



Reference manual for the Spatial Ecosystem and Populations Dynamics Model – SEAPODYM



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August 2005

Forewords

SEAPODYM is a numerical model initially developed for investigating physical-biological interaction between tuna populations and the pelagic ecosystem of the Pacific Ocean. Using predicted environment from ocean-biogeochemical models (primary production and physical environment), it simulates the development of the pelagic ecosystem in 2 trophic levels: tuna or associated species (one or several species, top level) and its forage (several components, mid-trophic level). SEAPODYM integrates spatio-temporal and multi-population dynamics and considers interactions among populations of different species and between populations and their physical and biological environment. The model also includes a description of multiple fisheries and then predicts spatio-temporal distribution of catch, catch rates, and length-frequencies of catch based either on observed or simulated fishing effort, allowing respectively to evaluate the model or to test management options (e.g., changing the fishing effort, implementing marine reserves, etc...).

Development of a first version of the model started in 1995 under the EU-funded SPRTRAMP project implemented at the Secretariat of the Pacific Community in Noumea, New-Caledonia. In 2000, the model was named SEPODYM for Spatial environmental Populations Dynamics Model when both sub-models for prey (forage) and tuna dynamics were fully coupled. A second EU-funded project (PROCFish) starting in 2002 at SPC allowed continuing the development of the model. An improved version was renamed SEAPODYM for Spatial Ecosystem And Populations Dynamics Model. This change corresponded to a better description of intermediate trophic levels in several vertical layers, and improvements in the approach to link the dynamics of multiple predators to these different prey populations.

All the spatial dynamic modelling of SEAPODYM is based on diffusion-advection-reaction equations in two horizontal dimensions. The numerical scheme for the transport initially developed for homogeneous grid was modified in 2004-05 with the support of the University of Hawaii-PFRP funded project "Mixed-resolution models for investigating individual to population spatial dynamics of large pelagics". The new numerical scheme allows the use of spatial stretched-grids. This was necessary step to increase resolution in regions of interest but keeping the time of computation at reasonable level by decreasing resolution elsewhere.

This document provides details on the different components of the model and the information needed to install and use the model. Details on the development of this model can be found in SCTB documents <u>http://www.spc.int/OceanFish/Html/SCTB/index.htm</u>) and several research articles.

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Chapter 1.

Software environment and preliminary steps before running simulations

1.01 SEAPODYM framework

The source code of SEAPODYM is developed in C++ oriented object language and executables are available for Windows and Linux platforms. Several softwares are developed in parallel in Java language (Figure 1-1): SeapodymView, GMB, and Seapodym-RC. These executables are available on the testing web site <u>www.seapodym.tk</u>

SeapodymView: visualization software reading DYM format and text column format with different tools to manipulate and analyze the data (see separate documentation). It includes a function to convert files from Netcdf format to DYM format.

GMB (for Grid and Mask Builder): software used to define the grid (regular or with stretching) and the corresponding mask based on topographic files (ETOPO). An interpolation function is provided to interpolate input environmental data files over the grid and corresponding mask (see separate documentation).

Seapodym-RC: visualization software for controlling a running simulation (see separate documentation).

Most of the input/output files needed/produced by SEAPODYM use a specific binary file format called DYM (*.dym). A DYM file contains a header and one 3D variable with dimensions nlong*nlat*ntime which correspond respectively to longitude, latitude, time. The header contains the values of nlong, nlat, ntime and the associated longitude, latitude, time (in decimal year) vectors. It also includes the mask and the grid (nlong*nlat) for the 3D variable. The DYM format can be viewed using SeapodymView software. See more details on format in section files formats.

A sample of files can be downloaded on the test web site <u>www.seapodym.tk</u>. They can be used to test a first simulation with the model.





SEAPODYM allows several types of simulations:

- <TestMap> is a test simulation that is recommended to use each time a new spatial grid is defined for a simulation. The simulation applies independently the advection and the diffusion scheme to a quantity which is uniformly concentrated in a square in the middle of the geographical domain at the first time step. This test simulation allows checking the mass conservation in the model.

- <Forage> run a simulation to predict the production and biomass of forage components based on environmental data provided in input (temperature, currents and primary production).
- <Habitat> simulates the habitats of the predator species with the predicted movement that would result from these habitats.
- <Seapodym> is the simulation for both forage components and predator populations. It can be run with or without fisheries.

Running a simulation requires to define a set of parameters. They are all listed in a parameter text file. By convention, the parameter file is identified by the extension *<.par>*, e.g. *<*first_simulation.par>. The parameter file includes several sections that are detailed in the following chapters. They are listed in a logical order that is imperative to follow (Table 1-1).

Running the <Testmap> simulation requires a parameter file with sections 1 and 2.

Running the <Forage> simulation requires a parameter file with sections 1 to 3.

Running the<Habitat> or <Seapodym> simulation without fisheries requires a parameter file with sections 1 to 4.

Running the <Seapodym> simulation with fisheries requires a parameter file with sections 1 to 6.

Section 7 is optional

Section 1: grid and time-space resolution
Section 2: parameters for transport
Section 3: parameters for the forage components
Section 4: parameters for predator species
Section 5: parameters for coupling between prey and predator
Section 6: parameters for the fisheries
Section 7: coordinates of regions to aggregate predictions

Table 1-1Different sections in the parameter file

1.02 Defining the grid and the mask

The GMB software allows to define a grid and to use a file of the global topography to define the mask. This is a first critical step. The grid can be regular or stretched using 2 types of functions to increase the resolution in some regions of interest (Figure 1-2).



Figure 1-2 Example of grid stretching defined in GMB combining 1-D and 2-D stretching functions

Once the grid is defined, it is also needed to create a mask. By default, the mask is put to 0 for land and 1 for ocean. Several options in GMB (see separate software documentation) allow to quickly match the mask to the grid and to modify special configurations that can produce instability (or "leak") with the advection-diffusion computation. This occurs when three cells of land surround one cell of ocean (Figure 1-3).

If the forage model is defined with several vertical layers (see chapter III), one mask should be created for each layer by selecting the depth boundary in GMB. After checking configuration of each layer mask they can be added together to provide the final mask that will be used for the simulation (Figure 1-4).

0 0 0 1	0 0 0 1	0 0 0 1
0 0 1 1	0 0 0 1	0 0 1 1
0 0 0 1	0 0 0 1	0 0 1 1
0 0 1 1	0 0 1 1	0 0 1 1
0 0 1 1	0 0 1 1	0 0 1 1

Figure 1-3 Special configurations (red circle) in the mask will lead to a "leak" with the transport model. It should be changed to one or the other alternative configuration proposed.



Figure 1-4. Example of a mask defined for the Pacific Ocean with three vertical layers. 0= black (land); 1=green (1 layer 0-100m); 2=blue (2 layers, 0-100m and 100-400m); 3=white (3 layers0-100m, 100-400m and 400-1000m)

1.03 Interpolating data

Before running a simulation, the files of environmental variables need to be interpolated over the grid that was created using GMB software. This can be done using GMB. However this requires to use the format dym. Files that are provided through the seapodym web are in this format. If you have your own files in NetCDF format you can use the NetcdfExtractor tool in SeapodymView to convert them in dym format. For other formats you would need to develop your own routine (see chapter V, files format).

When running SEAPODYM, the Main Menu also proposes an access to several tools:

*** SEAPODYM MAIN MENU *** S -> Simulations T -> Tools Q -> Quit

When entering the letter T + ENTER the Tools Menu appears:

*** SEAPODYM TOOLS ***
F -> Fisheries Text to Bin
C -> Create Climatology
M -> Monthly Average
I -> Interpolation
R -> Return to Main Menu

These tools are useful to prepare a SEAPODYM simulation and are briefly described below:

F->-> Fisheries Text to Bin

Convert a fishery text (column) file into the binary format used by SEAPODYM to have a rapid access to data.

You will be asked to enter the name of the input file and output file to create.

C -> Create Climatology

For a given variable, creates a monthly climatology out of a several-year 3D (longitude, latitude, time) time series.

You will be asked to enter the name of the input file and output file to create. The input/output file must/will be in DYM format.

M -> Monthly Average

For a given variable, averages over one or several months a 3D time series to create a lower-resolution time series.

You will be asked to enter the name of the input file and output file to create. The input/output file must/will be in DYM format.

I -> Interpolation

For a given variable at a spatial resolution higher than 1deg, the resolution is changed to a regular one-degree square.

You will be asked to enter the name of the input file and output file to create. The input/output file must/will be in DYM format.

1.04 Testing the mask

When creating for the first time a new grid and mask, it is recommended to test if the selected configuration allows the mass conservation in the model. In case of a mask with multiple layers, this rapid test can be run for each mask of individual layer before to add them to create the final mask.

After selecting T + ENTER in the Tools menu, the user is proposed to use a standard parameter file. Type "y + ENTER" to enter the name of a new parameter file, including its path.

The parameter files should include the section 1 and 2 as described below:

Section 1 of the parameter file (grid and time-space resolution)

Latmin Latmax L	onmin Lonmax	
reso		
deltaT deltaX de	taY	
nb_iteration		
nb_step_timeseri	S	
FirstDate La	stDate Fcst	

Notes:

Latmin, Latmax, Lonmin and Lonmax are the coordinates at the corners of the grid. reso is the original spatial resolution in degree (without considering stretching of the grid) deltaT is the time step of the simulation in day

deltaX and deltaY are the original size of the cells (nautical miles) in X and Y directions respectively

nb_iteration is the number of iteration to approximate the derivatives

nb_step_timeseries is the total number of time steps in the time series of the environmental files

FirstDate is the first date (decimal year) at which the simulation will start in the time series LastDate is the last date (decimal year) at which the simulation will stop in the time series Fcst is the forecast period (decimal year) after LastDate, based on a climatology.

Section 2 of the parameter file (input data access)

nb_layers
/DATA_PATH/mask.txt
/DATA_PATH/grid.txt
/DATA_PATH/Umean_layer1.dym
/DATA_PATH/Vmean_layer1.dym
/DATA_PATH/Umean_layern.dym
/DATA_PATH/Vmean_layern.dym
/DATA_PATH/mcl-Umean_layer1.dym
/DATA_PATH/mcl-Vvmean_layer1.dym
/DATA_PATH/mcl-Umean_layern.dym
/DATA_PATH/mcl-Vmean_layern.dym
/DATA_PATH/SaveDirectory/
Diff_F

<u>Notes:</u> nb_layers is the number of vertical layer. /DATA_PATH/.../ are the paths to the different input files. It is important to follow this order! Note that there are two series for these environmental variables. The first one is for files that provide the full time series for the simulation. The second is for monthly climatological files. By convention, file names of climatological files are the same than their corresponding time-series files but with the prefix 'mcl'. They can be created from the previous using the TOOLS->C+enter menu.

The diffusion coefficient (Diff_F) represents both the diffusion of water and the random movements of forage organisms. It is expressed in nautical miles $(n.mi.)^2.d^{-1}$.

Below is an example of a parameter file with the first two sections for 1 layer and using a monthly one-degree simulation over 1950-2002 (636 months), but used to test the mask over a period of 10 years.

```
-54.5
      64.5
             90.5
                   291.5
1
60
      60
             30
636
1990.0
                          0
             2000.0
1
\data\5002x30dx1deg\maskPac1deg-1L.txt
\data\5002x30dx1deg\gridPac1deg-1L.txt
\data\5002x30dx1deg\umean200m5002-30d-1deg.dym
\data\5002x30dx1deg\vmean200m5002-30d-1deg.dym
\data\5002x30dx1deg\mcl-umean200m-1deg.dym
\data\5002x30dx1deg\mcl-vmean200m-1deg.dym
\output\test\
250
```

If the parameter file and the path to it are correct, the simulation starts. The display will show the progress of the simulation, including the current time step and corresponding date, as well as the sum over the geographical domain of the quantity released in the center of the domain to test both diffusion and advection separately. These 2 quantities should remain constant for all the simulation.

Input/output file errors generate an error message.

At the end of the simulation, you can choose to save a copy of the parameter file or not. To properly stop an in-progress simulation, type "CTRL+c".

At the end of the simulation, the model will have recorded the results in the output directory provided in the parameter file, if this directory exists! You may want to see them using SeapodymView (Figure 1-5).



Figure 1-5. Example of testmap outputs for diffusion (top) and advection (bottom) after one (left) and twelve (right) monthly time step.

Chapter 2.

Modelling the mid-trophic forage components

2.01 Conceptual model of the pelagic ecosystem

When considering the definition of an ecosystem, i.e. how assemblages of species are organized in space and time, and how they interact with each other and the physical environment, modelling the ocean pelagic ecosystem is obviously a challenge that requires drastic simplifications. These simplifications need to be considered carefully in close relation with the level of observation and knowledge that we have for each component of the system (Figure 2-1) to be sure that the model can be properly developed and parameterized and then evaluated by comparing prediction to available observations.



Figure 2-1. Level of information (observation and knowledge) available for the components of the pelagic ecosystem and corresponding modelling approaches (GCM = general circulation model; NPZD = nutrients-phytoplankton-zooplankton-detritus models)

While the level of information for the physical and biogeochemical components is now sufficient to make possible detailed three-dimensional realistic planetary scale simulations of ocean physic and lower trophic (phytoplankton) level biology, it is clear that the information for the intermediate trophic levels (micronekton) is a weak link. Modelling this component of the system then requires an approach as simple as possible but that can be linked, however, to the other components without loosing the benefit of the better knowledge and detailed modelling possibility they offer. It seems therefore appropriate to define intermediate trophic

levels with several simple large functional groups with a dynamic linked to the one provided by ocean-biogeochemical models.

The intermediate or mid-trophic levels that provide the forage of tuna and other oceanic top predators consist of macrozooplankton and micronekton, i.e. small animals that can effectively swim. Organisms in these groups are typically crustaceans, fish, and cephalopods, with sizes in the range of 2-20 cm. However, at the scale of an oceanic basin, we can consider that they are largely influenced by the general circulation. Many of these species have optimized their behavior under the constraints of finding food in the productive upper layers while avoiding predators as far as possible, i.e. migrating in the upper layers after the sunset and leaving it during sunrise, so that vertical distributions and migrations are finally structuring all the pelagic foodweb.

From a literature review of several seminal works by King and Iversen (1962), Vinogradov (1981), Legand (1972), Granperrin (1975), Roger (1971), and Blackburn (1968), the pelagic micronekton can be divided into epipelagic (0~200m), mesopelagic (200~500m) and bathypelagic groups (below 500m), the last two groups being subdivided into migrant and non-migrant species. Of course, this is a simplified view of the system as it is difficult to establish clear vertical boundaries, which are influenced by local environmental conditions, and to group so many different species and even life-stage of species. The 200m vertical boundary between epi- and meso-pelagic layers in particular is likely too deep when considering the eastern Pacific. A better boundary definition could be based on the depth of the thermocline or the mixed-layed. 100m can be seen as a compromise to represent an average situation between western and eastern Pacific.

All these large groups include organisms of the main taxa: fish, crustacean and cephalopods, which, with the gelatinous filter feeders, are forage species of the top and apex predators (Figure 2-2). Therefore the micronekton (forage) components have been classified based on their vertical distributions (for details, see Lehodey 2004; Cianelli et al. 2005) that control their relationships with (and accessibility to) top predators.

2.02 A 3 layers – 6 components mid-trophic forage model

Primary production is the source for forage functional groups through ecological energy transfer. There is one coefficient *E* for the total energy transfer from primary production to all (*n*) forage components and one coefficient E_n ' for each forage component. The sum of E_n ' = 1 (Figure 2-3).

During the time that a forage component is occupying its day or night layer, it is redistributed by average currents in the corresponding layer. The time spent in one or the other layer is calculated from the day length (DL: nb of hours of daylight) equation (eq. 1) as a function of the latitude ϕ (in radians) between 65°N and 65°S and the Julian day of the year J (from 1 to 365).

$$DL = 24/\pi \arcsin(-\tan \phi \tan \delta) \tag{1}$$

where δ (in radians) is the solar declination angle:

$$\delta = 23.45 \cos(2\pi / 365 (J-172))$$
 (2)



Figure 2-2. A top to bottom schematic view of the pelagic food web. Most of the organisms in the mesoand deep-pelagic layers have nycthemeral migration patterns leading to higher concentration in the upper layer at night and in the deeper layer during the day. DOM, Dissolved Organic Mater; Bact., bacteria; Gel. org., gelatinous filter feeders; pk, plankton; Zpk, zooplankton; EpiPel, epipelagic micronekton; MesoPel, mesopelagic micronekton; BathyPel., bathypelagic micronekton; div. Pisc.; diverse piscivorous macronekton; skj, skipjack; yft; yellowfin; bet; bigeye; mar. mam., marine mammals



Figure 2-3. The different daily vertical distribution patterns of the micronekton in the pelagic ecosystem. 1, epipelagic; 2, migrant mesopelagic; 3, non-migrant mesopelagic; 4, migrant bathy-pelagic; 5, highlymigrant bathypelagic; 6, non-migrant bathypelagic. The part of energy (E) transferred from primary production (PP) to intermediate trophic levels is redistributed (E_n ') through the different components

To affect a realistic value to the ecological transfer, independent estimations of the efficiency coefficient of ecological transfer from primary to secondary levels of the pelagic food web have been obtained in the literature. Iverson (1990), compiling data in environments ranging from oceanic to coastal waters, calculated that for an average 2.5 trophic transfers from phytoplankton to carnivorous fish and squids (typically tuna prey species) the annual production can be described according to eq. 1a based on C transfer efficiency from total primary production or eq. 1b based on N transfer efficiency from new primary production.

$$F'_{yr} = P'_{lyr}. E_1^{2.5} * c_1$$

$$F'_{yr} = P'_{2yr}. E_2^{2.5} * c_2$$
(3)
(4)

With F'_{yr} the forage production, P'_{lyr} the total primary production in C and P'_{2yr} the new primary production in N.

 E_2 appears to be a constant value (0.28), while E_1 varies between 0.1 in oceanic environment and 0.2 in coastal environment. When using eq. 1a, we choose a value of 0.1 that gives E_2 = 0.00316. Coefficients c_1 and c_2 are used to convert between units of C and N respectively to grams of wet weight of forage.

For P_1 in mmol C, $c_1 = 12 \ 10^{-3}$ (g C) x 2.4 x 3.3 = 0.0948 With 2.4 the ratio between fish dry weight (g) and carbon (g) and 3.3 the ratio between fish wet weight(g) and fish dry weight (g) For P_2 in mmol N, $c_2 = 14 \ 10^{-3}$ (g N) x 2.4 x 3.3 x 3.6 = 0.3976

With 2.4 the ratio between fish dry weight (g) and carbon (g), 3.3 the ratio between fish wet weight(g) and fish dry weight (g), and 3.6 the ratio between carbon and nitrogen in fish.

In the special cases of shallow topography, the sum of transfer coefficients from forage components in the missing layer(s) is redistributed equally between the remaining components (Table 2-1). The mask is used to identify the number of layers: 0= land; 1= first layer only; $2=1^{st}$ and 2^{nd} layers; 3=3 layers. It can be easily created with GMB software.

 Table 2-1. Example of matrix of Energy transfer coefficients calculated from previous parameterisation according to the depth and the number of corresponding layers

			Forage component				
Mask	Nb of	epi	meso	m-meso	bathy	m-bathy	hm-bathy
value	Layers						
0	0	0	0	0	0	0	0
1	1	1	0	0	0	0	0
2	2	0.30	0.23	0.45	0	0	0
3	3	0.17	0.10	0.22	0.18	0.13	0.20

The dynamic of the forage components is based on time, temperature and transport. These functional groups are considered as single populations composed of different species, and then modeled using the same mathematics than in a single species population model, with continuous mortality and recruitment (e.g., Ricker 1975). Instead of having different age classes (cohorts) of a same species, there are different age classes of many different species.

But from a mathematical point of view, it is immaterial whether the cohorts are of the same species or not (Allen, 1971). However, the spatial dynamic is considered and described with an advection-diffusion equation using horizontal currents for the advective terms.

The concept of this tuna forage model can be simplified and discretised as follow: In the ocean, at any time, anywhere, there is a mixing of all kinds of eggs, cells, etc... that are the germs of the future organisms of the pelagic food web. In some places and time, the input of nutrient in the euphotic zone allows the almost immediate development of phytoplankton (Primary Production) that is the *input* (~ spawning) in the forage population model. This new production allows the development of a new "cohort" of organisms, i.e., true zooplankton like copepods as well as all larvae of fish and other larger organisms (meroplankton). The organisms having the longer life span and larger growth potential (larvae and juvenile of fish, squids, shrimps, etc) feed on the expense of the organisms with short life span and lower growth potential (phytoplankton, zooplankton). As the water masses are maturing, they are advected with these organisms (but a part of them can also diffuse due to the diffusion of water and their own random movements) and the currents create fronts of convergence where forage is aggregated. Of course this dynamic occurs as a continuous process in time and space. Following this time-trophic-continuum concept, the species should disappear selectively in the order of their trophic level related to their time of development.

Without spatial consideration, we can express the variation in time of the forage population F as:

$$\frac{dF}{dt} = S - (\lambda \ F) \tag{5}$$

where F is the forage population (biomass), S is the recruitment (or source) and λ the mortality coefficient. The recruitment consists of the new organisms that are entering in 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, this time of recruitment (T_r) allows to 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" (coinciding with the new primary production input) and their "recruitment" in the forage population. The fraction of biomass transferred (recruited) into the forage population from the primary production depends on ecological transfer coefficients (E).

Since the cohorts are identical in their growth and mortality, it is not necessary to consider effects due to the existence of more than one cohort (Allen 1971). This is illustrated in Figure 2-4 where the evolution in time of a single cohort is presented. Assuming that the source is constant in time and that $F_0 = 0$ at t = 0, the solution of (1) is:

$$F(t) = \frac{S}{\lambda} \quad (1 - e^{-\lambda t})$$
(6)

Because of the constant coefficient λ , a given source term will decrease exponentially, and in the case of a constant source, the biomass (*F*) would tend towards an equilibrium level (S/ λ). The total biomass integral by time of a single cohort is equal to the total biomass of the

population of successive and identical cohorts. The exponential mortality model used, with a constant instantaneous rate, implies a ratio production/biomass equal to the instantaneous mortality rate (Allen 1971) (3).

$$\lambda = \frac{F'}{F} \tag{7}$$

Therefore, in an equilibrium situation, the biomass $F \sim S/\lambda$ and the production F' = S.



Figure 2-4. Transfer with time of primary production to forage according to the model (S is assumed constant). The thin curve describes the evolution in time of a single source of primary production. The thick curve gives the total forage population, i.e., the sum of the shaded area. (redrawn from Lehodey 2001)

Assuming that the source term is constant and continuous also allows defining a mean age to the forage population. T_r being the time 0 of the forage population, the sum of the products t. S_t is:

$$\int_0^\infty t.St \, dt = S \int_0^\infty t \, e^{-\lambda .t} \, dt = \frac{S}{\lambda^2}$$
(8)

Since the forage population is S/λ , the mean time spent in the forage population is S/λ^2 divided by S/λ , that is $1/\lambda$. Adding T_r to $1/\lambda$ gives the mean age of the forage population

(Figure 2-4). The mean age can be assimilated to the interval between one generation and the next, that is, a mean generation time or turnover time (the mean time taken for the biomass of the population to be replaced by fresh production). It is also possible to define the maximum life span of organisms of the forage population as the time necessary to see the population reduced by a determined level (e.g., for 99%, $t = -1/\lambda \cdot Ln(0.01) + T_r$). Therefore λ and T_r which characterize F can be estimated using biological characteristics of key-species representative of the forage population.

Defining λ and T_r

It is well established that metabolic rates are correlated to temperature. Bergmann's rule, for example, describes the relation between temperature and body size, and age and size at maturity typically decrease in ectotherms with an increase in temperature (see a review in Atkinson 1994). These inverse relationships between temperature and age and size at maturity have been rationalized from the perspective of environmental physiology (Atkinson and Sibly 1997) and from life-history theory (Berrigan and Charnov 1994). Taking these macro-ecological principles into account requires linking the two parameters T_r and λ that characterize F with ambient water temperature. This is done using a simple decreasing exponential function (eq. 5) as illustrated on Figure 2-5.

$$1/\lambda = A e^{(-0.1 \text{ Tc})}$$
 (9)
 $T_r = B e^{(-0.1 \text{ Tc})}$ (10)

With T_c the environmental temperature, and A and B the maximal values (at 0°C). The exponential coefficient is set to 0.1, based on the '10°C rule' reflecting biochemical kinetics of metabolism (cf Charnov and Gillooly 2003).



Figure 2-5. Top: functions based on temperature used for the parameterization of T_r and λ that characterize the forage population. Bottom: spatial distribution of the forage "mean age" in months based on an average SST distribution and the equations 5a and 5b. The blue curve defines T_r and the red curve $1/\lambda$. The sum of both gives the mean age for a given temperature (black curve). Age at maturity is reported for capelin, herring, sardine, anchovy, oceanic anchovy, tropical squids, and tropical mesopelagic fish *Vinciguerria nimbaria*

Adding the transport

The spatial dynamic of forage organisms are described with a diffusion-advection equation, using zonal (u) and meridional (v) components of the current for the advective terms in the two horizontal dimensions and a diffusion coefficient (ρ) reproducing both diffusion of water and random movement of organisms (Lehodey et al. 1998). The transport in the two horizontal dimensions x and y by the diffusion-advection equation is described under a mathematical form by equation (7),

$$\frac{\partial F}{\partial t} = D\left(\frac{\partial^2 F}{\partial x^2} + \frac{\partial^2 F}{\partial y^2}\right) - \frac{\partial}{\partial x}(uF) - \frac{\partial}{\partial y}(vF) - (\lambda F) + S \tag{9}$$

During the time 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 or content of the primary production that is transferred toward the forage population.

The partial derivatives of equation (9) are approximated by second order finite differences with upwind differencing of advective terms as in Sibert et al. (1999). Zero-flux boundary conditions, representing zero transport of the biomass across the bounds are chosen in order to set impermeability of the computational domain. The resulting algebraic problem is solved with help of well-known alternate direction implicit (ADI) method. In this method the time discretization is split into two parts. Solver finds the solution for first half-step in one spatial direction and for second half-step in other direction. ADI method is stable and always converges to the unique solution of the given equation.

Note: Correction with latitude.

Rather than correcting the change of surface grid cells in the x direction with increasing latitude, the correction is done using a correction factor that is the inverse of the cosine function of the latitude in radian. This correction is applied either for computation of movement in the x direction or for surface calculation when necessary.

Section 3 of the parameter file (forage)

Once the grid and mask have been defined, and the environmental data required for the transport interpolated over this grid (see Chap. 2), the second sets of parameter to add in the parameter file for running a forage simulation has the following structure (in red, the parameters to estimate):

Nb_forage /DATA_PATH/PP.dym /DATA_PATH/Tmean_layer1.dym

/DATA_PATH/Tmean_layern.dym /DATA_PATH/mcl-PP.dym

/DATA_PAT	TH/mcl-Tmean_	_layer1	.dym
/DATA_PAT	TH/mcl-Tmean_	_layern	.dym
Tr_max	Tr_ex	р	
inv_lambda_	<mark>max</mark> inv_la	mbda_	exp
E c			
Fname ₁	Fname ₂		Fname _n
E'1	E'2		E'n
NighLayer ₁	NighLayer ₂		NighLayer _n
DayLayer ₁	DayLayer ₂	•••	DayLayer _n

Note:

Nb_forage is the number of forage components.

/DATA_PATH/.../ are the paths to additional input files required for this simulation: vertically integrated primary production and the average temperature for each layer. Here also both monthly climatologies and time series are needed.

Fname is the name of the component.

NightLayer and DayLayer are the layers where the forage component is present during night and day period and identified by the value used for the mask minus one (0=first upper layer; 1=second layer, etc ...).

 $\underline{Ex.}$ Section 3 of the parameter file with forage parameters. 3 layers - 6 components and total primary production in mmol C

6					
\data\PPtot0-400m.dym					
\data\7	mean0	-100m.c	lym		
\data\7	mean1	00-400r	n.dym		
\data\7	mean4	00-1000)m.dym		
\data\n	nclPPto	t0-400n	n.dym		
\data\n	nclTme	an0-100)m.dym		
\data\n	nclTme	an100-4	400m.dy	/m	
\data\n	nclTme	an400-1	1000m.c	lym	
450	-0.1				
1825	-0.1				
0.0031	6	0.0948	3		
epi	meso	mmeso	b bathy	mbath	y hmbathy
0.17	0.1	0.22	0.18	0.13	0.2
0	1	1	2	2	2
0	1	0	2	1	0
200					
3					

► The number of parameters that are needed to estimate here is 4+(n-1), n being the number of forage components.

2.03 Running a forage simulation

A forage simulation will record a production and a biomass file for each forage component (Figure 2-6) in the output directory, for the time period between first and last date entered in the parameter file (section 1). File names will have the form Fbiom_Fname.dym or Fprod_Fname.dym where Fname is the name of the forage component as provided in the parameter file.

A text file called \langle SumDym.txt \rangle is also created where the sums for biomass and production of all components are recorded for each time step since the beginning of the simulation. This simulation starts by a spin-up with a monthly climatological loop to build up the forage biomass before running the real time series. The spin-up is determined by the maximum value of T_r .

A second text file called <Nlayer_E_coeff.txt> record the matrix of Energy coefficients used in relation to the number of vertical layers.

At the end of the simulation, the user can decide to save a copy of the parameter file in the output directory. It may be useful to keep a record of the parameterization used to which correspond the files in the folder.

► It is necessary to run this forage simulation and to produce forage production and biomass files before running other types of simulations (habitat or seapodym) since they will use either one or the other as an input. Once the forage prediction is satisfying, it will be necessary to create monthly climatological files of these forage production and biomass series since they are used for initial phases of habitat standardization and spin-up of forage biomass and predator population.

Since the production of forage is simply determined by energy transfer from primary production and linked to temperature, it is independent of changes in forage biomass. Therefore it is much faster to use it as an input variable to build up the forage biomass in the seapodym simulation.



Figure 2-6. Example of forage biomass distributions (10-day period centred on 25 Dec. 1998) predicted in the surface layer (0-100m) during day (epi-pelagic forage biomass only) and night (sum of epi-pelagic, migrant meso-pelagic and highly migrant bathy-pelagic forage biomasses). Note the factor x4 in the color scales between day and night.

Chapter 3.

Top predators

Top predators in the marine pelagic ecosystem are essentially opportunistic omnivorous predators. Their diets reflect both the faunal assemblage of the component of the ecosystem that they explore and their aptitude to capture prey species at different periods of the day (i.e., daytime, nightime, twilight hours). It seems that most of them are in the upper layer during the night. But high sensory specialisation (e.g. olfaction in sharks, vision in bigeye tuna, swordfish and cephalopods or echolocation in marine mammals), and morphological and physiological adaptations (e.g., thermo-regulation) allow them also to exploit the dark and colder deeper layers (Figure 3-1).



Figure 3-1. Five typical vertical movement behaviors simulated using a 3-layer and 2-type of prey pelagic system (adapted from Dagorn et al. 2000): 1- epipelagic predators (e.g., skipjack, marlins and sailfish); 2-predators moving between the surface and intermediate layers during the day (e.g., yellowfin tuna); 3-predators mainly in the intermediate layer during the day (e.g., albacore tuna); 4- predators moving between deep and intermediate layer during the day (e.g., blue shark); 5- predators mainly in the deep layer during the day (e.g., bigeye tuna and swordfish).

The modeling approach for the tuna population dynamics has been first described in Bertignac et al. (1998), and modified in Lehodey (2001), Lehodey et al. (2003) and in this latest version (Table 3-1). Populations are age-structured and movements described with an advection-diffusion equation. Diffusion is used to represent undirected random movement, ie *kinesis*, while in contrast advection allows to describe directed movement in response to some external stimulus, ie. *taxis*. Here, the directed movement is following the gradient (slope) of a habitat index (klinotaxis). *Therefore, the movement of these top-predator species is modeled as a combination of kinesis and klinotaxis*.

While the spatio-temporal dynamics is applied at the time step of the model, the age structure for tuna and tuna-like predators is defined with three first monthly age-classes for larvae and juveniles, then quarterly age classes for young (from 2^{nd} quarter of age to age at first maturity) and adults (after age at first maturity). The last age class is a "+ class" where all oldest individuals are accumulated.

Surface currents passively transport tuna larvae, then, young and adult tuna movements are driven using a habitat index. Advection and diffusion are proportional to the size of the fish and the advection term is proportional to the gradient of the adult habitat, while the diffusion decreases when the habitat index increases. If spawning seasonality is not considered, the adult habitat is represented by the feeding habitat. In the other case, the adult habitat switches from the feeding to the spawning habitat to reproduce change in migration patterns of mature fish during the spawning season. The feeding habitat index has been modified from the previous version to take into account the changes in the modeling of the forage components (see in following section). The natural mortality is allowed to vary spatially in a certain range around the mean coefficient-at-age in relation with the habitat index. The growth and length-weight relationships are obtained from independent studies.

Table 3-1General framework showing the relationships between the age-structured population of
predator (tuna) populations and their bio-physical environment

	Spawning	Larvae	Juvenile	Young	Adult
Time / age structure	tO	1 st month	2 nd and 3 rd month	2 nd quarter to age of 1 st maturity	1 st maturity to last quarter
Size	2 mm	2 mm -5 cm	5-15 cm	15 - > 40 cm	> 40 cm
Transport / movement (advection- diffusion)		Currents in	upper layer	 Proportional to fish size Random movement (Diffusion) decreasing with increasing habitat Directed movement (Advection) following increasing gradient impact of currents 	
Habitat factors	Predators (F) in the epi- (all largest adult tuna) in (F) in all spawn		T°, oxygen, Food (F) in all layers, spawning seasonality	
Natural mortality		Independent estimates + habitat-related variability			
Growth		Independent estimates			

* Not implemented. In the current version juvenile habitat is set to a constant value of 0.5, ie with no effect on natural mortality.

3.01 Movement

Large-scale tagging experiments of tuna have demonstrated that movements at population level can be represented by a mixing of both kinesis and taxis. Kinesis, described as diffusion, reproduces a behavior of random search toward a favorable habitat, e.g. preferred temperature

or patch of prey species, while taxis, described by advection, is a directed movement following environmental stimuli, e.g. increasing gradient of temperature, or increasing concentration of food, or a combination of both. For both types of movements, the distance of displacement per time unit is obviously directly dependent of the size of individuals (cohorts). Therefore, for a given size, the movement is linked to a Maximum Sustainable Speed (MSS) expressed in Body Length per second. MSS could be defined as the average speed that an individual can maintain for a long period of time (e.g., during a few days). In addition, we can expect that individuals will tend to stay longer in presence of favorable conditions (low diffusion) but want to escape quickly unfavorable habitat (high diffusion), so that diffusion values should be linked to habitat condition. Finally there is an obvious trade-off between advection and diffusion. This is usually illustrated by the Peclet number, i.e. the ratio between advection and diffusion. However, Peclet number can help only when analyzing what is prevailing in movement (in what region), diffusion or advection, but not in estimating one or another, since we do not know this ratio *a priori*.

Nevertheless, we can define diffusion and advection according to a few realistic hypotheses. They are best illustrated with extreme conditions. For example, if the gradient is maximal, all individuals will tend to follow it, and then the population movement is dominated by advection with no or very low diffusion (statistically, there are always a few individuals that will not follow it). Conversely, in absence of gradient, the diffusion will dominate the population movement, and in particular, it will be maximal if in addition the habitat value is very low. These different cases are presented on the figure below.



Habitat = null (no gradient) All displacement is due to kinesis with individuals escaping at MSS in any straight direction. Population diffusion is maximal



Habitat = medium (medium gradient) Displacement is due to both kinesis and klinotaxis. Population diffusion and advection are medium





Habitat =low (high gradient) Displacement is mainly due to klinotaxis. Population diffusion is low and advection is high

Figure 3-2. Different cases of movements in changing habitat illustrating the link between individual movements and population density changes based on advection and diffusion.

In summary, while simulating population movement with advection-diffusion, it is necessary to reproduce the four extreme cases:

- 1- If habitat is null and there is no gradient: diffusion is maximum and there is no advection
- 2- If habitat is null and there is a maximum positive gradient: there is (almost) no diffusion and advection is maximum (positive sign)
- 3- If habitat is maximal and there is no gradient: there is (almost) no diffusion and no advection
- 4- If habitat is maximal and there is a maximum negative gradient: there is (almost) no diffusion and advection is maximum (negative sign)

Klinotaxis and Advection

Here we assume that MSS is reached for the maximal gradient G_{max} of the habitat distribution standardized between 0 and 1. The value of G_{max} is estimated first at the beginning of the simulation using a loop on a climatological series. G_{max} is defined as the average plus one standard deviation of all values of G calculated for this climatological series (and remaining values above this threshold are set to G_{max}). The klinotaxis coefficient X is given by equation (11), and the total advection (A) is the algebraic sum of movements due to currents and klinotaxis (12).

$$X = \frac{1}{G_{\text{max}}} \cdot MSS \cdot \frac{\text{time unit(s)}}{\text{Distance unit (m)}}$$
(11)

with G_{max} the maximum gradient of the standardized habitat, and total advection A_x (in the x direction) is:

$$A_x = \mathbf{u} + X. \ G_x \tag{12}$$

with u the zonal current and G_x the gradient of habitat index in the x direction (in the y direction, v, the meridional current, and G_y replace u and G_x).



Figure 3-3. Change in klinotaxis coefficient X (nautical miles day⁻¹) in relation with body size (FL) and Habitat gradient (with MSS = 1 BL.s⁻¹).

Kinesis and Diffusion

With the diffusion decreasing with habitat value, we need to find (i) what could be the maximal value of Diffusion when habitat is null, (ii) define a function describing the decrease of the diffusion coefficient for a given size of the fish, and (iii), verify that this definition agree with the extreme conditions that are listed above.

If we assume that fish are moving according to random walk in two-dimensional space (i.e. purely diffusively), then the diffusion coefficient D can be expressed in terms of mean square displacement of the individual from initial point over time of movement (see, for example, Okubo 1980, Turchin 1998), i.e. $D = R^2/4t$, where $R^2 = \langle x^2 + y^2 \rangle$ is average square displacement. Obviously, displacement is usually much shorter than fish path length, because it doesn't include all multiple turns and changes of direction, with the exception however, of the theoretical extreme case 1 above with null habitat and null gradient. This allows us to define maximal diffusion D_{max} . Presuming that $R^2 = (MSS \cdot FL)^2 \cdot t^2$, where FL is the body size (in m), MSS the Maximum Sustainable Speed (in body length.s-¹), and t the time step in the simulation (in s), we obtain maximal possible displacement and the diffusion coefficient is:

$$D_{\max} = \frac{1}{4} (MSS \cdot FL)^2 t \tag{13}$$

As said above the random movement should be linked to the habitat index that is standardized between 0-1. This is achieved using equation:

$$f(H_a) = \left(1 - \left[\frac{H_a}{\beta + H_a}\right]\right) \cdot \left(1 - \rho\right) \tag{14}$$

where H_a is the Habitat value, β a coefficient that defines the curvature of the function and the minimum asymptotic value, and ρ the ratio (in absolute value) between the gradient and the maximal gradient, to which corresponds a displacement at speed = MSS. However, since it is not possible to have zero diffusion with the numerical scheme used for the transport, a factor

0.9 is added. So finally, we have: $\rho = 0.9 \cdot \left| \frac{G}{G_{\text{max}}} \right|$.

The product of eq. (13) and (14) gives the value of diffusion D in relation to the body size, the habitat value and the gradient. We can verify that using this definition, the changes in diffusion with habitat and habitat gradient agree with extreme conditions as summarized in Table 3-2.

Ha	G	ρ	D	A
0	0	0	D _{max}	0
0	1/Δx	1	0	MSS
1	0	0	~ 0	0
1	-1/ Δx	1	0	MSS



 Table 3-2. Advection and diffusion terms in extreme conditions of habitat and habitat gradient.

Figure 3-4. Changes in diffusion according to habitat with $\beta = 0.1$.

3.02 Spawning Habitat

While the adult habitat index constrains the movement, a spawning habitat index (H_s) is used to constrain the recruitment to environmental conditions (Lehodey et al., 2003) and when spawning seasonality is considered, to drive the movement of mature fish during spawning period. The number of eggs released in each cell of the grid at a given time is the product of a constant number R_s and H_s , with the primary condition that adult fish, i.e. potentially mature, are present in this cell. After spawning, currents in the surface layer redistribute larvae during the first month, and a natural mortality coefficient is applied (cf section on natural mortality) before entering in the juvenile cohorts (cohorts of age 2 and 3 months). For a given cohort, the number of recruits entering into the exploited stock will depend of the total initial number of spawned eggs and the natural mortality coefficients applied spatially during the following time steps until the age of recruitment. Their spatial distribution will result of a combination of drift with the currents during the larval/juvenile phase with an increasing component (with size) of determined movements during young stages.

The spawning habitat is defined to represent three mechanisms that are assumed to control the survival of larvae and the subsequent recruitment:

- the changes in the spatial extension of the spawning temperature habitat;

- the coincidence of spawning with presence or absence (match/mismatch) of food for larvae (micro-zooplankton, that is approximated by primary production);
- the coincidence of spawning with presence or absence (match/mismatch) of predators of larvae (that are the forage organisms of adults).

A fourth mechanism is the redistribution by the oceanic circulation that can create retention of larvae in favourable areas (with lower natural mortality) or conversely move the larvae in unfavourable zones where the natural mortality will be higher (cf. section natural mortality).

Therefore, the spawning habitat function is given by eq. below.

$$H_{s} = \theta_{s} \cdot e^{\alpha \cdot \log\left[1 + \frac{P}{F_{l}}\right]}$$
(15)

with θ_s the spawning temperature function following a normal distribution N(T_s , σ_s) of standard deviation σ and optimal mean temperature T_s .

The primary production P is used as a proxy for the abundance of food for larvae, while the biomass of predator of larvae F_l is the sum of forage biomass in the epipelagic layer during the day and epi- and migrant-pelagic forage during the sunrise and sunset periods (practically a period of 2 hours is used).

$$F_l = (F_{epi} * DL) + ((F_{epi} + F_{mig}) * 2/24)$$
(16)

The amplitude of the match/mismatch effect between food and predator is proportional to a coefficient α , so that if $\alpha = 0$, only temperature has an effect on the spawning, while the match/mismatch effect between presence of food and predators exponentially increases relatively to the temperature effect with increasing α .

The spawning habitat index is standardised between 0 and 1 in dividing Hs by a maximum value Hs_{max} and setting remaining values above this value to 1. Hs_{max} is calculated using a climatological loop at the beginning of the simulation, and is defined as the average plus two standard deviations of all Hs values for this series, with the condition that they are in the temperature range of the species (based on upper layer temperature) defined by the optimum spawning temperature (θ_s) species +/- 2 σ_s .

3.03 Feeding habitat index H_f

To define the feeding habitat index of young and adult tuna, first, an accessibility coefficient (τ_n) is calculated for each forage component *n*, based on the constraints/affinities of the predator species for the physical conditions that characterize the water layer inhabited by the forage component.

Habitat functions for two critical parameters for tuna, temperature (θ_a) and dissolved oxygen content (O_a), are considered. The accessibility coefficient is the product of the indices obtained from these two functions (temperature and oxygen) for the layer considered.

$$\tau_n = I_{\theta_{a,n}} \times I_{O_{a,n}} \tag{17}$$

In the case of the migrant meso- and bathy-pelagic forage, it is necessary to calculate the mean temperature and oxygen based on the day length DL. For example, for the temperature, the index used in the accessibility coefficient for the meso-pelagic migrant component is:

$$I_{\theta_a} = \frac{\left[I_{\theta_{a1}} \times (24 - DL)\right] + \left[I_{\theta_{a2}} \times DL\right]}{24}$$
(18)

with $I_{\theta a_1}$ and $I_{\theta a_2}$ the indices from the temperature function calculated with the temperature in the upper and deep layer respectively.

The temperature function follows a normal distribution: $\theta_a = N(T_a, \sigma_a)$. All tuna species are known to spawn in warm waters (SST typically above 24°C), while their feeding habitat is covering a larger temperature range. Moreover, as they grow, their optimal temperatures decrease due to the development of the *rete mirabile* and higher accumulation of heat from larger body mass. Consequently, the optimal mean temperature T_a was linearly linked to the age by equation (19):

$$T_a = \frac{(T_{\min} - T_s)}{K} \cdot age + T_s \tag{19}$$

where T_{min} is the optimal mean temperature of the oldest cohort in the species population (Figure 3-5) and *K* the total number of cohorts of the species.

For the oxygen index I_O , a sigmoid function is used since only minimum values constrain the accessibility to the water layer associated to the forage component (Figure 3-5).

$$I_{O} = \frac{1}{\left[1 + e^{\left[b.(O-z)\right]}\right]}$$
(20)

where O is the dissolved oxygen value, z the oxygen value at $I_O = 0.5$ and b a curvature coefficient.

The feeding index for *n* forage (*F*) components is then:

$$H_f = \sum \left[\tau_n \frac{F_n}{F_{\text{max}}} \right] \tag{21}$$

 F_{max} being used for standardizing *F* between 0 and 1 (remaining values above 1 are set to 1). F_{max} is calculated for each species using a climatological loop at the beginning of the simulation, and is defined as the average plus two standard deviations of all *F* values for this series, with the condition that they are in the temperature range of the species defined by the optimum adult temperature (θ_a) of the oldest age class +/- $2\sigma_a$.



Figure 3-5. Left: change in temperature function with age from age 0 (spawning) to maximum age (with $T_s = 30^{\circ}$ C and $T_{min} = 20^{\circ}$ C); right: habitat function for the oxygen (with z = 2; b = -4).

3.04 Spawning seasonality

Typical tropical tuna species like skipjack and yellowfin are thought to spawn opportunistically in warm waters, and do not show clear spawning seasonality. With increasing affinities for colder waters and longer life span, in relation also with the extension of the feeding habitat to the temperate regions, tuna species appear to develop such seasonality, lightly marked for bigeye, more evident for albacore and fully obvious for the temperate bluefin tuna. Also, with the increasing seasonal effect, the spawning grounds seem becoming more limited in space (and time by definition). This is a good illustration of an evolutionary history between r- and K- strategies. In an r-situation, organisms invest in quick reproduction, in a K-situation they will rather invest in prolonged development and long life. Usually r-selection corresponds to an adaptation to a risky environment and K-selection to a more predictable (sure) environment. While seasonality is the strongest and "predictable" climate variability that affects bluefin tuna in temperate regions, it is the interannual and less predictable ENSO signal that controls the environmental variability in the western and central equatorial regions that is the core habitat of skipjack tuna. The seasonal cycle of reproduction and its associated maturation process can be easily believed under the control of strong seasonal factors, e.g. changes in temperature and light (day length), while the seasonal spawning grounds result from natural selection and evolution in the species life history under the constrain of environmental variability.

Trying to reproduce the seasonal effect on tuna species with colder temperature affinities, a seasonal signal is included, based on the following assumptions:

- (i) With the seasonal spawning period becoming closer in time, adult tuna tend to direct their movements to find a place with the same environmental conditions than those occurring during their birth.
- (ii) These conditions are defined by the spawning habitat index H_s .
- (iii) The seasonal effect is controlled by the cycle of day length (both in time and intensity, i.e. increasing with latitude).
- (iv) The triggering effect for switching from the feeding habitat to the spawning habitat is linked to a threshold in the increasing day of length (positive gradient).

Thus, using a function based on the day length, it is easy to change the directed movement according to either the feeding or the spawning habitat index. This switch will occur earlier for (mature) fish that are in higher latitudes, and then far from their spawning grounds in warm waters (Figure 3-6). In low latitudes, the gradient of day length is too low to have any effect and the habitat adult will remain driven by feeding habitat.

Since feeding and spawning habitats have opposite characteristics (high forage biomass and relatively low temperature for feeding, but low forage biomass (i.e. larvae predators) and high temperature for spawning), predicted movement of fish feeding in high latitudes can show drastic changes at the time of spawning migration; a behaviour that has been effectively observed for bluefin tuna or birds tracked with electronic tags.



Figure 3-6. Example of seasonal cycles in gradient of day length at different latitudes in the North hemisphere. With a threshold set above 0.02 hours per day, the adult habitat that constrains the movement of fish will switch from feeding habitat to spawning habitat at the end of December for mature fish at latitude 60°, and one month later at latitude 30°. Movement of fish at latitude below 20° remain always driven by the feeding habitat.

3.05 Natural Mortality

Natural mortality is described as the sum of two main causes. The mortality occurring during the juvenile and young phases (M_p) that is mainly due to starvation and predation, and the natural mortality associated to senescence and diseases in the adult phase (M_s) . These two sources are represented by equations 24 and 25, the sum of which gives the mean natural mortality-at-age, and illustrated on the Figure 3-7. The parameterization is defined to obtain coefficients of natural mortality-at-age in agreement with those estimated statistically with MULTIFAN-CL (Fournier et al. 1998; Hampton and Fournier 2001) and to have coherent parameters between species. For example, trends in natural mortality in early life stages are expected similar, although absolute values can decrease from skipjack to yellowfin and from yellowfin to bigeye in respect with their increasing life span associated to a more developed K- strategy (i.e., selection of better spawning time and spawning ground allowing a lower larvae mortality).

$$\overline{M}_{p_{age}} = M_{p_{max}} \cdot e^{\left(-k_1 \cdot age\right)}$$
(22)

$$\overline{M}_{s_{age}} = \frac{M_{s_{max}}}{1 + e^{(k_2 \cdot [age - k_3])}}$$
(23)



Figure 3-7. Natural mortality of skipjack, yellowfin and bigeye tuna species defined in the model (thick curves) and compared to estimates from MULTIFAN-CL (dotted curves).

In addition, the natural mortality-at-age coefficients obtained from eq. (24) and (25) are expressed in terms of the habitat (eq. 26); increasing for habitat values below 0.5 and decreasing for values above 0.5 (Figure 3-8). The parameter ε gives the range of variability, the natural mortality-at-age coefficient remaining constant for ε = zero. The habitat index used is the spawning habitat for the first age class, the juvenile habitat for second and third monthly age class and the adult habitat for the older age classes.

$$M_{age} = M_{\max} \cdot e^{\left(\delta \cdot H_a\right)} \tag{24}$$

th
$$M_{\text{max}} = \overline{M}_{age} + (\overline{M}_{age} \cdot \varepsilon)$$
 and $\delta = 2 \cdot \ln \frac{M_{age}}{M_{\text{max}}}$

with





3.06 Growth

There is one length and one weight coefficient by cohort.

3.07 Running a habitat simulation

Before running a simulation coupling forage and predator dynamics, it is possible (and recommended) to run habitat simulation(s) producing the adult and spawning habitat as defined in the parameter file, either for a fixed age (in quarter), or with a growing age to see the evolution of habitat of a given cohort. It is necessary to add the section 4 to the parameter file.

Section 4 of the parameter file (predator species)

Section 4 of the parameter file includes all parameters required for the species dynamics as described in the present chapter. Following the previous 3 sections of the file, this fourth set of parameters has the following structure (in red, the parameters to estimate):

Nb_species /DATA_PATH/Omean_layer1.dym ... /DATA_PATH/Omean_layern.dym /DATA_PATH/mcl-Omean_layer1.dym ... /DATA_PATH/mcl-Omean_layern.dym

Name_sp
seasonality
Tau_s
sigma_s
alpha
Rs
Tau_a
sigma_a
Oxy_half
Oxy_slope
MSS
beta_diff
unit_age_class_jv
nb_age_class_jv
juv_length[0]juv_length[n]
juv_weight[0]juv_weight[n]
unit_age_class_ad
nb_age_class_ad
ad_length[0]ad_length[n]
ad_weight[0]ad_weight[n]
Mp_mean_max Mp_mean_exp Ms_mean_max Ms_mean_slop Ms_mean_half
M_epsilon
age_autonomous
age_mature
age_recruit

Notes:

Nb_species is the number of predator species.

/DATA_PATH/.../ are the path to files for oxygen distribution in the different layers. Name_sp is the name or code for the predator species.

Seasonality is a Boolean to indicate if seasonality is considered (1) or not (0).

Tau_s and sigma_s are mean and standard error of the spawning temperature function.

Alpha is the exponential coefficient of the spawning function.

Rs is the scaling factor in the spawning function.

Tau_a and sigma_a are mean and standard error of the feeding temperature function.

Oxy_half and Oxy_slope are coefficients of the oxygen sigmoid function.

MSS is the maximum sustainable speed (in body length per second).

beta_diff is the coefficient of the decreasing diffusion function.

unit_age_class_jv is the time unit in day of the juvenile age classes and nb_age_class_jv the number of classes.

juv_length[0].....juv_length[n] and juv_weight[0].....juv_weight[n] are length and weight coefficients by age class.

unit_age_class_ad is the time unit in day of the young and adult age classes and

nb_age_class_ad is the number of age classes.

 $ad_length[0]....ad_length[n]$ and $ad_weight[0]....ad_weight[n]$ are length and weight coefficients by age class.

Mp_mean_max, Mp_mean_exp, Ms_mean_max, Ms_mean_slop, Ms_mean_half are coefficient of natural mortality functions

M_epsilon is the coefficient to scale the range of variability of natural mortality in relation to time-space variability of habitat
age_autonomous is age at which fish movement starts to be driven by the adult habitat; 0 being the first age class after the juvenile phase. age_mature is age at first maturity. age_recruit is age at recruitment.

Ex. Section 4 of the parameter file for skipjack tuna

1 z:\data\oxy10deg\oxyml200m-ext.dym z:\data\oxy10deg\oxym1500m-ext.dym z:\data\oxy10deg\oxym11000m-ext.dym z:\data\oxy10deg\Levitusqcl-1deg-oxyml200m-ext.dym z:\data\oxy10deg\Levitusqcl-1deg-oxyml500m-ext.dym z:\data\oxy10deg\Levitusqcl-1deg-oxyml1000m-ext.dym skj 1 29 3.0 1.5 2000 26 3 2.5 -4 1.0 0.1 30 3 3.333 10.00 16.667 0.034 0.103 0.172 90 15 26.08 40.10 46.09 52.15 57.60 63.73 67.53 70.58 73.03 74.99 76.57 77.84 78.86 79.68 80.33 0.330 1.271 1.977 2.929 4.024 5.557 6.688 7.703 8.592 9.354 9.998 10.537 10.984 11.351 11.652 0.300 0.050 0.167 -0.267 30 0.5 0 2 1

The menu will ask to enter the parameter file and then the path to the folder where are the forage production and biomass files, including both full time series <dym> files and the corresponding monthly climatologies, that can be easily created using tools "Create Climatology" and "Monthly Average" if needed.

Chapter 4.

Forage-Predators Coupling

Given that there are several forage components, it was necessary to revise the approach used for coupling the forage mortality to the density of predators that was initially described in Lehodey (2001). In the previous version, the forage mortality was linked to the tuna density by applying first a specific local mortality ω resulting from the food requirements of tuna population described in the model, then a mean residual mortality λ' which is the difference between the total mortality λ and the mean specific mortality ϖ over the area occupied by tuna. Therefore, the total forage biomass over the whole area remains equal to the total forage biomass calculated in the case of a constant λ , but the spatial distribution linking the density of tuna may be different (see previous reference). This approach is useful as it is possible to have from zero to all potential predators species explicitly described in the model. As a counterpart, this is based on the assumption that the predators present an 'ideal free distribution', such that the total forage mortality by these species would be the same everywhere and equal to λ . This assumption does not appear unrealistic when considering both the horizontal and vertical distribution of the main tuna species together with those of other large oceanic predators (e.g. Fig. 2-3).

It is possible to use the same approach with several forage components, at the condition of defining for each predator species the forage required from each component. This is done using the accessibility coefficient τ_n defined in eq. (17). The ratio of forage of a given component that contributes to the total food ration is:

$$\gamma_n = \frac{\tau_n}{\sum \tau_n} \tag{25}$$

then, the forage required from the component *n* by the tuna species (F_{Rn}) is calculated by knowing a daily food ration *r* relative to its weight-at-age *w* and the ratio γ_n obtained from eq. (25). The specific mortality rate is defined as the ratio of the forage biomass requirement (F_{Rn}) for the species to the forage biomass available F_n (eq. 27):

$$F_{Rn} = \sum_{age,i,j} \left(N_{age,i,j} \cdot w_{age} \cdot r_{age} \cdot \gamma_{n_{age}} \right)$$
(26)

and the local specific mortality ω_n on the forage component *n* is the ratio between the forage required and the forage available, calculated for each age class in each cell of indices *i* and *j*.

The mean specific mortality over the whole area occupied by the predator species is:

$$\overline{\omega}_n = \frac{\sum F_{Rn}}{\sum F_n} \tag{27}$$

Section 5 of the parameter file (forage-predator coupling)

Section 5 of the parameter file is really simple! There is only one parameter for each predator species that is the mean daily ration of food relatively to individual weight. If better knowledge of change in food ration according to age/size were available, we could however introduce such details here, after a few changes in the code.

Also, it is worth to note that putting this parameter equal to zero is equivalent to run uncoupled simulation. This can be interesting to test the difference, and the impact of forage mortality due to one predator species.

Food_ration

 $\underline{Ex.}$ Section 5 of the parameter file for skipjack tuna, ie., we consider that skipjack tuna daily ration is in average 8% of their body mass.

0.08

Running a SEAPODYM coupled simulation

Once the parameter file is ready and the forage production files created, it is possible to run simulation coupling both forage and predator dynamics by choosing <coupled> in the menu simulation. The menu will ask to enter the path to the parameter file and then the path to the directory where are the forage production files.

Before starting the simulation over the selected period of the time series, there are three preliminary steps (Fig. 4-1):

- 1- Habitat standardization.
- 2- Forage spin-up. Using climatological series of environmental data and forage production, the forage populations (biomass) are built up over a number of months corresponding to the maximum "mean age" of all the forage groups.
- 3- Predators spin-up. Also based on climatologies, the predator populations are built up over a number of months corresponding to the oldest age of the species that has the longest lifespan.

Then, the simulation switch on the "real" time-series of environmental data until the last date provided in the parameter file. If the value of the parameter "Fcst" in the parameter file is >0, the simulation continues and records the forecast based on the climatologies.

An example of parameter file for multi-species simulation is given in Annex 3. Predictions are recorded in dym files (cf Annex 2). The text file <sumdym.txt> records values at each time steps of total production and biomass of each forage component, the biomass in the predator area, the biomass required by the species, and the corresponding mean specific mortality (eq. 27).



Figure 4-1. Chronology of a simulation in SEAPODYM

Chapter 5.

Fisheries

For each fishery, the actual fishing effort is used to predict catch of tuna species by cell, time step and by age class of species. When fishing data are at a lower resolution than the resolution used for the simulation, the fishing effort is redistributed proportionally to the surface of the cells. The fishing mortality, for a given cell and at a given time step, is proportional to the sum of fishing efforts in the cell, the catchability coefficients of the corresponding fisheries and the selectivity coefficients for the gear and age (size) considered. The fishing mortality (f), added to the natural mortality (M), gives the total mortality rate (Z).

Fishing data files provide observed fishing effort by time step and geographical position and the associated catch of one or several species. The format used is a binary format to allow a faster access for reading data during simulation. A special tool can be use to convert a file of the form of text column into this special format using the extension ".bin" (c.f. format in annex I).

5.01 Catchability and predicted catch

Each fishery has a single catchability coefficient by species that is scaled to obtain an average level of predicted catch close to the level of observed catch for the time series of the simulation. Catchability coefficients are corrected to the surface of the cell. Since this coefficient is constant it is recommended to define homogeneous fisheries. A first obvious criterion for example is the fishing gear, but it may be also necessary to consider some large spatial-scale stratification, different fishing strategies, or different periods of time associated to large changes in the fishing strategy or gear technology.

Time series of total catch by species and by fishery is recorder in a text file called <sumdym.txt> (cf Annex 2). Another text file, <species_Spatial_Corr.txt>, records the correlation for each time step and fishery of spatially disaggregated catch, with the number of observations and the probability that the correlation is not significative. These records allow evaluating the simulation by comparison of observed and predicted total monthly catch and spatial distribution of catch for each fishery.



Figure 5.1. Example of plots for one fishery directly produced from the generated file <sumdym.txt>. Comparisons between observed (black curve) and predicted (red curve) total catch and CPUE.



Figure 5.2. Example of plot for one fishery directly produced from the generated file <species_Spatial_Corr.txt >. Spatial correlation coefficients between observed and predicted catch (crosses) with a 12-month moving average (curve) and the corresponding number of observations (bars)

The parameter "type_fishery" is a number (enter) that is used to aggregate predicted catch through fisheries that have the same code and to produce dym files of spatial distribution of this catch. The result can be visualized using the SeapodymView software as illustrated on Fig 5.3. Similarly the observed catch can be superimposed using original fishing data text files.



.....

Figure 5-3. Example of spatial distribution of predicted biomass of one tuna species (skipjack) with observed catch superimposed as proportional circles, produced with the software SeapodymView

5.02 Selectivity and predicted length frequencies

In addition to its catchability coefficient, a fishery is characterized by an age (length)-based selectivity function. The selectivity coefficients are adjusted to obtain predicted length frequency distribution of catch in agreement with observation. Fishing effort of each fleet varies according to the time step and spatial resolution used in the simulation. To check that selectivity is well defined for predicting observed catch length frequencies, two text files are generated. The file <species_LF_Q_sum.txt> provides the sum of catch of a given species by length for each fishery and for each quarter, aggregated over all years of the fisheries. The file <species_LF_Q_fishery.txt> provides the same records but disaggregated by year.



Figure 5-3. Example of selectivity function for one fishery (left) and the corresponding distribution of length frequencies (right) of predicted (black curve) and observed (histogram) catch, as produced from the file <species_LF_Q_sum.txt>.

Section 6 of the parameter file (fisheries)

To run a simulation with fisheries, the section 6 needs to be added to the parameter file

nb fisheries code fishery[0] code fishery[n] ... type fishery[0] type_fishery[n] ... /DATA_PATH/fishery_file[0] /DATA PATH/fishery file[n] N_fishery_species code_fishery1 code_fisheryN nb_sp_fishery1nb_sp_fisheryN code_sp1 code spN code_sp1 code spN catchability_coeff[0] ... catchability_coeff[n] selectivity_age_species[age] ... selectivity_age_species[age_max]

Notes:

nb_fisheries is the total number of fisheries

code_fishery is the code name of the fishery

type_fishery is the type of the fishery that can be used to aggregate spatial prediction of catch (e.g. all purse seine fisheries together, all pole and line, all longline,...)

/DATA_PATH/fishery_file is the path to the fishery file (format bin)

N_fishery_species is the number of fisheries by species

nb_sp_fisheryN is the number of species in the fishery file N

code_sp1.. code_spN is the list of code names of species corresponding to the species in a given fishery file

catchability_coeff are catchability of fishery for a given species

selectivity_age_species are selectivity-at-age coefficients for a given species and fishery.

Ex: Single species (skipjack, 16 quarterly age classes) simulation with 9 fisheries.

9 PLSUB PLTRO WPSASS WPSUNA EPSASS EPSUNA RINGNET ARTSURF COMMHL 2 2 2 3 3 2 3 1 1 z:\data\Fisheries\PLSUB.bin z:\data\Fisheries\PLTRO.bin z:\data\Fisheries\WPSASS.bin z:\data\Fisheries\WPSUNA.bin z:\data\Fisheries\EPSASS.bin z:\data\Fisheries\EPSUNA.bin z:\data\Fisheries\RINGNET.bin z:\data\Fisheries\ARTSURF.bin z:\data\Fisheries\COMMHL.bin 9 PLSUB PLTRO WPSASS WPSUNA EPSASS EPSUNA RINGNET ARTSURF COMMHL 4 3 3 3 3 3 3 4 4 alb skj yft bet skj yft bet alb

```
yft
           bet
skj
     yft
           bet
skj
     yft
           bet
skj
     yft
           bet
ski
skj
     yft
           bet
skj
     yft
           bet
                  alb
skj
     yft
           bet
0.077 0.013 0.028 0.060 0.019 0.036 0.0103 0.0055 0.000008
0
  0.001 0.01 0.1 0.5 0.8 0.95 1 1 1 1 1 1 1 1 1
0 0.001 0.01 0.1 0.5 0.8 0.95 1 1 1 1 1 1 1 1 1
0 0 0.01 0.3 0.6 0.8 0.95 1 1 1 1 1 1 1 1 1
0 0 0.01 0.05 0.3 0.6 0.8 0.95 1 1 1 1 1 1 1 1
 0 0.1 0.5 0.7 0.85 0.95 1 1 1 1 1 1 1 1 1
0
                                          1
                                            1
0
 0 0.01 0.1 0.4 0.6 0.8 0.95 1 1 1 1 1
                                        1
 0.002 0.02 0.2 0.5 0.8 0.95 1 1 1 1 1 1
                                            1 1
0
                                          1
0 0.002 0.02 0.2 0.5 0.8 0.95 1 1 1 1 1 1 1
                                            1 1
0 0 0.002 0.02 0.2 0.5 0.8 0.95 1 1 1 1 1 1 1 1
```

5.03 Aggregating predicted catch by regions

Section 7 of the parameter file

Section 7 is the last one of the parameter file. It includes coordinates of rectangular areas for which values of biomass of larvae, juvenile, young, recruit, adult and sum of young and adults of the predator species of the simulation are aggregated by time step. Another possibility to aggregate predicted biomasses is through the use of a mask with the zones identified by different numbers (enters). The file mask is a text file identical to the mask used for section 2. The path to this file is provided after the number of zones (Nb_zone) and before the list of numbers identifying these zones. While different rectangular areas can be used for different species, the zones are used for all species. An example of use is the definition of Exclusive Economic Zones (Fig. 5-4). Aggregated estimates of biomass are recorded in the text file <SumArea.txt>.

```
Nb_area
area1 minlong maxlong minlat maxlat
...
areaN minlong maxlong minlat maxlat
Narea_species1
area1 ... areaN
Nb_zone
/DATA_PATH/mask_zones.txt
Zone1
....
ZoneN
```

Note:

Nb_area is the number of rectangular areas.

area1 is the code (enter) of the area followed by the coordinates, minimum and maximum longitudes and latitudes (latitude south is negative; longitude west is negative or >180).

Narea_species1 is the number of areas used for the first species.

area1...areaN is the list of the code for a given species.

Nb_zone is the number of zones, followed by the path to the file and the list of numbers identifying these zones.

If only zones are used, it is necessary to put 0 for Nb_area and then skip to Nb_zone. This section can be used even when there is no fisheries. In that case, it is necessary to put 0 for the parameter Nb_fisheries of section 6 before skipping to this section 7.

<u>Ex.</u> Section 7 of the parameter file for two species, with 7 rectangular areas, 4 being used for the first species and 5 for the second and 3 zones corresponding to EEZs as identified in the text file "mask_EEZ_1deg.txt" (Fig. 5-4).

7					
1	120.5	140.5	25.5	35.5	
2	140.5	165.5	25.5	45.5	
3	165.5	210.5	25.5	45.5	
4	115.5	210.5	15.5	25.5	
5	115.5	165.5	-20.5	15.5	
6	165.5	210.5	-20.5	15.5	
7	210.5	280.5	-20.5	25.5	
4	5				
1	2	3	4		
1	2	5	6	7	
3					
c:\seapodym\param\mask_EEZ_1deg.txt					
16	36	42		C	



Figure 5-4. Example of file mask at spatial resolution of 1 degree square used for defining Pacific Islands EEZs for which biomass can be aggregated.

Chapter 6.

Conclusion

Since its early development in 1995, this model has been continuously enhanced to provide a general framework allowing to integrate the knowledge on the biology and ecology of tuna species and to test hypotheses on the mechanisms that link behaviors and dynamics of these species to the environmental and climate variability. Obviously the model will continue to evolve in the coming years, and hopefully will become more and more realistic in its predictions. The implementation of an optimization function for a statistical estimation of the parameters is now a priority and this approach is already explored. Though the spatial context makes this development a difficult task, it is worth to note that this model is strongly constrained by the environment and the mathematical description of the relationships between tuna and this environment. Consequently, there are a limited number of parameters that would need to be considered in the optimization process.

In parallel with the improvement of the model, there are already several fields of applications that can be explored to assist management decisions, particularly thanks to the spatial approach and the multi-species multi-fisheries structure. The model can be used to test interactions between fisheries and the impacts of management options on the different species. Biomass of tuna can be calculated by EEZ for discussions at National level, and conservation measures can be tested, for example, the potential impacts and relevance of no-fishing areas on tuna stocks and fisheries.

Finally, some important by-catch (e.g., marine turtles, sea birds) and associated species (e.g., billfish, blue shark) could be included in the model with the same approach used for tuna or by coupling (online or off-line) to an IBM model.

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Annex 1. Files formats

Format dym

Binary format (IEEE float) with a Header as follow:

IdFormat	(Character, identification of the version of dym format)
IdFunc	(Integer, identification of the function used for grid stretching)
MinVal	(float, minimum value of the data file)
MaxVal	(float, maximum value of the data file)
Nlong	(Integer, number of longitude points in the grid)
Nlat	(Integer, number of latitude points in the grid)
Ntime	(Integer, number of time steps in the series)
FirstDate	(decimal first date of the series, e.g., 1948.0416 for 15 Jan 1948)
LastDate	(decimal last date of the series, e.g., 1999.9584 for 15 Dec 1999)
Xlon[Nlat][Nlong]	(2D vector of floats with all longitude values)
Ylat[Nlat][Nlong]	(2D vector of floats with all latitude values)
Zlevel[Nlevel]	(vector of floats with all level values, i.e. dates)
Mask[Nlat][Nlong]	(2D vector with mask values: 0=land, 1= 1 layer, 2=2 layers, 3)

To skip the header for reading the data directly the number of bytes (4 bytes per number) to skip is: nbytetoskip = $[9 + 3 \times (Nlong + Nlat) + Nlevel] \times 4$

To access the first value of the matrix n, the number of bytes (4 bytes per number) to skip is: $nbytetoskip = [9 + 3(Nlong + Nlat) + Nlevel + (Nlong Nlat(n-1))]^4$



Format bin

Binary format for observed fishing data. One file by fishery

Header:

yydeb	(first	year :	in the	e ser	ries)				
mmdeb	(first	(first month in the series)							
yyfin	(last [.]	year in	ı the	seri	les)				
mmfin	(last	month :	in the	e ser	ries)				
nbsp	(numbe	r of sp	pecies	S)					
filereso	(spati	al reso	olutio	on ir	ı deg s	square)		
yysp[0] mms	ɔ[0]	(first	year	and	first	month	for	the	first species)
									2 nd species)
			-						-
yysp[n] mms	p[n]	(first	year	and	first	month	for	the	last species)

Then data are sorted by column:

Year	Month	Lond	Latd	Fishing	Catch	Catch	 Catch
				effort	1 st	2 nd	last
					species	species	species

Note: latitudes south are negative, and longitudes east of 180 can be either negative or ${\sf>}180$

Example:

2001 4 5 1986 1982	2 11 7 2 2 2							
	2 2 2 3	-22.5 -17.5 -17.5 -22.5	182.5 187.5	131.63 32.37 475.74 557.82	0 0 0 0	0.162 11.06	0.216 0 1.187 1.349	0.108 2.518

Annex 2. Output Files

After a **forage simulation**, the following files of spatial distributions are saved:

File Name	Description	Unit
For each forage component:		
Fprod_name-forage.dym	Production of forage	g of wet weight. m ⁻² . time step ⁻¹
Fbiom_name-forage.dym	Biomass of forage	g of wet weight. m ⁻²

They are at format dym and can be viewed using SeapodymView software that provides tools to extract data or create time series in sub-regions.

A text file is also produced where sums by time steps are aggregated:

File Name	Description	Unit
	Sum of Primary Production over all the	origin unit
SumDum tut	surface of the grid	
	Sum of production for each forage	metric tonnes of wet weight per
SumDym.txt	component over all the surface of the grid	time step unit
	Sum of biomass for each forage component	
	over all the surface of the grid	metric tonnes of wet weight

After a **coupled simulation**, only forage biomass <dym> files are recorded with in addition the following files of spatial distributions:

File Name	Description	Unit
For each forage component:		
Fbiom_code-forage.dym	Biomass of forage	g WW. m ⁻²
For each species:		
sp_larve.dym	Biomass of larvae (from age 0 to one month)	
sp_juvnl.dym	Biomass of juveniles (from age 1 month to 3 month)	-2
sp_ young.dym	Biomass of young (from age 2 quarter to age mature)	mg WW. m ⁻² or kg WW. km ⁻²
sp_ recru.dym	Biomass at age of recruitment	Kg W W. KIII
sp_ adult.dym	Biomass of adults (from age mature to age max)	
sp_totbm.dym	Total biomass (from age 2 quarter to age max)	
For each fishery type:		
sp_Cpred_typeX.dym	The total catch predicted for all fisheries of type	t. cell ⁻¹
	X, the type of fishery being defined in the	
	parameter file. There are one file per type	
	defined	

They are at format dym and can be viewed using SeapodymView software that provides tools to extract data or create time series in sub-regions.

Text files are also produced where sums by time steps are aggregated:

SumDym.txt	 Sums of Primary Production over all the surface of the grid 	origin unit
	 Sums of production for each forage component over all the surface of the grid 	t WW . time step ⁻¹
	 Sums of biomass for each forage component over all the surface of the grid 	t WW
	 Sums of biomass of juvenile, young, adult and total population by species over all the surface of the grid 	t WW
	 Total fishing effort by fishery 	origin unit
	 Total observed catch by fishery and by species 	origin unit
	 Total predicted catch by fishery and by species 	t WW
SumArea.txt	Sum of biomass by time step by region, and/or zone	t WW
	if required, for larvae, juvenile, young, recruit, adult	
	and total population	
Sp_spatial_Corr.txt	Number of observation, r-correlation coefficient, and associated probability for the spatially-	
	disaggregated predicted and observed catch by time	
	step.	
Sp_LF_Qsum.txt	Length Frequency of catch by fishery and by	1000x fish
-	quarter (see format below)	
sp_LF_Qfishery.txt	Length Frequency of catch by fishery and by quarter and by year (see format below)	1000x fish

The **length frequency files** (one by species) provide frequency of catch by length for each fishery. If a number of regions have been defined the frequency is given by fishery and region.

Format:

