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A Spatial Ecosystem And Populations Dynamics Model (SEAPODYM) for tuna and associated oceanic top-predator species: Part I – Lower and intermediate trophic components

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A Spatial Ecosystem And Populations Dynamics Model (SEAPODYM) for tuna and associated oceanic top-predator species:

Part I – Lower and intermediate trophic components

Introduction

The Spatial Ecosystem And Populations Dynamics Model (SEAPODYM) is an improved version of SEPODYM that was developped at the Oceanic Fisheries Programme since 1995 and presented in previous SCTB meetings. A first major change in this new version is the introduction of several forage components to account for different behaviour of tuna species. This is described in this first part after a review of the previous developments in the modelling of tuna forage organisms. With these changes, it was also necessary to reconsider the approach to link the dynamics of the predators (tuna) to these different prey populations. Several other changes have been introduced; in particular, the possibility to have a seasonal behaviour for the reproduction. This is presented in part II with the results of a first application to skipjack and yellowfin tuna.

Epi- and mesopelagic forage

The forage of tuna and other oceanic top predators consists 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. Smaller zooplankton (micro- and mesozooplankton) is drifting horizontally with the currents, but can migrate vertically at relatively high speeds and show daily migration driven by light intensity. One important benefit of this evolutionary adaptation is likely a decrease of the predation pressure in the deeper layer during daytime. However, most of the mesozooplankton biomass remains permanently in the upper 200 m layer in the tropical ocean, at the difference of temperate regions where zooplankton migrate seasonally below 200m during the winter season. Forage species have also optimized their behaviour under the same constraints, i.e. finding food and avoiding predators, so that vertical distributions and migrations are finally structuring all the pelagic foodweb. Therefore, according to Legand (1972), and Grandperrin (1975), about 90% of the biomass of macroplankton and micronekton (that is roughly equivalent to 25% of the mesozooplancton biomass) is typically concentrated in the 0-500m upper layer during the night and 50% in the 0-100m, but only 10% would remain in the first 200 m during the day.

It seems therefore appropriate to classify the micronekton (forage) components based on their vertical distributions that control their relationships with (and accessibility to) top predators. Based on several seminal works by King and Iversen (1962), Vinogradov (1981), Legand (1972), Granperrin (1975), Roger (1971), 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. All these 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 (Fig. 1). 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.

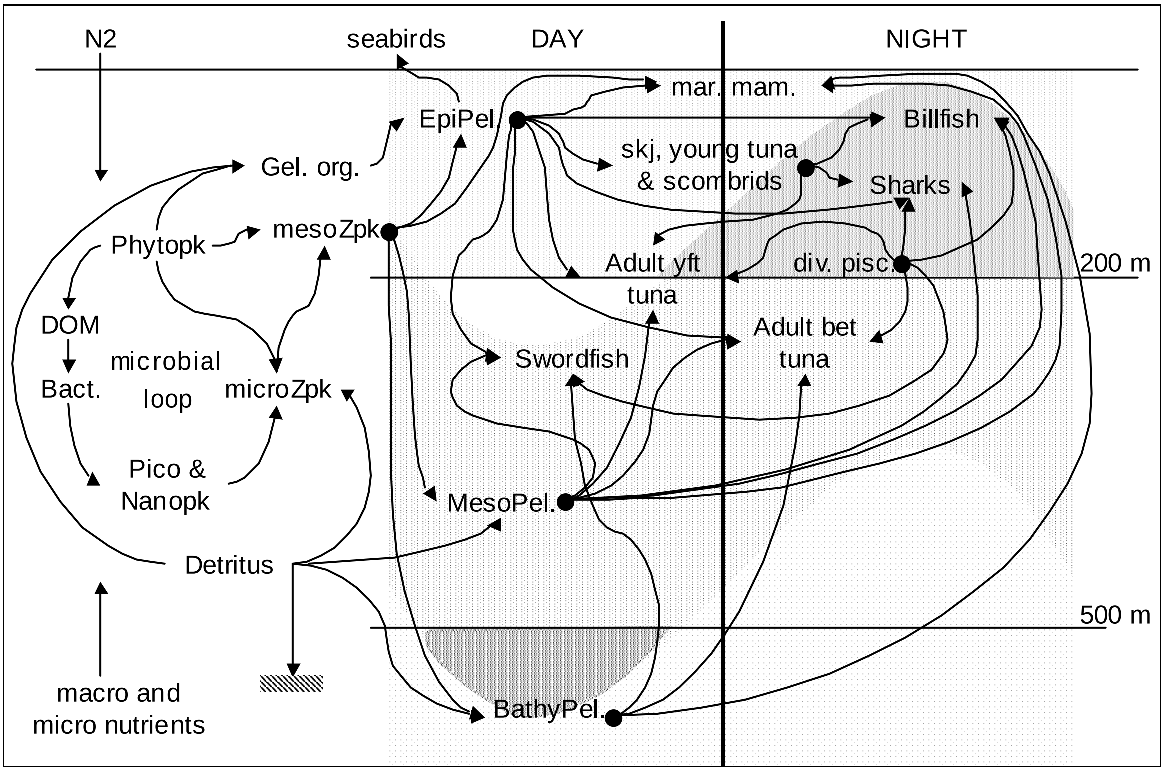

Figure 1. A top to bottom schematic view of the pelagic food web. Most of the organisms in the meso- and deep- pelagic layers have nycthemeral migration patterns leading to higher concentration in the upper layer at night and in the deeper layer during the day. DOM, Dissolved Organic Mater; Bact., bacteria; 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

Crustaceans of epipelagic micronekton include small size (< 20 mm) euphausids (e.g., *Stylocheiron carinatum*, *Euphausia tenera*, *S. affine*), larvae of crabs, shrimps, and stomatopods and pelagic adults decapods. In particular, the pelagic phase of the red crab (*Pleurocondes planipes*) is very abundant in the Eastern Pacific and represents an important source of food for skipjack (Blackburn and Laurs 1972). Almost all amphipods of the family Phronimidae appear also concentrated in the epipelagic layer (Repelin, 1978). The main epipelagic planktivorous fish families are Engraulidae (anchovies), Clupeidae (herrings, sardines), Exocœtidae (flyingfish), and small Carangidae (scads), but an important component also is represented by all juvenile stages of large-size species (Bramidae, Coryphaenidae, Thunnidae, etc…). The oceanic anchovy (*Enchrasicholinus punctifer*) seems to be a key species in the epipelagic food chain in the warmpool as it is growing very quickly (mature after 3-5 months) and can become very abundant after episodic blooms of phytoplankton. Cephalopods encountered in the epipelagic layer are mainly at larval and juvenile stages or from the small-size squids of the family Onychoteuthidae (*Onychoteuthis banksi, Onychia spp*.). More generally, Legand et al. (1972) noted that there was a relationship between depth and age for the Cranchidae, young larvae being in the surface 0-50m, oldest larvae between 50 and 100m, post-larvae between 100 and 250 m, and adults in deeper layers.

The layer 200-500 m seems to be mostly a transition zone occupied during the day by relatively few permanent species like some euphausids (*Nematoscelis tenella, S. maximum, S abbreviatum, S longicorn*) and migrant species, e.g., *Phronima sedentaria* - one of the species in the Phronimidae that does not stay in the epipelagic layer at day - and the cephalopods of the family Enoploteuthidae, that move to the upper layer at nightime. Almost all meso- and bathypelagic fish appear to stay deeper during the day, ~90% of them belonging to the four families of Myctophidae (lanternfish), Gonostomatidae (bristlemouth, mainly *Cyclothone sp*.), Sternoptychidae (hatchetfish) and Phosichtyidae (lightfish, mainly *Vinciguerria nimbaria*). Many bathypelagic species (i.e., inhabiting the depth below 500m at least during daytime) migrate across this layer during sunset to reach the upper epipelagic layer, and during sunrise to move back in the deeper layer, while some other stay in this intermediate layer all the night. All possible patterns occurs (Fig. 2): (i) species moving to the surface layer, e.g., many euphausids (*E. diomedae, T. tricuspidata, T. aequalis, E. paragibba*), deep shrimps of the Sergestidae, and numerous fish of the families Myctophidae (*Ceratoscopelus warmingi, Diaphus elucens D. bracycephalus, D. lucidus, D. mollis, Notolychnus valdiviae Lobianchia gemellari*), Astronesthidae, Melanostomiatidae, Nemichthyidae, Idiacanthidae (*Idiacanthus sp*.), Melamphaeidae (*Melamphaes sp*.), and Gonostomatidae (*Vinciguerria nimbaria*), (ii) species migrating to the intermediate layer, e.g., euphausids (*N. microps, N. gracilis, T. pectinata, T. rnonacantha T. orientalis and N. flexipes*), deep shrimps of the Peneidae, fish of the families Melamphaidae (*Scopelogadus mizolepis*, *Scopelogadus sp*.), Myctophidae (*Lampanyctus niger*), Chauliodidae (*Chauliodus sloani*), Gonostomatidae (*Gonostoma atlanticum, G. elongatum*), Percichthyidae (*Howella sp*.), and Stomiatidae, and (iii) species dispersing in all the column between 0-500m (e.g., deep shrimps of the Caridae).

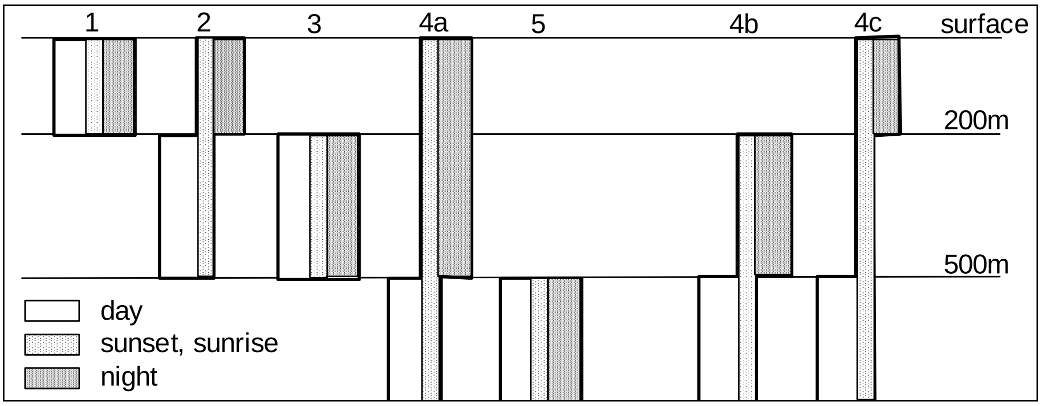

Figure 2. The different daily vertical distribution patterns of the micronekton in the tropical pelagic ecosystem. 1, epipelagic; 2, mesopelagic migrant; 3, mesopelagic non-migrant; 4, bathy-pelagic migrant; 5, bathypelagic non-migrant. Group 4 can be detailed into bathypelagic migrant into the surface layer (4c), intermediate layer (4b) or both (4a).

Finally, a part of the micronekton biomass remains permanently below 500 m. It is constituted by bathypelagic non-migrant species or very deep species that do not migrate above this limit. Here again, there are several species of euphausids (*Nematoscelis boopis, Thysanopoda cristata, Bentheuphausia amplyops*), and deep shrimps (Mysidaceae). Fish are represented by species of the families Gonostomatidae (genus *Cyclothone*: *C. alba* and *C. microdon*, *Margrethia obtusirostra*), Myctophidae (*Taaningichthys sp.*, *Diaphus anderseni*), Sternoptychidae (*Sternoptyx diaphana*), Trichiuridae (*Benthodesmus tenuis*), Scopelarchidae (*Scopelarchus guntheri*), and Maurolicidae (*Valenciennelus tripunctulatus*). Many species of cephalopods also inhabit this deep layer (Cranchidés, Chiroteuthidés, Mastigoteuthidés, Histioteuthidés, Enoploteuthidés) but they are difficult to sample with usual micronekton nets.

A simple forage population dynamic model

Oceanic top predators in the pelagic food web 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 (olfaction in sharks, vision in bigeye tuna, swordfish and cephalopods or echolocation in marine mammals), and morphological and physiological adaptations (e.g., rete mirabile) allow them also to exploit the dark and colder deeper layers. Interestingly, Dagorn *et al.* (2000) using computer simulations to predict different potential evolution of predators in a simplified (3 layers) pelagic system similar to what is described in Figure 2, showed that the five most frequent predicted vertical movement behaviours were remarkably similar to those observed in different apex predators (Fig. 3).

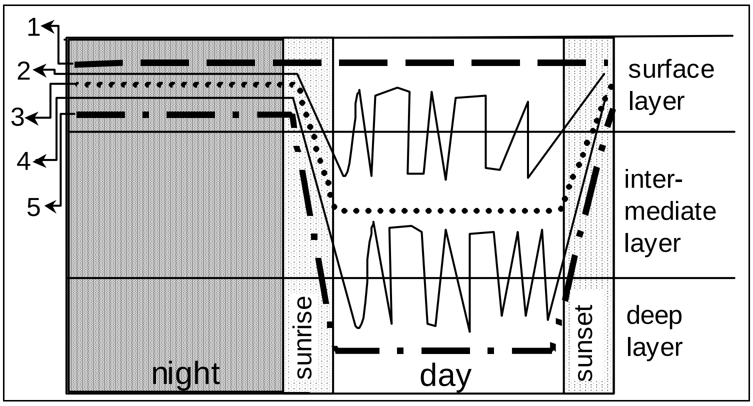

Figure 3. Five typical vertical movement behaviours simulated using a 3-layer and 2-type of prey pelagic system (adapted from Dagorn et al. 2000). 1, epipelagic predators (e.g., skipjack, marlins and sailfish); 2, predators moving between the surface and intermediate layers during the day (e.g., yellowfin 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). All predators move to the surface layer during the night.

Given the large spectrum of prey organisms of tuna and other top oceanic predators and the lack of information on their spatio-temporal dynamics, the tuna forage components are modeled as single populations composed of different species, using the same mathematics than in a single species population model, with constant and 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:

$$\frac{dF}{dt} = S - (.\ \ F) \qquad (1)$$

where *F* is the forage population (biomass), *S* is the recruitment (or source) and . 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 an ecological transfer coefficient (*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 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:

$$F(t) = \frac{S}{\cdot}\,(1 - e^{-\cdot\, t}) \tag{2}$$

Because of the constant coefficient . , 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/.). 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).

$$\cdot = \frac{F'}{F} \tag{3}$$

Therefore, in an equilibrium situation, the biomass *F* ~ S/. and the production *F'* = *S*.

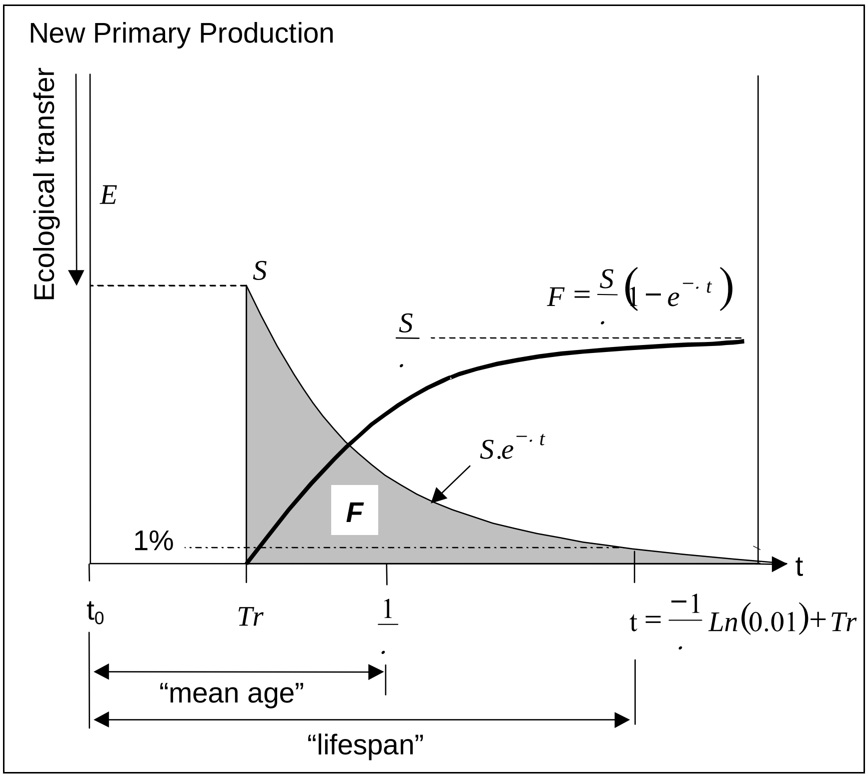

Figure 4. Transfer with time of primary production to forage according to the model (*S* is assumed constant). The thin curve describes the evolution in time of a single source of primary production. The thick curve gives the total forage population, i.e., the sum of the shaded area.
(redrawn from Lehodey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

$$\int_0^8 t.S_t\,dt = S\int_0^8 t\,e^{-.\;t}\,dt = \frac{S}{.^{2}} \qquad (4)$$

Since the forage population is *S/.* , the mean time spent in the forage population is $S/.^{2}$ divided by *S/.* , that is 1/. . Adding T_r to 1/. gives the mean age of the forage population (Fig. 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%, $t = - 1/. \; . \mathrm{Ln}(0.01) + T_r$). Therefore . and T_r which characterize *F* can be estimated using biological characteristics of key-species representative of the forage population.

Characterizing the forage heterogeneous population with . and T_r

Biological characteristics of the main tuna prey species or group of species can be found in the literature. In the tropical region, cephalopod species (Jackson and Choat 1992), size-at-age data suggests a rapid growth, with achievement of full size in less than 200 d. and short life span (less than one year). In the eastern tropical Pacific, a key prey species of skipjack appears to be the red crab (Galatheidae), *Pleuroncodes planipes* (Forsbergh 1980). Its larval phase is about 130 d. (five zoeal stages) and postlarval phase (2 to 6 mm) about 4 or 6 months, while the individuals reach sexual maturity (at ~ 16 mm) in about 1 year (Gomez-Gutierrez and Sanchez-Ortiz 1997). In the western tropical Pacific, schools of skipjack and yellowfin regularly feed on high concentrations of the zooplanktivore oceanic anchovy, *Encrasicholina punctifer* (Hida 1973), a species with a short life cycle (less than 1 year), a rapid growth and a maturity age of 3-4 months (Dalzell 1993). Regarding the euphausids that are also frequently found in skipjack stomach contents, their life span appears to be ~1 year (10 to 15 months) with sexual maturity reached at 8-10 months (Roger 1971).

Tuna also migrate seasonally in the subtropical areas (e.g. the Kuroshio extension or the southern subtropical convergence zone), or move close to coastal upwelling areas (e.g., California, Peru), where they can exploit the frontal zones with highly productive colder waters. Some tuna species (e.g. bigeye tuna) are also able to exploit deep forage species at depths below 300-400m. In these cases, forage species have different biological characteristics, typically older age at maturity and longer life span, in relation with lower ambient temperature. For example, compared to the tropical oceanic anchovy above, temperate anchovy species (SST ~15-22°C) have a much longer life span and turn-over rates. In the north west Pacific for example, the Japanese anchovy *Engraulis japonicas* has a life span of ~3 years and mature at ~1 year (Whitehead et al., 1988). Anchovies in the upwelling systems of Peru and Chili have similar biological characteristics. Indeed, 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 macroecological principles into account requires linking the two parameters T_r and . that characterize *F* with ambiant water temperature. This is done using a simple decreasing exponential function (eq. 5) as illustrated on Figure 5.

$$1/. \ = A\ e^{(-0.1\ \ Tc)} \qquad (5a)$$

$$T_r \ = B\ e^{(-0.1\ \ Tc)} \qquad (5b)$$

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

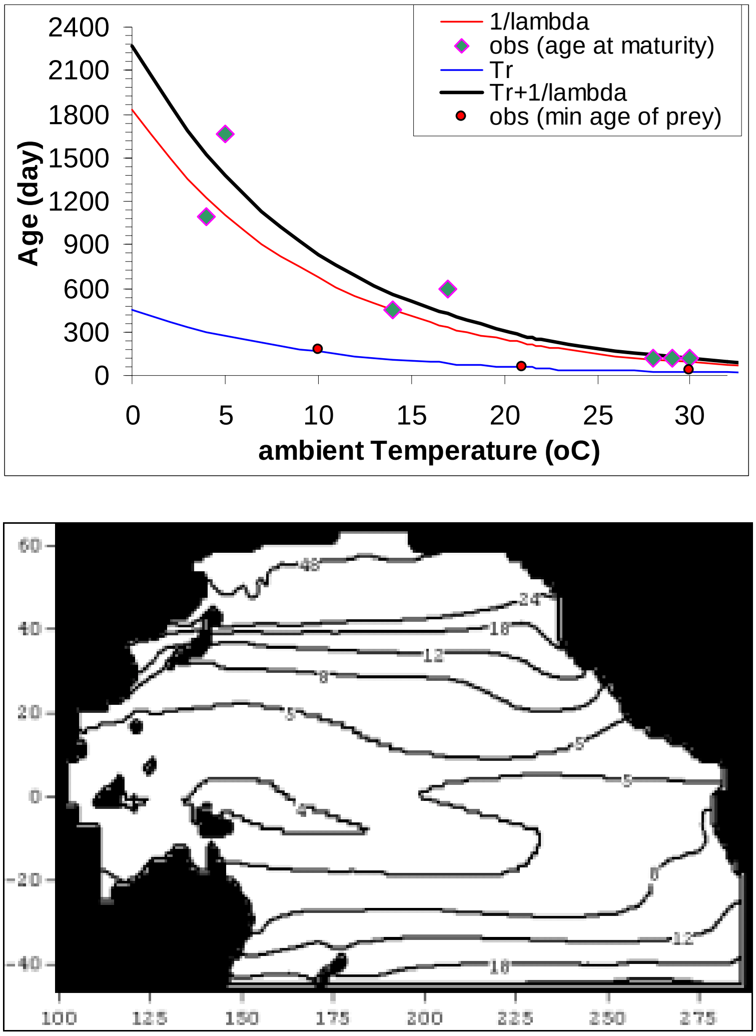

Figure 5. Top: functions based on temperature used for the parameterization of T_r and . that characterize the forage population. Bottom: spatial distribution of the forage “mean age” in months based on an average SST distribution and the equations 5a and 5b. The blue curve defines T_r and the red curve 1/. . 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* (ref)

Ecological transfer toward forage production

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. 6a based on C transfer efficiency from total primary production or eq. 6b based on N transfer efficiency from new primary production.

$$F'_{yr} = P_{1yr}' \,.\, E_1^{\,2.5} * c_1 \qquad (6a)$$

$$F'_{yr} = P_{2yr}' \,.\, E_2^{\,2.5} * c_2 \qquad (6b)$$

E_2 appears to be a constant value (0.28), while E_1 varies between 0.1 in oceanic environnment and 0.2 in coastal environment. When using eq. 6a, we choose a value of 0.1. Coefficients c_1 and c_2 are used to convert between units of N or C respectively to grams of fish wet weight.

For P_1 in mmol N, $c_1 = 12\ 10^{-3}$(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 C, $c_2 = 14\ 10^{-3}$(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.

Using these equations we can easily link the primary production to the forage production, that is the source (recruitment) of the forage population. We do not use a growth model for the forage population but simply convert the fraction of N or C accumulated in the population in a biomass of wet weight using the adequate coefficient.

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 (.) 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),

$$\frac{.\,F}{.\,t} = .\left(\frac{.\,^2F}{.\,x^2} + \frac{.\,^2F}{.\,y^2}\right) - \frac{.}{.\,x}(uF) - \frac{.}{.\,y}(vF) - \left(.\,F\right) + S \qquad (7)$$

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 differential equations are numerically solved by finite-difference techniques using a network of regularly spaced grid points, as in Sibert and Fournier (1994) and Sibert et al (1999). The equation (7) is applied over a discret time step and at a spatial resolution of one degree or less.

Results

1-layer, 1-component forage simulations

In a first phase of development, only one single forage population was simulated (Lehodey 1998, 2001, 2003) integrating the biomass over all the vertical structure. Predicted fields from two different coupled physical biogeochemical models were used. One is nitrogen-based and the second is carbon-based. The nitrogen-based biogeochemical model is driven by a physical model that is a full 3D ocean general circulation model (Li et al, 2001). The surface forcing uses the Comprehensive Oceanic and Atmospheric Data Set (COADS) monthly wind and heat flux. The biogeochemical model is a 10-component improved Nutrient-Phytoplankton-Zooplankton-Detritus (NPZD) ecosystem model designed originally for the equatorial Pacific (Chai et al., 2002; Dugdale et al., 2002). The model includes both nitrate and silicate as major potential nutrients, two sizes of phytoplankton and zooplankton, nonliving detrital particles, as well as total CO2. The carbon based biogeochemical model (Hackert et al. 2001, Christian et al. 2002) is coupled to the sigma-coordinate general circulation model of Gent and Cane (1989) as further developed by Chen et al (1994) and Murtugudde et al. (1996), and the ecosystem model of Leonard et al. (1999).

For simulating the 1-component forage, currents are averaged over the surface layer (0-50m), and new (N) or total (C) primary production are integrated over the euphotic zone. Figure 6 gives an illustration of the predicted primary production from these two models. Though total and new primary production cannot be directly compared, both models capture the main basin-scale features with the rich cold-tongue associated to the equatorial upwelling, the low productive central gyres, the seasonal enrichment in temperate latitudes and the interannual (ENSO) and decadal (PDO) variability. The most obvious features in the simulated forage (Figure 7) is the latitudinal shift of maximum concentration on each side of the equator, the very high biomass in high latitudes due to lower turn-over associated to cold temperature, and as for the primary production, but with a time lag of a few months, the decrease of biomass in the central Pacific during El Nino events.

Interestingly, the comparison of average forage biomass predicted from the two models gives remarkable similar results, both in absolute values and in fluctuations in the different equatorial geographical boxes as defined in Figure 8. For extratropical regions, discrepancies are observed that are clearly due to differences in temperature used for constraining the turn-over rate (“mean-age”) of the forage. The reason of these differences has been identified (lack of ice-model) and new versions of the OGCM will be modified to solve this problem.

2-layer, 3-component forage simulations

We have tested a 2-layer, 3-component forage model consisting of an upper- (0-200m) and a deep- (200-500m) pelagic layer with corresponding epi- and deep- forage components, plus a third component of migrating species moving from the deep layer in the day to the upper layer in the night. During the time that a forage component is occupying the upper or deep layer, it is redistributed by average currents in the corresponding layer and coefficients T_r and . are calculated on SST or temperature at 200 m respectively. The time that the migrant meso-pelagic forage spends either in the upper or the deep pelagic layer is calculated from the day length (DL: nb of hours of daylight) equation (eq. 8) 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).

$$DL = 24/\pi \ \mathrm{acos}(-\tan\phi \tan\delta) \qquad (8)$$

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

$$\delta = 23.45 \cos(\ 2\pi\ /\ 365\ (J-172)\ ) \qquad (9)$$

In absence of information on the level of energy transfer from primary production to each of these components, a first simulation was run based on the previous parameterization (equation 6) with equal part transferred to each component (i.e. 1/3, 1/3, 1/3). Then, results were compared to a few observations found in the literature, leading to a new parameterization of 1/6 (epi), 3/6 (migrant) and 2/6 (deep). Climatological and ENSO spatial distributions for these three components are presented on Figure 9 to 11. The use of average currents on 0-200m produced more diffuse distributions for the epi-pelagic forage when compared to previous simulations based on the average in the 0-50m layer. This trend is obviously increased for the migrant and deep pelagic forage, under the influence of deeper and less dynamical circulation. As expected the range of biomass values are much higher for the migrant and deep forage (Fig 12), due both to higher energy transfer coefficient and also to lower temperature. The biomass of epi-pelagic forage is about 10% of the total biomass in agreement with observations by Legand et al. (1972) and Grandperrin (1975). All series in the equatorial regions present clear ENSO-related interannual variability, and a decadal change after 1975 is visible in the central and eastern regions.

Discussion

The EASTROPAC cruises in 1967-1968 (Blackburn and Laurs, 1972) provided night and day distribution of micronekton in the eastern equatorial Pacific in the upper 200m. A comparison of these observations with predicted biomass of epipelagic forage during the day and the sum of epipelagic and migrant forage during the night is presented on figure 12 and figure 13, assuming that 1ml ~1g for converting measure of volumes in wet weight. It should be noted that estimates of forage biomass by net sampling are likely underestimated due to difficulties to collect the most agile organisms like squids that can avoid the micronekton net. Roughly, the simulation produced a range of values in agreement with the observation, with an order of magnitude between day and night values. The model also predicted a maximum along the coast and another along the equator or just above as observed during the cruises. However, the predicted maximum at the equator seems to be shifted in the east when compared to the observation.

Predicted biomass of the migrant pelagic forage was also compared to abundance of migrating mesopelagic fishes off New Zealand (McClatchie and Dunford, 2003) that were estimated from acoustic surveys during night hours (Figure 15). While the simulated migrant pelagic biomass includes all type of organisms, acoustic data (38 kHz) are asssumed to represent migrant mesopelagic fishes only. In particular, gelatinous organisms, krill, shrimps and squids are not included. Therefore, higher values in the predicted biomass are expected. The simulated biomass also suggests a decrease in the northeast as observed. Comparison in the southern region (region 4) is of less value, as there is likely an overestimation of biomass by the model due to artificial accumulation along the closed boundary of the grid.

Obviously, these comparisons provide a useful but very rough evaluation. Only level of biomasses and large-scale spatial features should be compared, both in reason of the interpolation of the observations and the type of models used. These models are basin-scale models parameterized to reproduce oceanic process and the boundaries of the grid are delimited by the 200m isobath. Also, the 0-200m layer used to define the epi-pelagic layer is likely too deep in the eastern Pacific where the thermocline is much shallower than in the west. A better definition of the boundary between the two layers could use the thermocline or the depth of the mixed-layer. Further comparisons are needed to evaluate the model results and to refine the parameterization. With acoustic and net sampling data, analyses of stable isotopes (Allain, 2004) should help in estimating the energy transfer from primary production to the different micronekton components. Increased resolution and improvements in the model to reproduce meso-scale oceanic features will also allow detailed studies, while success in reproducing behaviour of tagged individual tuna based on predicted distribution of their prey (Fig. 16) would also provide indirect validation of the spatial simulation of forage organisms.

Acknowledgment

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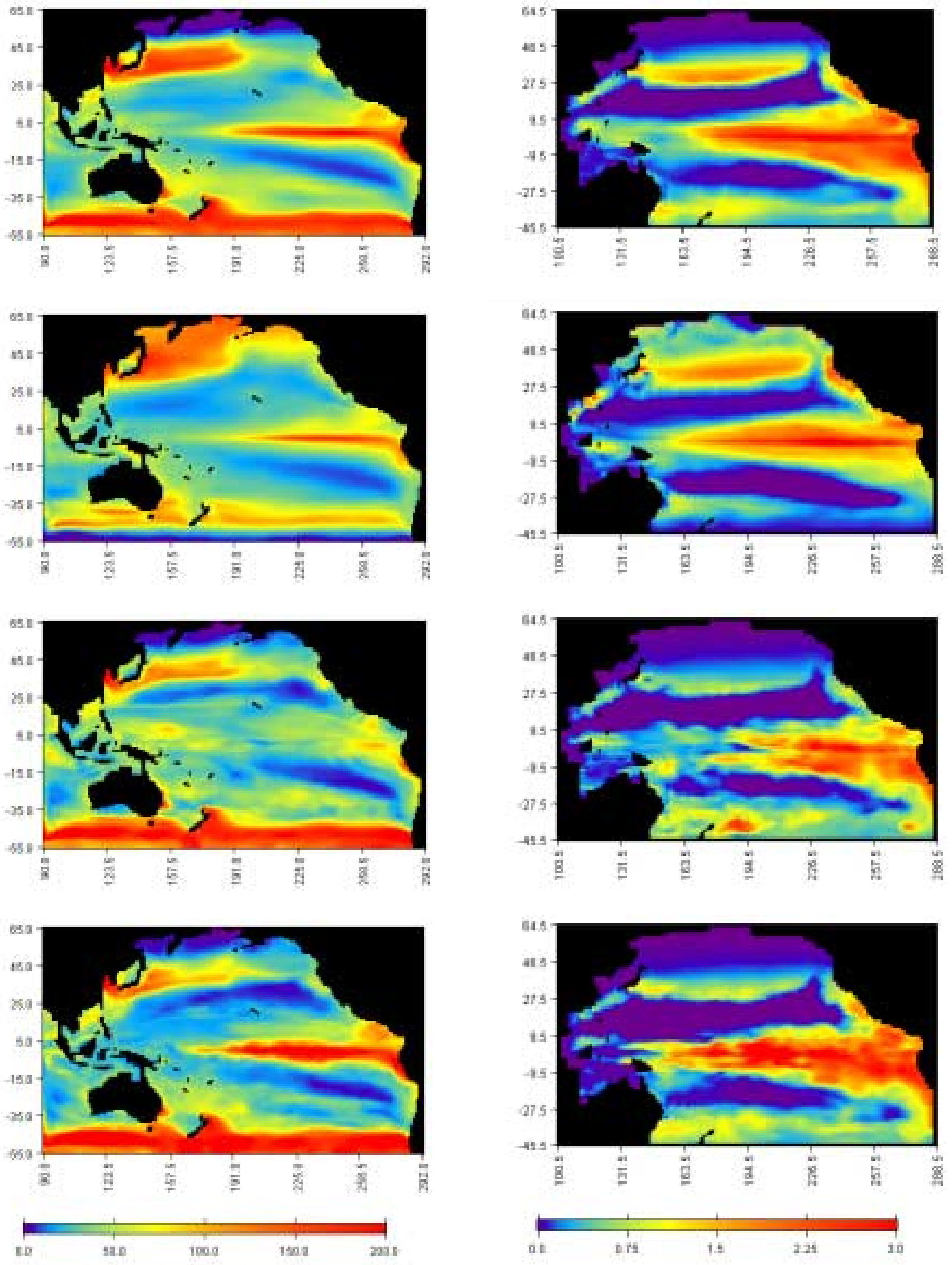


Figure 6. Predicted primary production in the Pacific Ocean from two coupled physical biogeochemical models. Left: total primary production in mmol C m^{-2} day^{-1} from the ESSIC model. Right: new primary production in mmol N m^{-2} day^{-1} from the Maine model. From top to bottom: Climatology in January, Climatology in June, December 1982 (El Niño), December 1988 (La Niña). Note that latitudinal boundaries are different in the south.

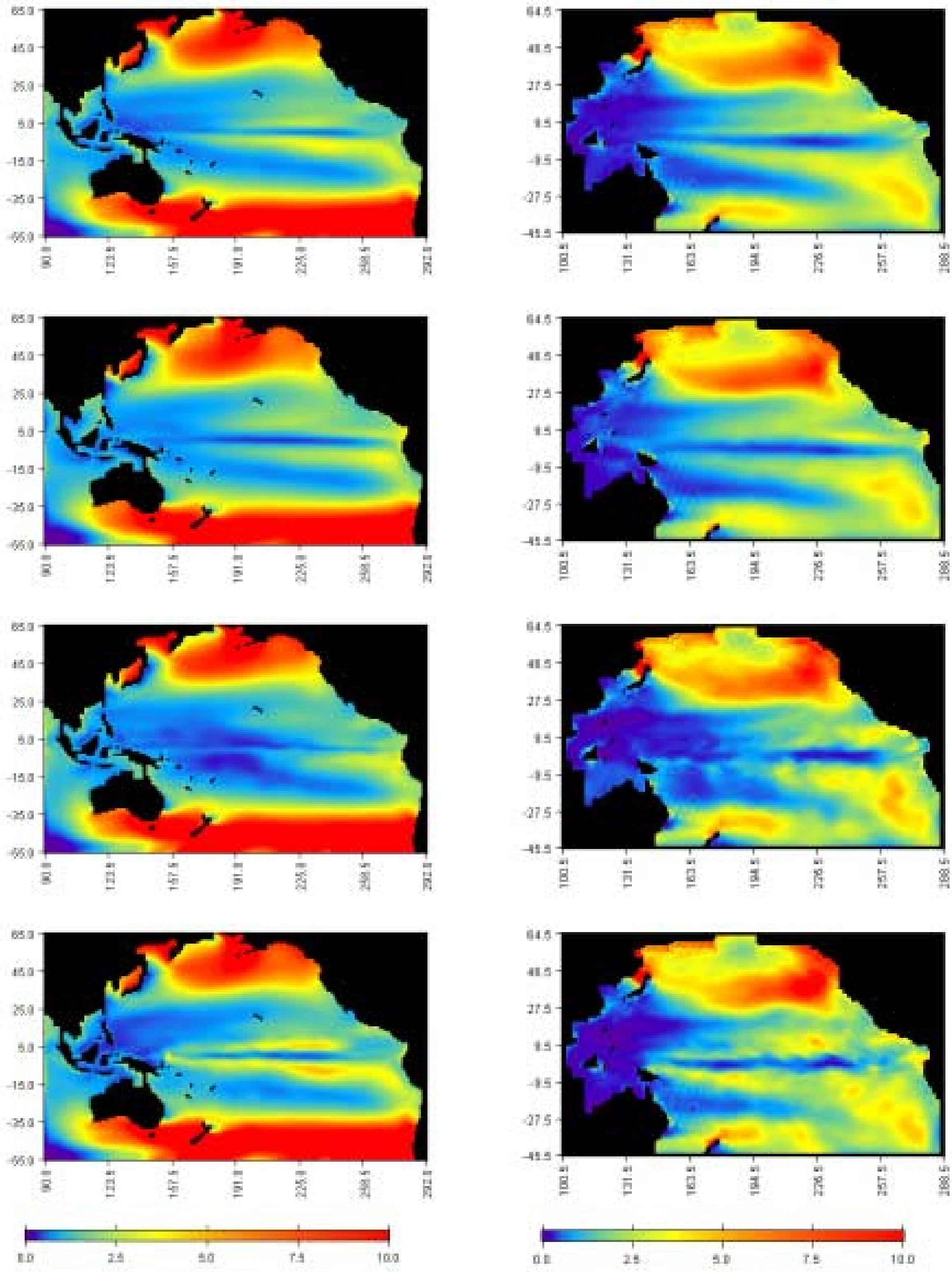


Figure 7. Predicted forage biomass in the Pacific Ocean based on total (left) and new (right) primary production from the two coupled physical biogeochemical models in Fig. 6. From top to bottom: Climatology in January, Climatology in June, December 1982 (El Niño), December 1988 (La Niña).

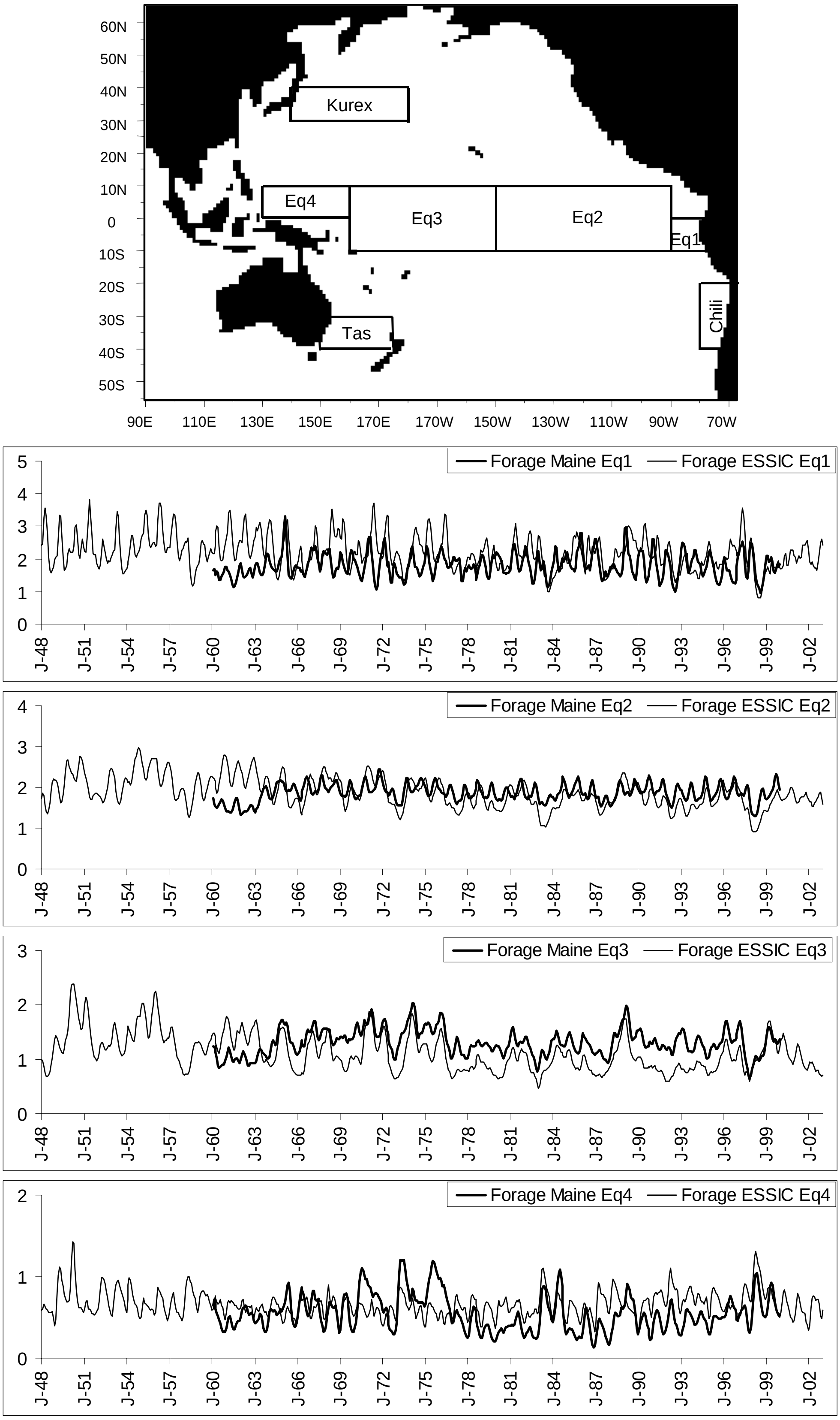


Figure 8 – Mean forage biomass (g of WW m^{-2}) time series in the geographical boxes identified on the map predicted with different inputs from two coupled physical-biogeochemical model (see text for explanation)

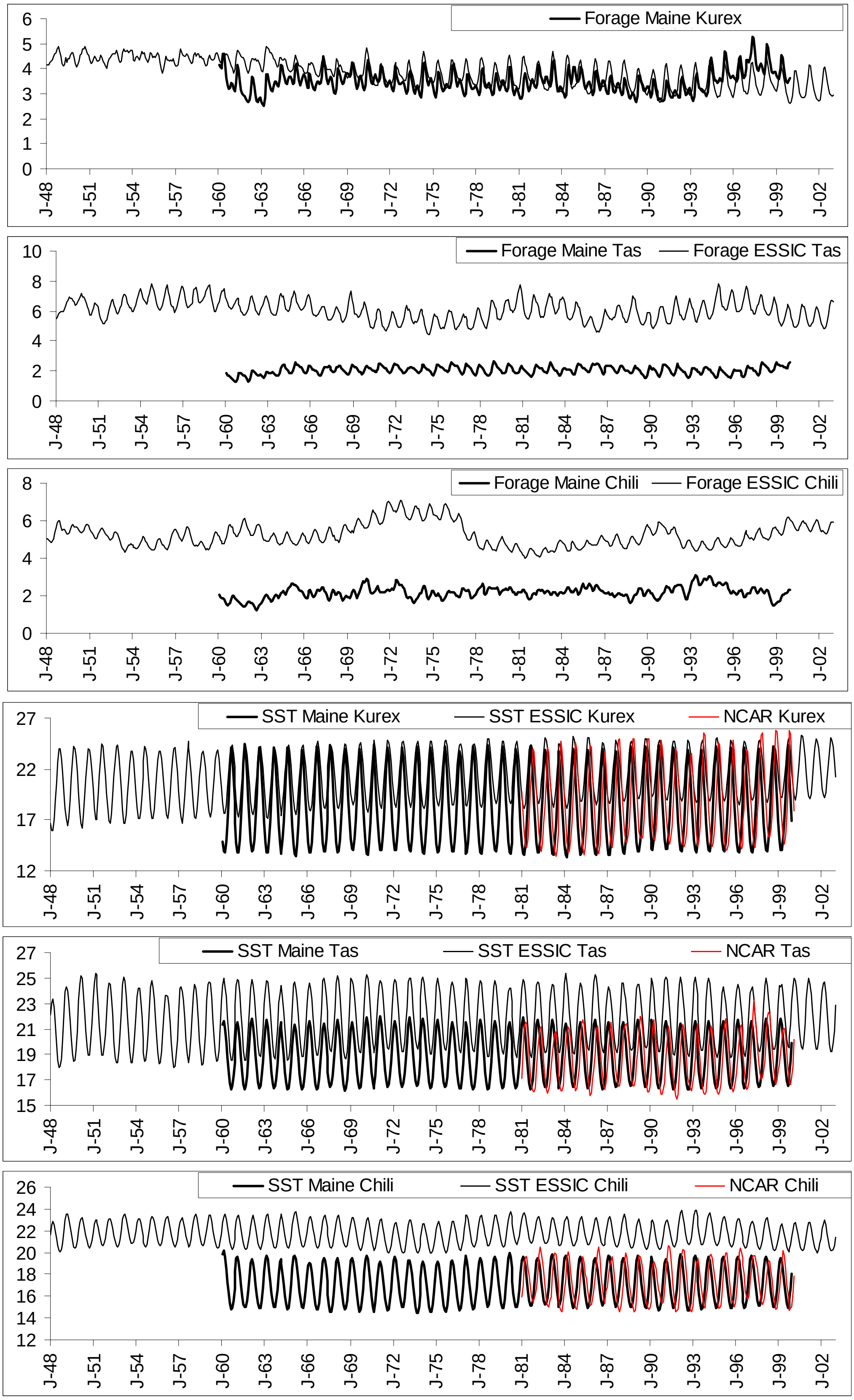


Figure 8 (cont.) Mean forage biomass (g of WW m^{-2}) time series in the three extra-tropical boxes identified on the map, and corresponding SST from the two models and observation (red) from the NCAR OI data sets.

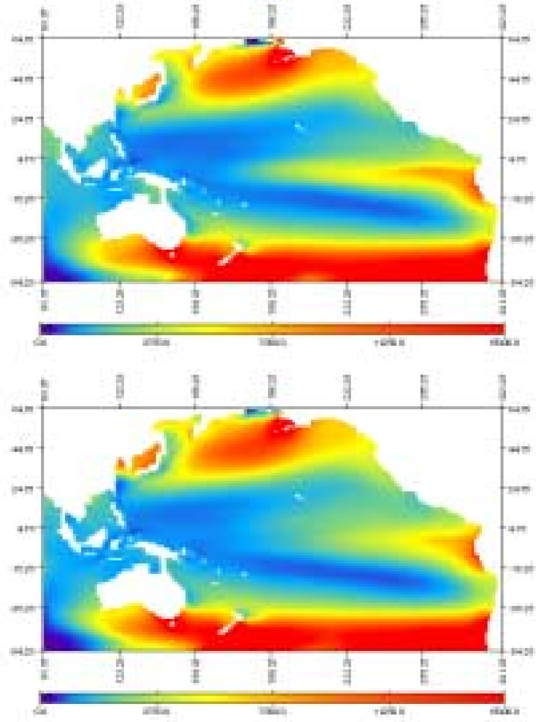


Figure 9 – Predicted epipelagic (0-200m) forage biomass (t of WW deg^{-2}). Left: Climatology in January (top) and December (bottom). Top right: December 1982 (El Niño). Bottom right: December 1988 (La Niña).

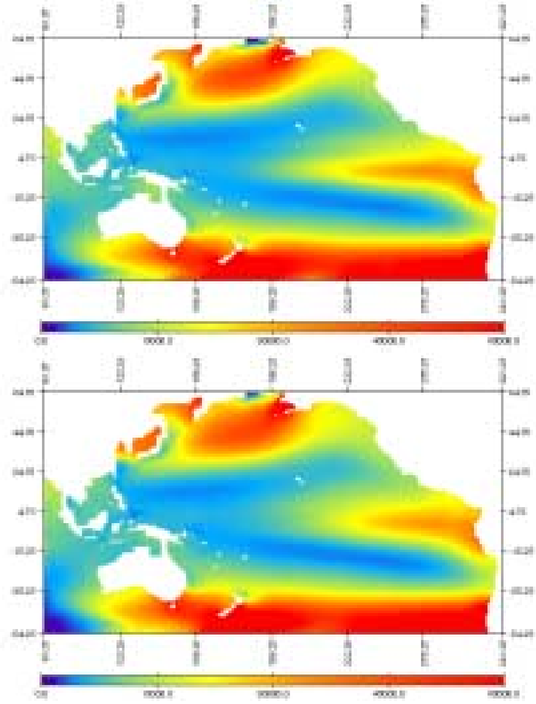


Figure 10 – Predicted migrant mesopelagic (0-200m <-> 200-500m) forage biomass (t of WW deg^{-2}). Left: Climatology in January (top) and December (bottom). Top right: December 1982 (El Niño). Bottom right: December 1988 (La Niña).

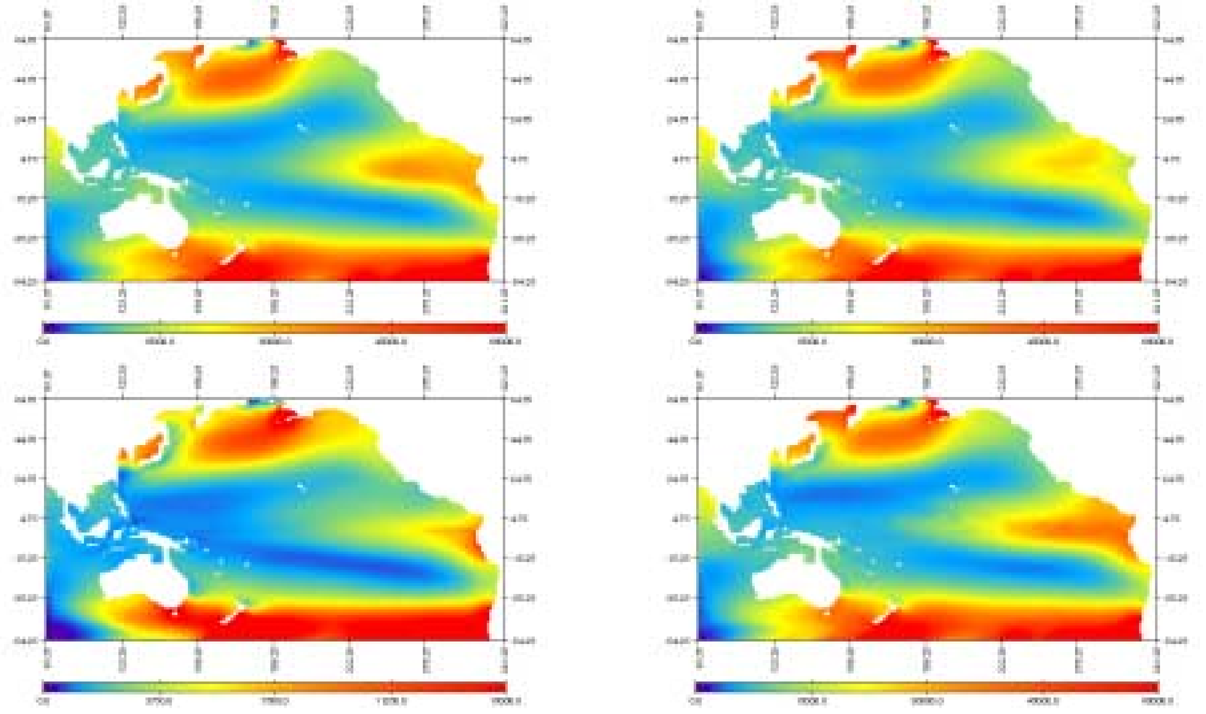


Figure 11 – Predicted mesopelagic (200-500m) forage biomass (t of WW deg^{-2}). Left: Climatology in January (top) and December (bottom). Top right: December 1982 (El Niño). Bottom right: December 1988 (La Niña).

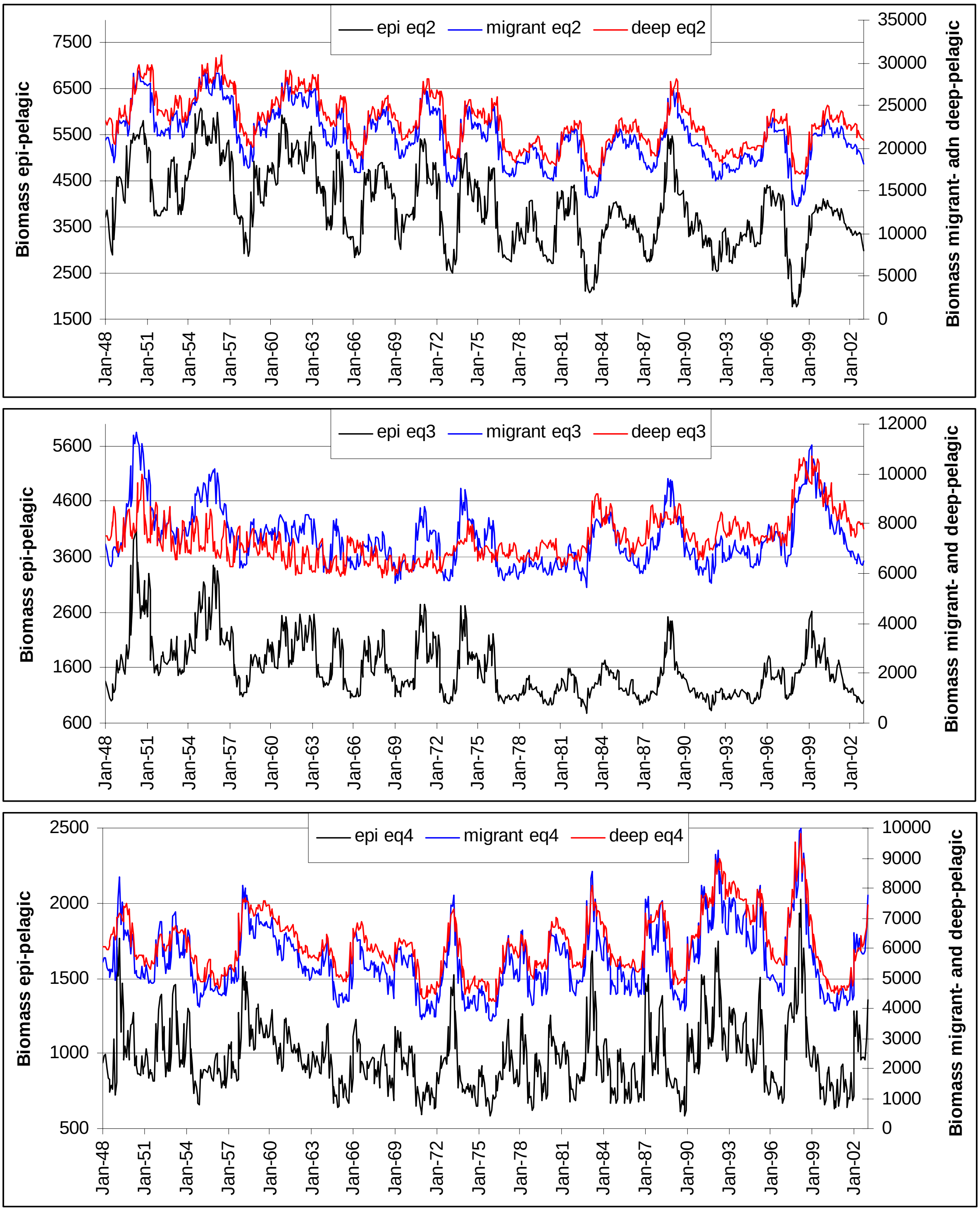


Figure 12. Average biomass (tonnes deg^{-2}) for the different forage components in the equatorial boxes 2, 3, and 4 presented on figure 8.

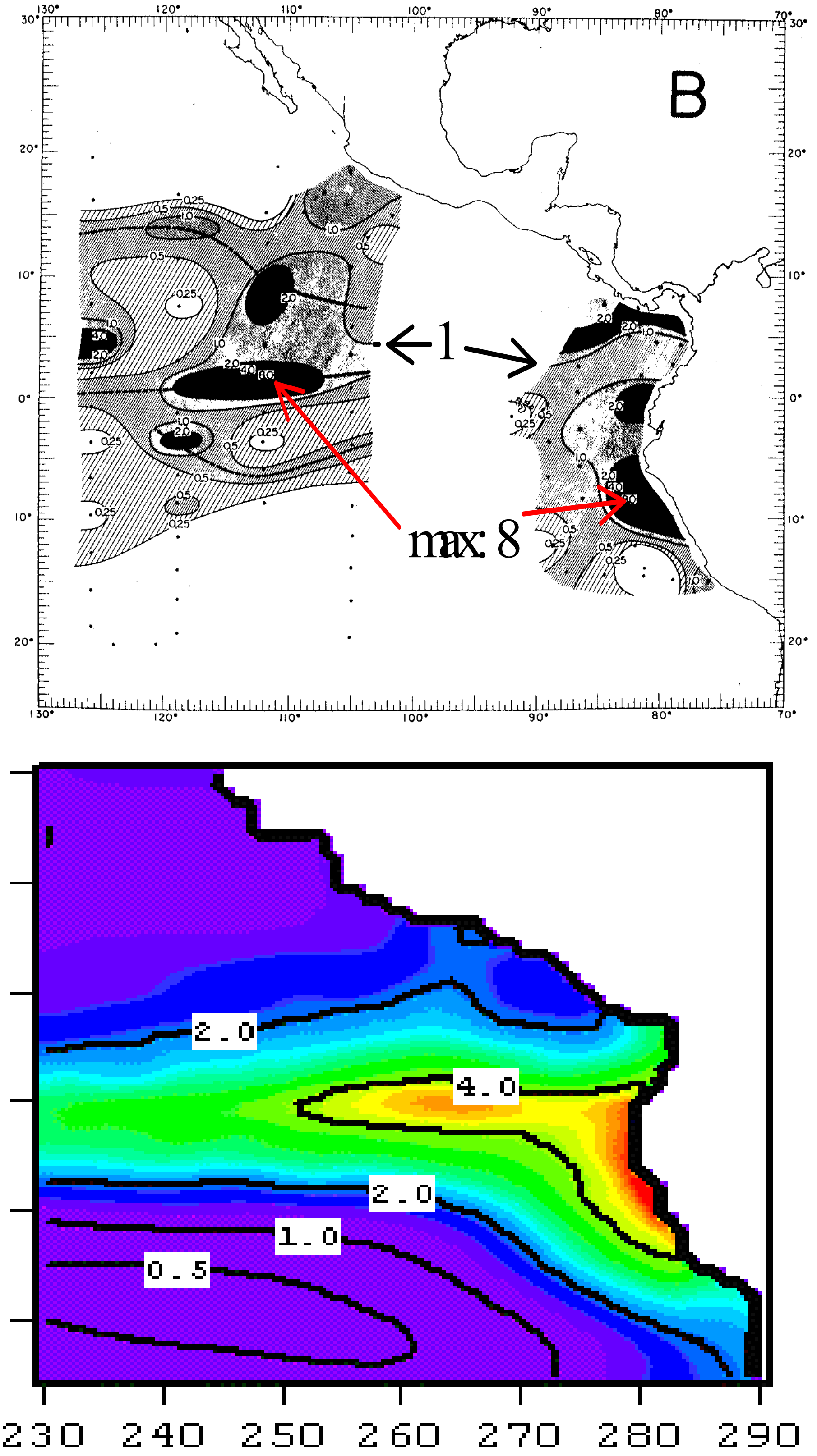


Figure 13 –Day concentrations (ml / 1000 m^3) of “skipjack forage” measured during the EASTROPAC cruise (left) and biomass of epi-pelagic forage predicted by the model for the same period (February-March 1967).

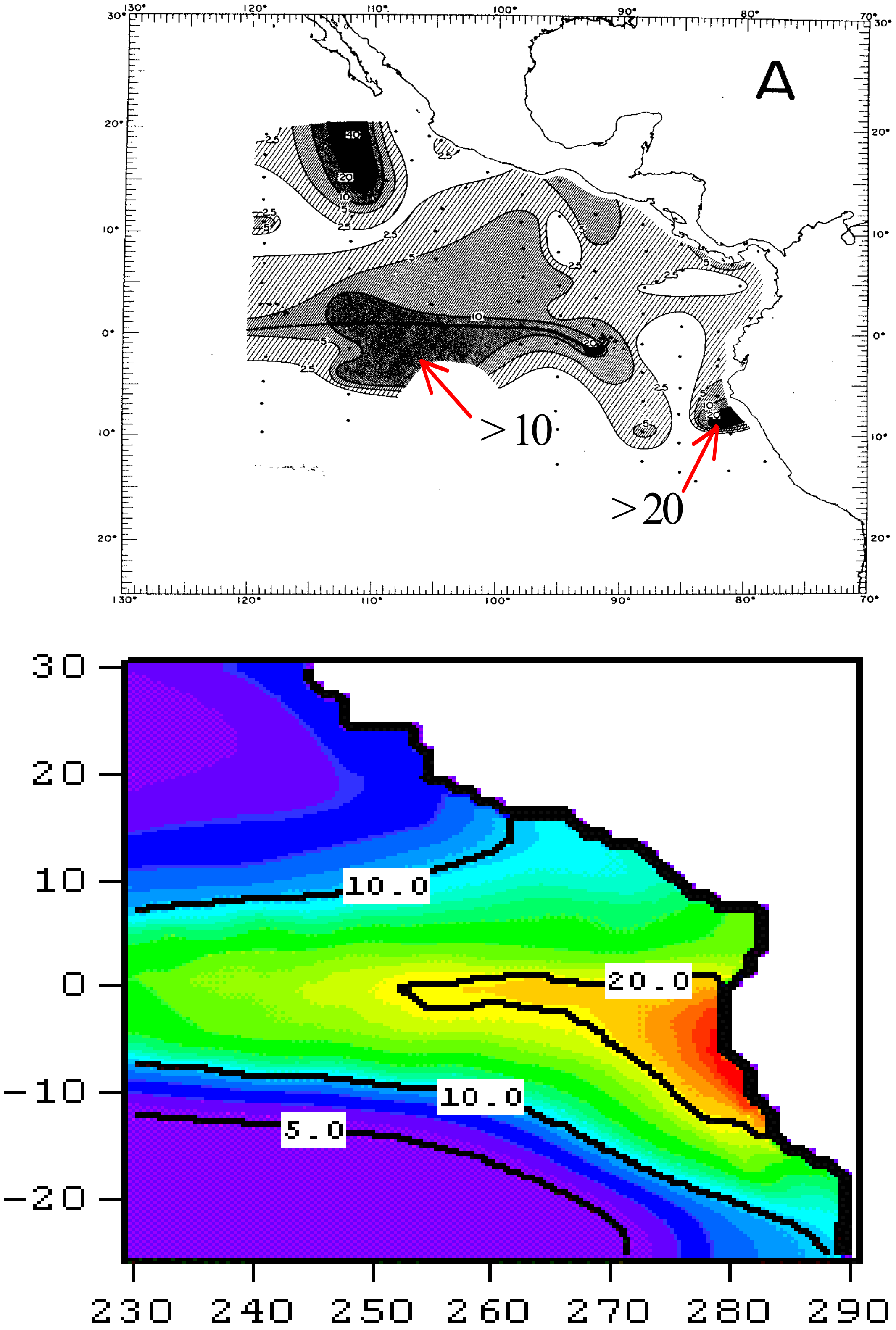
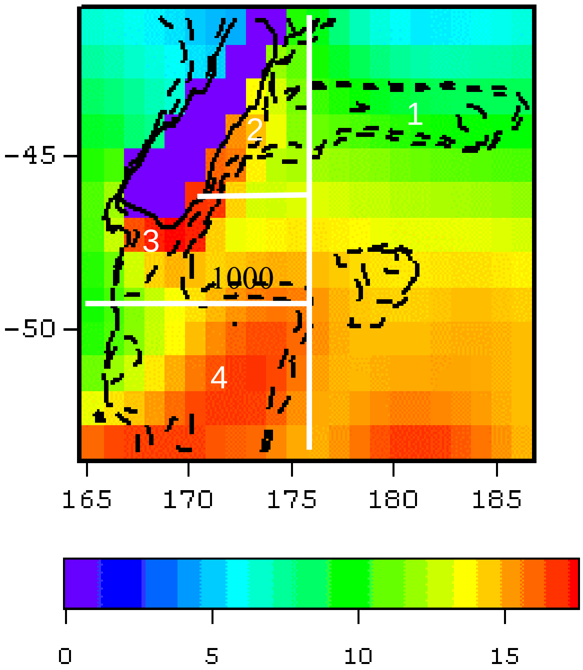


Figure 14 – Night concentrations (ml / 1000 m^3) of "skipjack forage" measured during the EASTROPAC cruise (left) and sum of epi- and migrant- pelagic forage biomass predicted by the model for the same period (Aug-Sept 1967).



Region	Data	Model
1	0.2 g.m^{-2}	8.5 – 11.5 g.m^{-2}
2	8.15 g.m^{-2}	12 – 16 g.m^{-2}
3	5.37 g.m^{-2}	13 – 17.5 g.m^{-2}
4	0.13 g.m^{-2}	12 – 17 g.m^{-2}

Figure 15 – Predicted migrant mesopelagic forage biomass (g WW. m^{-2}) around the Southern Island of New Zealand in Nov-Dec 2000, and comparison with acoustic data in 4 sub-regions with depth shallower than 1000 m.

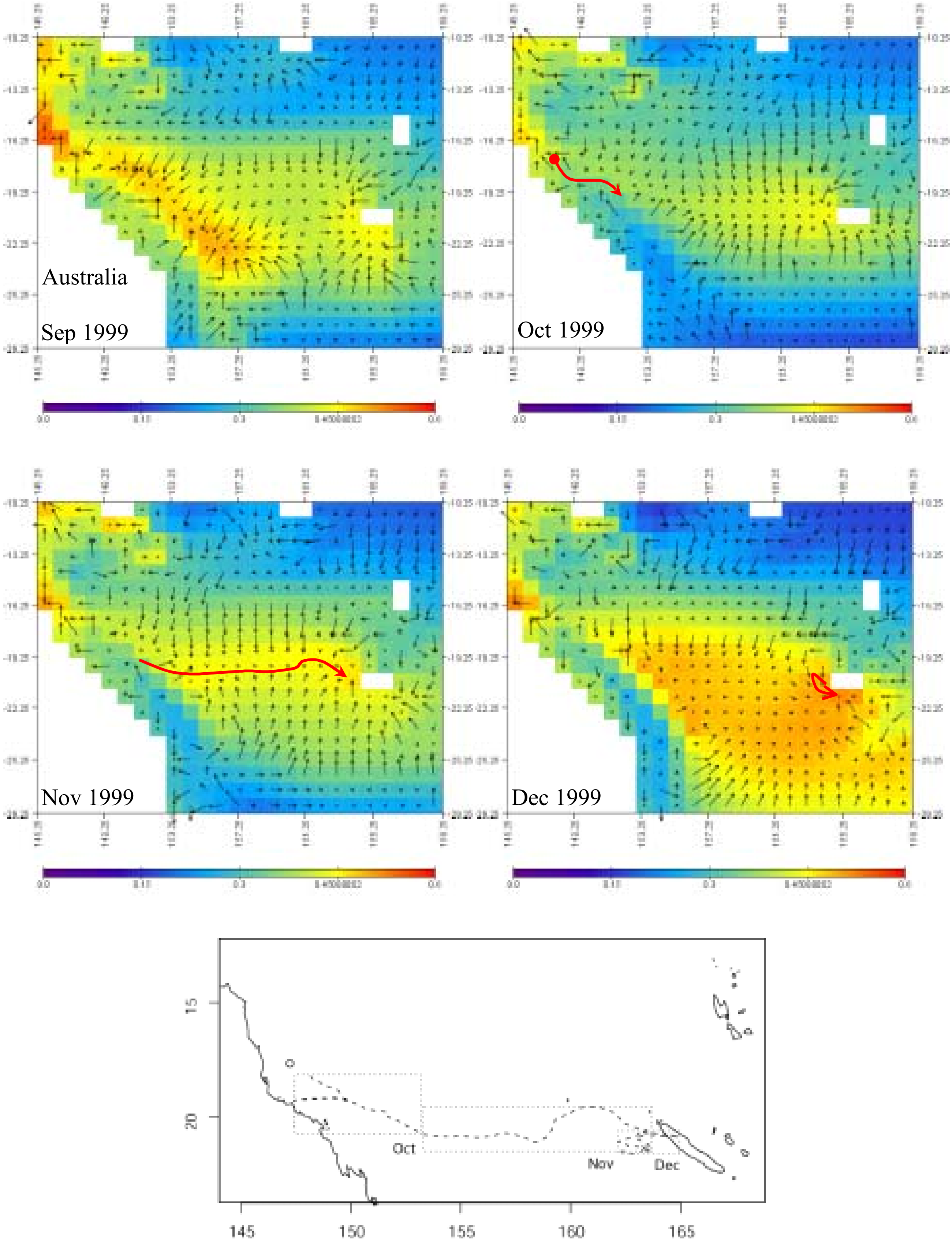


Figure 16. Predicted movement (cf part II) of bigeye tuna (FL ~ 80 cm) based on the gradient of habitat (combining forage, temperature and oxygen) from Sep to Dec 1999. One bigeye tagged with an archival tag crossed the Coral Sea from East Australia to New Caledonia in November 1999 (bottom map, cf Kirby et al 2004). Approximated track is reported in red.