The tuna fisheries in the Pacific Ocean have economical importance for the majority of Pacific countries. The 1999 Pacific tuna catch (2,380,271 mt) represented 67% of the provisional estimate of world tuna catch (3,571,114 mt). This global tuna catch is dominated by two tropical species, skipjack and yellowfin, species inhabiting the surface mixed layer (Figure 1). Amongst the top predators of the tropical pelagic ecosystem, these two species have the greatest biomass and the largest forage requirement (Kitchell et al., 1999). Main results for the tuna species from the western Pacific are shown below.
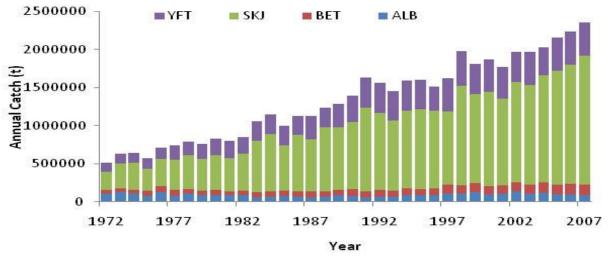

Figure 1. Total western central Pacific Ocean (WCPO) tuna catch by species (SKJ; skipjack, YFT; yellowfin, BET; bigeye tuna, ALB; albacore)

Skipjack

Development and testing of the first SEAPODYM version were carried out in 1995 with climatological series of predicted currents from the OPA ocean model (LODYC) and CZCS-satellite-derived chlorophyll data as a proxy for the primary productivity. This first climatological "forage index" was used in the definition of an habitat index for skipjack tuna and used in the spatial population model (Bertignac et al., 1998).Results agreed with the general knowledge on the spatial distribution of this species. However, the spatial correlation between predicted and observed catch remained very low and it became clear that the inter-annual variability due to the El Niño Southern Oscillation (ENSO) had to be taken into consideration, particularly as other results based on fishery and tagging data demonstrated the importance of ENSO on the movement of skipjack.
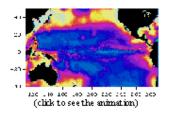

(click to see the animation)

Figure 1. Time series of CZSC satellite chlorophyll data used as proxy for primary production in the Pacific Ocean.
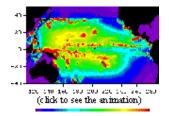
(click to see the animation)

Figure 2. Time series of the habitat index used in the first test for SEAPODYM in 1995.

The development of a biogeochemical model coupled to an Ocean General Circulation model at the LODYC (Stoens *et al.*, 1998, 1999) allowed testing the impact of the interannual variability on the forage species in the equatorial 20N-20S area (Lehodey *et al.*, 1998).

In 1999, an important development in the model regarding the interaction between predicted tuna density and forage density was made. In the first version, the forage mortality due to tuna species was assumed to be included in the total mortality Λ. However, the use of the predicted distribution of forage for constraining the movement of tunas without considering the feedback effect of tuna density distribution has implicit hypotheses. Either the forage mortality due to the tuna predation is assumed very low and relatively negligible to the total mortality of forage, or the predators present an "ideal distribution", where forage predators would have a natural ideal distribution, such that forage mortality would be the same everywhere and equal to λ. This hypothetical situation presents an analogy with the "ideal free distribution" proposed by Fretwell and Lucas (1970) and Fretwell (1972) for the density dependent habitat selection theory, whereby individuals differentially occupy available habitats so that realized "suitability" is equal for all occupied habitats.
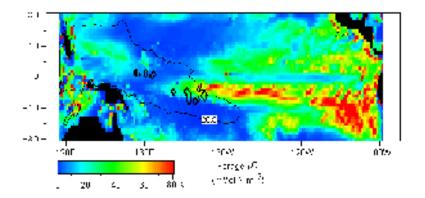

Figure 3. Spatial distribution of new primary production (PP) simulated by the coupled OPA biogeochemical model and the tuna forage biomass (FO) for the month of June 1994 in the Equatorial Pacific Ocean. The delineation of the warmpool is approximated by the 28.5 C isotherm and the contours of US purse seiners' CPUE > 10t/day when superimposed (Lehodey *et al.*, 1998)

Forage mortality

To include more realistic predator-prey interactions the forage mortality must depend on tuna density. The approach used was to calculate and apply a specific local mortality $w_{i,j,t}$ depending on the food requirements of tuna population; then, a mean residual mortality l' which is the

difference between the total mortality l and the mean specific mortality $\overline{\dot{a}\dot{x}}$ over the area occupied by the tuna species. Therefore, the total forage biomass over the whole area remains equal to the total forage biomass calculated in the case of a constant l, but the spatial distribution linking the density of tuna may be different. An increasing density of tuna increases the forage mortality, and if there is no additional supply of forage, decreases the habitat index value. Since the movement of tuna is based on the gradient of the habitat index, tuna will start to leave the zone when forage is not abundant enough to support the local tuna population density. On the other hand, tuna will continue to concentrate if the index value remains higher than in neighbouring zones. This approach seems appropriate for reproducing tuna behaviour, particularly the frequent huge aggregations of tuna feeding on large patches of prey organisms.

The new SEPODYM version was tested with the previous LODYC's run of new primary production. Despite some limitations in the input data set and a simplified parameterization, this first simulation improved the prediction of catch and was helpful to interpret the observed ENSO-related spatial-temporal changes in the distribution of skipjack population (Lehodey, 2001).

However, the run presented a short time-series (1992-95) and was limited to the 20oN–20oS equatorial region when tuna stocks extend to sub-tropical and temperate oceanic regions. Furthermore, both observations relative to the development of the recent El Niño – La Niña sequence (1997-2000) and results from Multifan-CL providing the first statistical recruitment estimates suggested that a simple temperature constrain was not sufficient to explain the recruitment fluctuation.
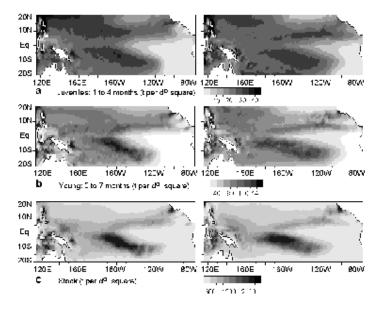

Figure 4. Larvae-juveniles spatial distribution (passive transport), young and virgin skipjack stock in first quarter (average from 1993 – 1995) and third quarter (average from 1992 – 1994), from Lehodey (2001).

Skipjack

The first SEAPODYM application was for the skipjack tuna population and its fisheries. Three fishing gears were modeled for that fishery: purse-seine, pole-and-line and a group of mixed domestic gears from the Philippines and Indonesia. A total of ten fleets were included, each with a separate catchability coefficient.

An age-based selectivity function was used for each gear (Figure 1). Fishing effort of each fleet varies monthly and spatially, with a one degree square resolution except for the Philippines and the Indonesia fleets that provide data aggregated annually with a five degree resolution.
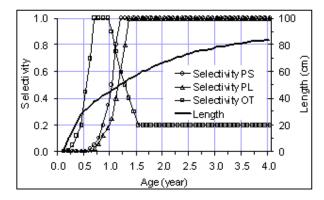

Figure 2. Gear selectivity, (PS, purse seine; PL, pole and line; OT, mixed domestic gears) and the growth equation (Length) used in SEAPODYM.

Catchability coefficients were estimated fitting SEAPODYM to observed fishing data by region. In particular, results from the estimation were compared to total monthly catch, spatial distribution of catch, and fishery size composition. In general, there was a good fit between the observed and estimated data, as shown below (Figures 3, 4 and 5).
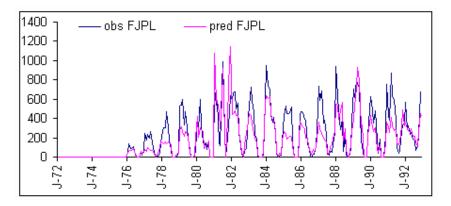

Figure 3. Fit to total monthly catch of Fidji pole an line fleet data, (obs FJPL, observed monthly catch; Pred FJPL estimates monthly catch).
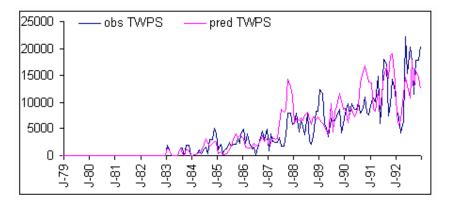
Figure 4. Fit to total monthly catch of Taiwan purse seine fleet data, (obs TWPS, observed monthly catch; Pred TWPS estimated monthly catch).
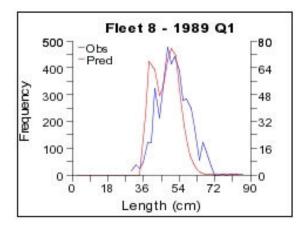

Figure 5. Fit to size composition data for fleet 8, (obs observed size composition; Pred estimated size composition).

Recent developments

The opportunity to consider a longer time-series over the whole Pacific basin arose with the recent developments in NPZ models. Besides temperature, additional environmental effects in the spawning habitat index were also investigated. With the inclusion in SEAPODYM of temperature and physical constraints like the advection (creating favourable zones of retention for larvae), food availability and predation are likely the other major factors affecting larval survival and pelagic fish recruitment. Food of larvae depends directly on primary production, while their predators are organisms included in the tuna forage. Therefore, it was interesting to investigate these two opposite effects on the recruitment by using the ratio P/F.

The use of this new input data and the spawning habitat index set provided important results. The skipjack recruitment defined by environmental constrains in SEPODYM agreed with the independent statistical estimate from Multifan-CL. As mentioned, the spatial correlation between observed and predicted catch was high.
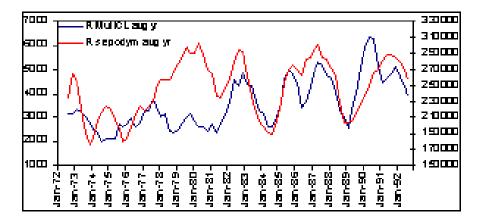
Figure 6. Comparison of skipjack recruitment estimates from the SEAPODYM model and the Multifan-CL model.

When the spawning habitat index is only dependent of SST, the skipjack recruitment and biomass did not show large fluctuation as suggested by the MULTIFAN-CL analysis. Using the P/F ratio in the spawning habitat index produced fluctuations showing an evident correlation with the MULTIFAN-CL estimates. The high spatial correlation between observed and predicted catch even with a relatively homogeneous recruitment depending of SST only (a = 0) suggests that the dynamics are relatively well described in the model, at least at this large spatial scale. In particular, the redistribution of larvae by currents and the movement of young and adults tuna constrained by the habitat index are fundamental processes that might be able to explain the population distribution.
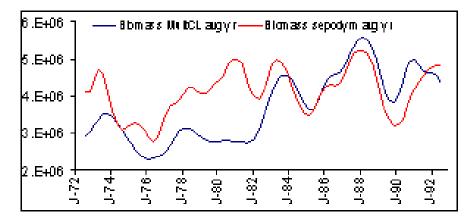

Figure 7. Comparison of skipjack biomass estimates from the SEAPODYM model and the Multifan-CL model.

The large interannual variations in the recruitment are related to the ENSO (El Niño Southern Oscillation) events, the recruitment had higher values during El Niño years (1972, 1982-83, 1987, 1990) and the lowest during La Niña years (1974-76, 1988-89). The simulations predicted that the main skipjack spawning ground occurs in the western Pacific between Indonesia and Papua New Guinea, with a general decreasing gradient from west to east. During El Niño events the

recruitment of juvenile increases drastically with a spatial extension to the central Pacific, while during La Niña it is contracted in the western Pacific with a lower recruitment level. A large proportion of recruits moves either to Japan following the Kuroshio or to the central Pacific in the convergence zone between the warm pool and the cold tongue as early described (Lehodey et al., 1997; Lehodey et al., 1998; Lehodey, 2001) and in agreement with the results from the skipjack MULTIFAN-CL analysis (Bigelow, 2000; Hampton et al., 2001).
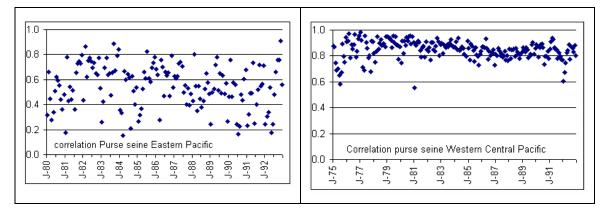

Figure 8. Monthly spatial (1 degree square) correlation between observed and predicted skipjack catches for Japanese purse seiners fleets in the eastern central and western Pacific Ocean.
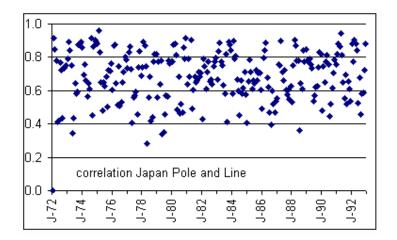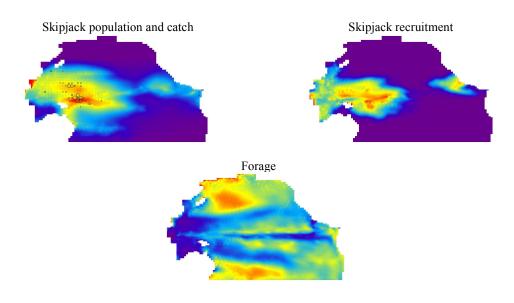

Figure 9. Monthly spatial (1 degree square) correlation between observed and predicted skipjack catches from Japanese pole and line fleet in the Pacific Ocean.

Despite some limitations, the use of a new set of predicted primary production and physical data has considerably extended the analysis because the simulations now cover all the Pacific Ocean since 1955, and also because the prediction of the primary production has improved. The next simulations should include a longer period of time, starting in 1992 up to the current date, allowing comparisons with recent and numerous observed data (e.g., SeaWiFS) including the strong El Niño of 1997-98 followed by the long La Niña event of 1998-2001. These results reinforce the suggestion of the impact of the ENSO variability with a positive (negative) effect of El Niño (La Niña) events on recruitment that is propagated into the stock in the following two years. Therefore, after the 1997-98 El Niño event and the associated high record of skipjack catch in 1998-2000, the last La Niña episode of 1998-2001 should lead to a decrease of the skipjack stock biomass in the next two years.

Recruitment mechanisms are fundamental processes in population dynamics. The spatial model SEPODYM is particularly well suited to test hypotheses on these mechanisms and on the stock-recruitment relationships. The results concerning the skipjack recruitment are encouraging. However, the improvement of recruitment prediction requires the improvement of the parameterization of young and adult migrations. In particular, the advection and diffusion coefficients of tuna could be set up as age-dependent to have a realistic description of the physical capability for movement associated to fish size.

Skipjack population and catch

Skipjack recruitment

Forage

Animations (click on the image to see the animation)
You can download a free video viewer (753 Kb) at http://www.gromada.com/Moyager.html