all the more since ENSO-related displacements of tuna have been demonstrated from fishing and tagging data (Lehodey et al. 1997).

Overview of the modelling approach

A major feature of SEPODYM is the use of an environmental-based habitat index to constrain the movement of tuna. The habitat index, at this stage of development, combines temperature and forage density effects, both of which are supposed to be the main factors determining tuna distribution, at least at the large horizontal scale investigated for management purposes. All the spatial dynamic modelling of SEPODYM is based on a diffusion–advection equation in two horizontal dimensions. However, the advective terms applied to this equation are different according to the movements simulated. For the movement of small organisms of the forage and for the larvae and juveniles of tuna, the advective components in the two horizontal dimensions are oceanic currents, while they are gradients of habitat index for adult tuna. Therefore, we can explicitly incorporate population movement and spatial structure in the population dynamic model.

The forage model

Instead of developing a detailed explicit food web through the whole pelagic ecosystem, which is a complex and very long task, the tuna forage species are considered a single population composed of different species. Therefore, it is possible to apply the fish population dynamic mathematics to this forage population. The difference is that instead of having different age classes of a same species, there are different age classes of different species. Following the time-trophic-continuum concept of the pelagic food web, these species should disappear selectively in the order of their trophic level related to their time of development. The simplest approach is to start from the classical fish population dynamic model in the case of a fish population with a constant continuous recruitment and a constant mortality. In this case the variation in time of the forage population F can be expressed as:

$$\frac{dF}{dt} = S - (\lambda\ F)$$

(1)

where F is the forage population (biomass), S is the recruitment (or source) and λ the mortality coefficient (Z in fishery sciences). The recruitment consists of the new organisms that are entering the forage population at a given time. Since the tuna forage does not include all the organisms developing along the food chain from the primary level, the time at recruitment (T_r) can select the adequate spectrum of organisms of the forage. In other terms, the time T_r is the minimum time necessary for the development of organisms between their "birth" and "recruitment" in the forage population.

In a classical fish population model, the origin of the recruitment is the biomass of spawning adults. In the case of the forage population, we consider that the development of a new primary biomass during a period of time (primary production) allows the development of a new cohort of many different organisms, a fraction of which will be recruited after a time T_r into the forage population. The level of fraction transferred depends of an ecological transfer coefficient (concept of biomass size spectrum). In the hypothesis of a constant source (recruitment), it is not necessary to consider effects due to the existence of more than one cohort since the cohorts are identical in their growth and mortality. This is illustrated in Figure 1 where the evolution in time of a single cohort is presented.

The transport in the two horizontal dimensions x and y by the diffusion-advection equation is described under a mathematical form by equation (2),

$$\frac{\partial F}{\partial t} = \rho\left(\frac{\partial^2 F}{\partial x^2} + \frac{\partial^2 F}{\partial y^2}\right) - \frac{\partial}{\partial x}(uF) - \frac{\partial}{\partial x}(vF) - (\lambda F) + S$$

(2)

with ρ, the diffusion coefficient, and u, v the zonal and meridional components of the current in the euphotic layer. The same transport model is used for spatial tuna dynamics, and the numerical resolution based on the work of Sibert and Fournier 1994) and Sibert et al. (1999).

During the period T_r, the cohort of organisms that is developing from a new contribution of primary production is also under the influence of the motion of water masses. As a consequence, the transport model has to be applied during this period to the fraction of N content of the primary production that is transferred toward the forage population. To keep the parallel with a fish population model, it will correspond to transport applied to larvae, juveniles and young fish before their recruitment to the exploited stock.

The tuna population model

The tuna population dynamic is described in the two dimensions x and y by the equation (3),

$$\frac{\partial N}{\partial t} = D\left(\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2}\right) - \frac{\partial}{\partial x}\left(\chi_0 N \frac{\partial I}{\partial x}\right) - \frac{\partial}{\partial y}\left(\chi_0 N \frac{\partial I}{\partial y}\right) - ZN + R \qquad (3)$$

where N is the number of fish, D is the constant diffusive component, I is the habitat index and $\partial I/\partial x$ and $\partial I/\partial y$ are the gradients in habitat index respectively in the east-west and north-south directions. χ_0 is a coefficient of proportionality between advection and gradient in habitat index. Z is the total mortality rate (sum of natural and fishing mortality) and R is the recruitment. Since the model is age-structured, the fishing mortality is applied by age class in each spatial cell.

The recruitment is assumed to be independent of the adult population density. However, the spatial distribution of recruits is environmentally constrained by the processes occurring in the pre-recruitment period. First, the spawning area is limited by the conditions of presence of mature tuna and of sea surface temperature (SST) above a limit value. This latter condition is supported by the high correlation found between SST and occurrence of reproductively-active tropical tuna (Schaefer 1998). Thereafter, during a short period of development, larvae and young juveniles are passively transported by the currents, then they move according to the gradient of habitat index as the adults. Finally, when reaching the age of first capture, they are recruited on the spot in the first age class of the exploitable fraction of the population.

The tuna population model is parameterized using an approximate tuning procedure. The recruitment is adjusted so that the stock biomass estimates roughly equal those obtained independently from other studies. The catchability coefficients are then scaled to obtain estimated catches at the same level as observed catches. Finally, results of the simulation are compared to observed fishing data by fleets, i.e., total monthly catch, spatial distribution of catch and distribution of length frequencies.

Coupling Forage and Tuna models

The λ coefficient used to build the forage biomass represents the instantaneous rate of the total mortality applied to the forage population. In classical fish population dynamic, it is similar to Z, the total mortality, that is the sum of the fishing ($\sim$ predation in the case of forage) and natural mortality of the species. Therefore, λ is the sum of all the predation mortality ω_{sp} due to each species sp feeding upon this forage plus all the natural mortality η_{sf} relative to the total forage biomass of the species sf of the forage population (eq. 4).

$$\lambda = \sum \omega_{sp} + \sum \eta_{sf} \qquad (4)$$

For each predator species that is explicitly described in the populations dynamic model, the contribution to the total predation mortality due to this species is removed from the total mortality λ, so that we get a residual total mortality λ', as illustrated in equation (5) for one predator species. Since ω_{sp} is related to the biomass of the species sp, ω_{sp} and λ' vary in time.

$$\lambda_t' = \lambda - \omega_{sp,t} \qquad (5)$$

On the other side, an explicit mortality by predation due to the same species is applied locally in each spatial cell. To calculate $\omega_{sp,t}$, we use estimates of food consumption by the predator species (sp) relatively to its weight. Therefore, $\omega_{sp,t}$ is defined as the ratio of the forage biomass requirement for the species to the total forage biomass. Locally, at each time step, the forage biomass is reduced in the same way.

In the case of a model in which all the predator species are explicitly described, λ' represents the sum of natural mortality (relative to the forage biomass) of forage species only. The forage distribution given in this case will tend to be the same as the forage distribution obtained with a constant λ

coefficient if the sum of the predation mortality by all the predator species is the same everywhere, although the species differentially occupy the space. This hypothetical situation presents some analogy with the "ideal free distribution" proposed by Fretwell and Lucas (1970) (*in* McCall 1990) for the density dependent habitat selection theory, when individuals differentially occupy available habitats so that realized "suitability" is equal for all occupied habitats.

Discussion

The present model SEPODYM tries to integrate in the simplest possible way knowledge of the biology and the ecology of tuna, to develop a management tool that will allow investigating the environmental interactions and impacts on the tuna stocks. Such an approach inevitably implies a switch from the single species model towards an ecosystem model, even if the ecosystem is drastically simplified. Now that the overall structure of the model has been designed, many improvements can be envisaged in the light of these promising results.

First, it is necessary to encompass the whole tuna stock range. This should be realized in a next version by using a new set of oceanographic data. The understanding of the recruitment mechanisms is fundamental to obtain a model totally based on the environment and hence truly capable of predicting the impacts of the environmental variability. Already, preliminary investigations indicate that the ENSO variability influences the tuna recruitment (cf. SCTB WP RG-1), and the model SEPODYM is an ideal tool for analyzing these mechanisms. More work also needs to be conducted on the definition of the tuna habitat, combining observations, experimental studies, and statistical analyses.

Finally, although SEPODYM is obviously far from being able to describe the complexity of the real pelagic ecosystem, it is a very useful tool, with multiple possible applications. The approach for coupling the species to their forage gives high flexibility to the model. We can examine the dynamics of a single population, or at the opposite include all the tropical tuna species and the other top predator species of the pelagic ecosystem, like billfishes or sharks, if sufficient information is available on their biology and fisheries. The mechanisms of energy transfer through the ecosystem can be investigated as well as the impact of the large and mesoscale physical processes. Once the parameterization can be more accurately fixed, it would be also helpful to test scenarios of climate variability.

Reference List

Bertignac, M., Lehodey, P., Hampton, J. 1998. A spatial population dynamics simulation model of tropical tunas using a habitat index based on environmental parameters. *Fisheries Oceanography* 7(3/4), 326-335.
Lehodey, P., Andre, J.-M., Bertignac, M., Hampton, J., Stoens, A., Menkes, C., Memery, L., Grima, N. 1998. Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical bio-geochemical model. *Fisheries Oceanography* 7(3/4), 317-325.
Lehodey, P., Bertignac, M., Hampton, J., Lewis, A., Picaut, J. 1997. El Nino Southern Oscillation and tuna in the western Pacific. *Nature* **389**, 715-718.
Schaefer, K.M. 1998. Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. Bayliff, W. H. La Jolla, California, USA, Inter-Amerinca Tropical Tuna Commission. Bulletin. **21**(5), 205-272.
Sibert, J.R., Fournier, D. A. 1994. Evaluation of advection-diffusion equations for estimation of movement patterns from tag recapture data. Shomura, R. S., Majkowski, J. and Langi, S. *Summary report and papers on interaction*. Rome, FAO. Interactions of Pacific tuna fisheries. 108-121.
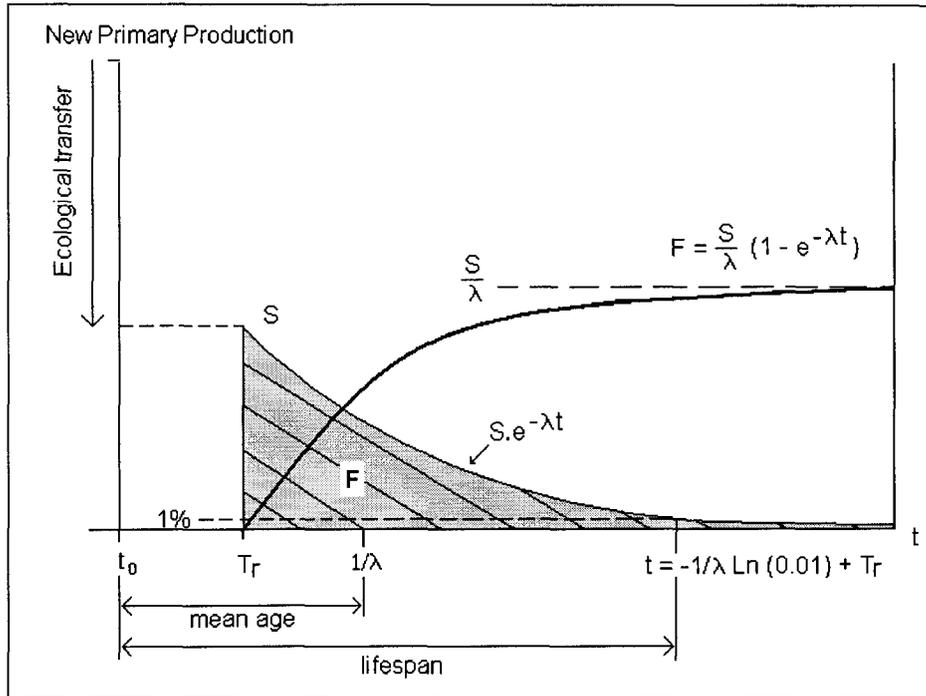
Figure 1. Transfer with time of primary production towards forage according to the model (S is assumed constant), and parameters characterizing the forage population. The thin curve describes the evolution in time of a single source of primary production. The thick curve gives the total forage population