## Tuna model

Tuna are highly specialized migrating species. They swim continuously to counterbalance their negative buoyancy, travelling hundreds of miles. This strategy has a high energy cost, forcing them to move in search of food and has resulted in morphological and physiological adaptations for thermoregulation and high oxygen extraction efficiency. Therefore, temperature and dissolved oxygen concentration affect tuna behavior significantly (Brill, 1994). Sea surface temperature and oxygen concentration have been used to define large-scale limits for potential tuna habitat (Barkley, Neill, \& Gooding, 1978). The tuna forage distribution might have also a major influence on tuna distribution. Surface tuna like skipjack and yellowfin tuna feed during daylight hours. Thus, water clarity is also likely to influence their distribution.
In SEAPODYM we have defined some indices playing an important role in the tuna spatial population dynamics. In general, physical and biogeochemical conditions influence tuna population dynamics through changes in spawning conditions, habitat suitability, and food resources distribution, thus inducing migration behavior, reproduction and mortality. Therefore, Environmental data are used in SEAPODYM to characterize the population habitat depending on tuna's thermal biochemical and forage preferences. There are four types of indices in the model:

1) thermal
2) spawning,
3) feeding
4) movement

These considerations are included in SEAPODYM. In particular, it is assumed that the recruits' spatial distribution is environmentally constrained by processes occurring in the pre-recruitment period. The spawning area is limited by the presence of mature tuna and limiting surface temperatures (SST). Subsequently, during a four months development period, larvae and juveniles are passively transported by currents. Later, young tuna become independent and move with the same adult pattern following a habitat index gradient. Finally, young tuna are recruited to the fishery, entering to the exploitable fraction of the population. Tuna population dynamics include tuna migration through spatially advection- diffusion-reaction (ADR) equations, birth, death and growth processes:

$$
\frac{\partial N_{a}}{\partial t}=\frac{\partial}{\partial x}\left(D \frac{\partial N_{a}}{\partial x}\right)+\frac{\partial}{\partial y}\left(D \frac{\partial N_{a}}{\partial y}\right)-\frac{\partial}{\partial x}\left(X_{0} N_{a} \frac{\partial I}{\partial x}\right)-\frac{\partial}{\partial y}\left(X_{0} N_{a} \frac{\partial I}{\partial y}\right)-\left(M_{a}+F_{a}\right) N_{a}+S_{a}
$$

In last equation, $N_{a}$ is the abundance of age-class $a$ tuna, $D$ is a diffusion coefficient, $X_{0}$ is a coefficient of proportionality between the advection term and the habitat index (refer to Movement Index) ( $I$ ) gradient, $M$ is the natural mortality, $F$ is the fishing mortality and $S_{a}$ is the population surviving from the previous age class or recruitment in the corresponding case.
Additional equations are used to account for the age class decay:

$$
N_{t+1, a}=p_{n, a-1} N_{t, a-1}+\left(1-p_{n, a}\right) N_{t, a}
$$

Where $p$ is a survival coefficient, $n$ is the ratio between the time step in the population age structure and the time step of discretization in the numerical approximation used in the last two equations. The survival coefficient is calculated as:

$$
p_{n, a}=\frac{e^{-n\left(M_{a}+F_{a}\right)}}{\sum_{i=1}^{n} e^{-i\left(M_{a}+F_{a}\right)}}
$$

Recruitment is assumed to be the product of the Beverton-Holt relationship and a spawning index (refer to Spawning habitat) $H_{s}$ :
$S_{0}=\frac{a N}{1+b N} H_{s}$
The larvae natural mortality $M_{0}$ is assumed depending on the surface temperature $T_{0}$, the primary production $P P$ and the forage density $F O$. For juveniles (ages 1 and 2 ) the natural mortality $M_{1,2}$ depends on the surface layer temperature and the adult tuna density. In general, the average natural mortality $m$ depends on an exponentially decreasing component (starvation and predation) and an increasing component for the adult phase (aging and disease):
$m(\tau)=\bar{m}_{p} e^{-\tau \beta_{p}}+\bar{m}_{s}\left(1+e^{\beta_{S}(\tau-A)}\right)^{-1}$
where $\tau$ is the time measured in months, $\bar{m}_{s}$ is the maximum aging mortality and $\bar{m}_{p}$ is the maximum predation mortality. $\beta_{p}$ and $\beta_{s}$ are slope coefficients and $A$ is the age at which the mortality is one half of the maximum aging mortality. The addition of environmental variability is achieved using a standardized index $I$ :
$M=m(\tau)(1-I+\varepsilon)$
In the case of larvae, the feeding index (refer to Feeding habitat index) is used in last equation; for juveniles and adults, two indices are defined as follows. The juvenile index $I_{J P}$ combines the thermal habitat index (refer to Thermal habitat index) and a component related to predation by adults:
$I_{J P}=\left(1-\frac{N_{\text {tot }}}{h+N_{\text {tot }}}\right) H_{T}$
$N_{t o t}$ is the total adult population and $h$ determines the predation intensity. In the adult case, we define the adult food requirement index as the ratio between available forage and the food required by adult tuna (age $a$ ):
$I_{F R, a}=\frac{\sum_{n} F O_{n}}{\psi \sum_{n} r w_{a} N_{a} \vartheta_{a, n}}$
where $r$ is the individual food ration, $w$ is the weight at age, $\psi$ is the consumption of forage by other predators and $\vartheta$ is the relative accessibility coefficient given by:

$$
\vartheta_{c, a}=\frac{\theta_{c, a}}{\sum_{n} \theta_{c, a}}
$$

where $\theta_{c, a}$ is the accessibility coefficient (refer to feeding habitat index). The adult food requirement index can be normalized as:

$$
I_{F R, a}=\frac{1}{1+I_{F R, a}^{v}}
$$

Regarding the fishing mortality, several fisheries are included in the model. For each fishery the fishing effort, the catchability coefficient $q$ and the selectivity at age $s$ are used to estimate the fishing mortality by cell, time step and by age class to estimate the catch:

$$
F_{a}=\sum_{f} s_{f, a} q_{f} E_{f}
$$

In this version of SEAPODYM, the selectivity is defined as a sigmoid function (type I) or an asymmetric normal distribution (type II). The total mortality at age $Z_{a}$ is the sum of the natural mortality and the fishing mortality.

The statistical estimation of SEAPODYM parameters is based on fisheries data. Keeping the computation time low requires a balance between the number of fisheries included, the domain size, the spatial and temporal resolution, and the time series size used in the estimation. Since in SEAPODYM each fishery is characterized by a constant catchability coefficient and selectivity parameters, it is also important to aggregate homogeneous fishery data. For tuna species, there is monthly spatially distributed effort (in days or number of hooks) and catch data (in weight). Size composition data is also available, usually aggregated by fishery and area.

SEAPODYM describes the tuna spatial dynamics influenced by intrinsic processes and extrinsic environmental variability. Several model predictions depend on environmental forcing. However, we need to combine the simulations with a formal statistical framework to produce the best fit to the observed fisheries data.

In particular, the current SEAPODYM version assumes only observation error on fisheries data and a maximum likelihood estimate approach is used for the estimation of the parameters. The likelihood objective function has several components depending on the availability of fisheries data. In particular, the Poisson distribution was used for the Pacific skipjack (Senina et al. 2008) and the WCPO purse seine fleet:

$$
L\left(\theta \mid C^{o b s}\right)=\prod_{t, f, i, j} \frac{C_{t, f, i, j}^{\text {pred }}{ }^{c_{t, f, i, j}^{\text {obs }}} e^{-C_{t, f, i, j}^{p r e d}}}{C_{t, f, i, j}^{\text {obs }}!}, \quad f=1,2,3,4
$$

where the predicted catch $C_{t, f, i, s}^{p r e d}$ is calculated using observed fishing effort $E_{t, f, i, j}$ with the following equation:

$$
C_{t, f, i, j}^{\text {pred }}=q_{f} E_{t, f, i, j} \sum_{a=1}^{K} s_{f, a} w_{a} N_{t, a, i, j} \Delta x \Delta y
$$

where $w_{a}$ is the fish mean weight at age $a, s_{f, a}$ is the selectivity at age for the fishery $f$ and $N_{t . a, i, j}$ is the population density. It is important to point out that when catch data contain many zeros, it may be more appropriate to use a negative binomial distribution with zero inflation:
where $\beta_{f}$ and $p_{f}$, are the negative binomial parameter and the probability of getting a null observation respectively. Both parameters are statistically estimated. Regarding the size composition data, it was assumed that fish lengths from are normally distributed, therefore the likelihood component is:
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$$
-L_{3}\left(\theta \mid Q^{o b s}\right)=\frac{1}{2 \sigma_{Q}^{2}} \sum_{t=1}^{T} \sum_{f=1}^{6} \sum_{a=1}^{K} \sum_{r=1}^{7}\left(Q_{t, f, a, r}^{\text {pred }}-Q_{t, f, a, r}^{o b s}\right)^{2}
$$

where the predicted catch composition at age in the region $r$ is:

$$
Q_{t, f, a, r}^{p r e d}=\frac{s_{f, a} \sum_{i, j \in r} E_{f, i, j} N_{a, i, j} \Delta x \Delta y}{\sum_{a=1}^{K} s_{f, a} \sum_{i, j \in r} E_{f, i, j} N_{a, i, j} \Delta x \Delta y}
$$

the proportion at age $a$ in the catch computed from the observed length-frequency data is:
$Q_{t, f, a, r}^{\text {obs }}=\frac{C_{t, f, l, r}^{o b s}}{\sum_{l} C_{t, f, l, r}^{o b s}}, l \in\left[l_{a}, \bar{l}_{a}\right)$.
where $C_{t, f, l, r}^{\text {obs }}$ is the number of fish of length $l$ in region $r$ that belongs to the age-class $a$. The variance $\sigma_{Q}^{2}$ is assumed to be constant ( 1.5 cm ). The total negative log-likelihood to be minimized is the sum of the mentioned components:
The total negative log-likelihood to be minimized is the sum of the mentioned components:
$L^{-}=-\ln L_{1}\left(\theta \mid C^{o b s}\right)-\ln \left(\theta \mid C^{o b s}\right)-\ln \left(\theta \mid Q^{o b s}\right)$
SEAPODYM has been used for three tuna fisheries from the west Pacific Ocean. You can review the results for skipjack, yellowfin tuna, and albacore on the Seapodym section of the web site.

## References

Barkley, R A, Neill, W H, \& Gooding, R M. (1978). Skipjack tuna (Katsuwonus pelamis) habitat based on temperature and oxygen requirements. Fishery Bulletin, 76, 653-662.
Brill, R. 1994. A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. Fisheries Oceanography 3:3, 204216.

