

SCTB15 Working Paper
SKJ-5

## SEPODYM development and application to skipjack population and fisheries



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

## SEPODYM development and application to skipjack population and fisheries

Patrick Lehodey

## Background

To explore the underlying mechanisms by which the environmental variability affects the pelagic ecosystem and tuna populations, a spatial environmental population dynamic model (SEPODYM) has been developed at the OFP-SPC (Bertignac et al. 1998; Lehodey et al. 1998; Lehodey 2001a). The model is a 2D coupled physicalbiological interaction model at the ocean basin scale, combining a forage (prey) production model with an age structured population model of targeted (tuna predator) species. The model contains environmental and spatial components used to constrain the movement and the recruitment of tuna. Input data set for the model are sea surface temperature, dissolved oxygen concentration, oceanic currents, and primary production that can be predicted data from coupled physicalbiogeochemical models, as well as satellite-derived data distributions.

Development and test of a first version of the model were carried out in 1995 with a climatological series of predicted currents from the OPA ocean model (LODYC) and CZCS-satellite-derived chlorophyll data as a proxy of the primary productivity. Predicted data from a biogeochemical model coupled to an Ocean General Circulation model developed at the LODYC (Stoens et al. 1999) allowed to testing the impact of interannual variability on the forage in the equatorial $20 \mathrm{~N}-20 \mathrm{~S}$ area (Lehodey et al., 1998). Then, the interaction between predicted tuna density and forage density was considered by coupling the forage (prey) mortality to the tuna predation. The modelling approach was tested with the previous LODYC 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 spatio-temporal changes in the distribution of skipjack population (Lehodey 2001a). However, the run represented a short time-series (1992-95) and was limited to the $20^{\circ} \mathrm{N}-20^{\circ} \mathrm{S}$ equatorial region, whereas tuna stocks extend to sub-tropical and temperate oceanic regions.

A new input data set predicted by a coupled physicalbiogeochemical model (F. Chai, Univ. Maine) allowed extending the analysis to the Pacific basin over a long time series (1960-1992). In addition, new developments in the model were realized with an improved parameterization, and results were presented during SCTB14 (Lehodey 2001b). To consider change in tuna behaviour according to the quality of habitat, e.g., leaving rapidly a poor habitat region, functions were added to increase the diffusion and the advection at low values of habitat index. A spawning habitat index $\left(H_{s}\right)$ was defined to constrain the recruitment to environmental conditions. With the previous assumptions for defining the spawning conditions (i.e., presence of mature tuna and limiting sea surface temperature), effects of food availability and predation on larvae were investigated through a proxy variable: the $P / F$ ratio. These results indicated that El Niño (La Niña) events have a positive (negative) impact on the recruitment that is propagated into the stock in the following two years.

## Physical-NPZD simulation

A new run produced by a coupled physicalbiogeochemical model has been used in this analysis. The 3D physical model is based on the Modular Ocean Model (MOM 1.1) developed at GFDL/NOAA, and modified for the entire Pacific Ocean $\left(45^{\circ} \mathrm{S}-65^{\circ} \mathrm{N}, 100^{\circ} \mathrm{E}-70^{\circ} \mathrm{W}\right)$. The resolution is 2 degrees in longitude, and decreases in latitude from 0.5 degrees near the equator ( 10 S to 10 N ), and 2 degrees close to the north and south boundaries. There are 40 layers with 10 m resolution within the euphotic zone ( 120 m ). The biological NPZD model is a 10 -component ecosystem model designed ariginally for the equatorial Pacific (Chai et al., 2001; and Dugdale et al., 2001). The model includes both nitrate and silicate as limiting nutrients, two sizes of phytoplankton and zooplankton, nonliving detrital particles, as well as total $\mathrm{CO}_{2}$. The physical-biological model was forced with the Comprehensive Oceanic and Atmospheric Data Set (COADS) monthly wind and heat flux from 1955 to 1993 and with a similar product after 1993.

Predicted data for 1960-93 are similar to those obtained from the previous run. The physicalbiogeochemical model is capable of reproducing many observed features and their variability in the Pacific Ocean (Li et al, 2001; Chai et al 2002). In particular it simulates the equatorial region very well with elevated high biomass in the cold tongue region, as well as the effect of ENSO events with higher temperature anomaly during the El Niño and lower primary production in the cold tongue. Also, the model captures the slowdown of the meridional overturning and decrease of the equatorial upwelling transport, which causes primary production and phytoplankton biomass to decrease by about $10 \%$ after 1976-77 in the equatorial Pacific. In the central North Pacific, the modeled primary productivity and phytoplankton biomass in the transition zone (30N-45N) increase after the 1976-77 climatic shift. Elevated chlorophyll level in the central North Pacific expends the transitional zone and push the transition zone chlorophyll front (defined as surface chlorophyll $=0.2 \mathrm{mg} / \mathrm{m} 3$ ) equatorward (Chai et al, submitted). Overall, the physicalbiogeochemical model responds to the abrupt climate shift reasonably well, and the modeled results are consistent with the limited observations in the Pacific Ocean.

However, it seems that the second forcing data se produces higher upwelling velocity. Moreover, the predicted new primary production does not reproduce the peak of primary production in the western equatorial region ( $5 \mathrm{~N}-5 \mathrm{~S}$; 160-170E) occurring in April-June 1998, as observed from SeaWiFS Satellite data (Murtuggude et al 1999). This bloom of phytoplankton is expected to be responsible for the very high peak of skipjack recruitment in 1998 (Lehodey 2000). This phenomenon requires more investigations and results concerning skipjack population are presented here for 1960-1996.

Currents and primary production are averaged over the 030 m surface layer and interpolated with the sea surface temperature (SST) on a grid of one degree square resolution to be used with SEPODYM.

## Tuna Forage ( $F$ )

With the extension of the model to the whole Pacific basin, the parameterization of the forage population has been revised to take into account regions as different as the warm pool and the subarctic gyre. It is well established that metabolic rates are correlated to temperature. For example, while oceanic anchovy (Encrasicholinus punctifer) in the warmpool (SST $>28^{\circ} \mathrm{C}$ ) are mature at 4 months with a life span of $\sim 1$ yr, temperate anchovy species (SST $\sim 15-22^{\circ} \mathrm{C}$ ) have a much longer life span and turn-over rates (or population doubling time). For example, in the north west Pacific, the Japanese anchovy, Engraulis japonicas has a life span of $\sim 3$ years and mature at $\sim 1$ year (Whitehead et al 1988), that is 3 times the values indicated for the oceanic anchovy. Anchovies in the upwelling systems of Peru and Chili have similar biological characteristics. Therefore the two parameters $\mathrm{T}_{\mathrm{r}}$ and $\lambda$ that characterize F have been linked to SST (Figure 1). A first parameterization gives a "mean age" $\left(T_{r}+1 / \lambda\right)$ ?or turn-over time for F ranging from 4 months in the warmpool to $12-16$ months in the subarctic region (Fig. 2).


Figure 1. Functions based on SST used in for the parameterization of Tr and lambda that characterize the forage population. The step-like function for Tr is due to the one month time resolution of the model.


Figure 2. Distribution of the forage "mean age" based on an average SST distribution and the function shown in Figure 1.

Though detailed analyses are needed to refine and validate this preliminary parameterization, the predictions suggest realistic patterns both in terms of seasonal fluctuation and spatial dynamics. An illustration is given in the north transition zone chlorophyll front (TZCF) as defined by Polovina et al. (2001). Satellite telemetry data on movements of loggerhead turtles and detailed fisheries data for albacore tuna showed that both apex predators travel along this front as they migrate across the North Pacific (Polovina 2001). The predicted forage similarly reproduces a clear front of forage biomass (Fig. 3). The biomass of forage shows seasonal fluctuations in abundance with a minimum in February-March, and the position of the front varied substantially both at seasonal and interannual scales. It seems also possible to discern two different regimes coinciding with the decadal regime shift that occurred in 1976. After 1976 the front was shifted southward by 5 degrees in average. Since 1997, the front has returned to its pre-1976 position suggesting a possible new regime shift.


Figure 3. Latitude-time plot of the forage biomass averaged in the Transition Zone Chlorophyll Front box defined by latitudes $25 \mathrm{~N}-45 \mathrm{~N}$ and longitudes $180-150 \mathrm{~W}$ localised on the map above. The plot shows a seasonal fluctuation of the biomass and a latitudinal displacement in the position of the southern front. Two different regimes seem apparent before and after 1976 and a new shift may be occurring since 1997.

In the Kuroshio extension region ( $45 \mathrm{~N}-35 \mathrm{~N}$ ) the seasonal peak of forage biomass predicted in the previous simulation with constant parameters occurred in May-June. With this new parameterization these peaks occur later in summer between July and October (Fig. 4). This seems more realistic and in agreement with the sequence of biological events in that region, i.e., the spring bloom of phytoplankton in March-April followed by the peak in zooplankton biomass in May (Sugimoto and Tadokoro 1998). The peak in spawning season of small pelagic fish coincides with the peak in phytoplankton, e.g., $95 \%$ of eggs of the Japanese sardine, Sardinops melanostictus are released between February and May and dispersed in the Kuroshio extension zone (Heath et al., 1998). Then, after 12 months of larval stage these small pelagic fishes metamorphose to juveniles. Interestingly, the new parameterization improves the synchronism between seasonal peaks of forage abundance and skipjack catch in this Kuroshio extension zone (Fig. 4). As expected, increasing the mortality coefficient $\lambda$ of the forage population with decreasing temperature leads to lower turnover but higher biomass. In summary, predicted large scale features appear realistic in this region, but the coarse resolution of the model does not resolve the Kuroshio current, which is a strongly narrow ( $50-100 \mathrm{~km}$ ) jet following the southern coast of Japan.


Figure 4. Forage biomass in the Kuroshio region (average in the geographical box: 45N-35N, 180140 E ) for previous (constant) and new parameterization (varying with SST) of the forage population, and skipjack catch in the same area.

## Tuna habitats

Few changes have been made for the definition of skipjack adult tuna habitat index $\left(H_{a}\right)$ that combines the spatial distribution of forage with a temperature function. Several parameters have been tested for the temperature function and the retained function (1) slightly increases the range of temperature comparatively to the function used in previous simulations.

$$
\begin{equation*}
\mathrm{I}_{\mathrm{SST}}=1 /\left(1+\mathrm{e}^{(-0.5(\mathrm{SST}-23))}\right) \tag{1}
\end{equation*}
$$

A first definition of the spawning habitat index $\left(H_{s}\right)$ used to constrain the recruitment to environmental conditions was given in Lehodey (2001b). Impacts of temperature, primary production and forage biomass on this index were tested and results compared to the recruitment and biomass predicted in several regions by the statistical model MULTIFAN-CL (Fig. 5).


Figure 5. Geographical areas defined for the skipjack Multifan-CL application.

While the use of $\mathrm{P} / \mathrm{F}$ ratio produced high spawning and recruitment in region 5, i.e., the western equatorial Pacific, the primary production alone predicted high spawning and recruitment in the region 6 , that is the central equatorial Pacific. According to the recruitment predicted by MULTIFAN-CL (Hampton, 2002), the highest recruitment occurs in region 6 followed by region 5 . Therefore, with the temperature, the primary production would have the main impact on the spawning. The large peak of recruitment likely associated with the bloom of phytoplankton at $165^{\circ} \mathrm{E}$ on the Equator in 1998 would confirm this hypothesis. Therefore the spawning habitat index $H_{s}$ was simplified to take into account SST and primary production only (2). However, it was necessary to reduce the range of the spawning temperature (3) to keep a realistic overall distribution and a good agreement between predicted and observed catch (Fig 6). A priority was also given to the prediction of recruitment and biomass at similar levels than those predicted from MULTIFAN-CL estimates in the main regions (i.e., 5 and 6).

$$
\begin{align*}
H_{s} & =\theta_{s} \mathrm{e}^{(\alpha \operatorname{Ln}(P)}  \tag{2}\\
\text { with } \quad \theta_{s} & =1 /\left(1+\mathrm{e}^{(-2(\mathrm{SST}-29))}\right) \tag{3}
\end{align*}
$$



Figure 6. Temperature function of the skipjack spawning habitat.

## Tuna population

## Movement

The tuna movement is described with an advection-diffusion equation (see previous references and Sibert et al. 1999) with the advective term proportional to the gradient of the habitat through a coefficient of proportionality $X_{o}$ In previous simulations this coefficient was constant whatever the age, and a function was used to increase the diffusion $(D)$ and the advection $\left(X_{o}\right)$ at low values of habitat index (to mimic change in tuna behaviour according to the quality of habitat). In this new version both $D$ and $X_{o}$ are now proportional to the size of the fish. A simple preliminary linear relationship is used:

$$
\begin{align*}
& \mathrm{X}_{a}=\mathrm{X}_{\mathrm{o}} \cdot \mathrm{~L}_{\mathrm{a}} \cdot \mathrm{c}  \tag{4a}\\
& D_{a}=D . \mathrm{L}_{\mathrm{a}} \cdot \mathrm{c} \tag{4b}
\end{align*}
$$

with $L_{a}$ the fish length at age $a$, and $c=0.01 . X_{o}$ and $D$ become maximal values of advection and diffusion coefficient respectively. The change of these parameters according to values of habitat and habitat gradient are illustrated in Fig 6 and Fig. 7. The value of $X_{o}$ and $D$ were scaled to be in agreement with the range of values estimated from tagging data by Sibert et al. (1999). However, additional information, e.g. observed tuna movements from electronic tags and comparisons with Individual-Based Models would be helpful to improve this parameterization.


Figure 7. Change in the diffusion coefficient for tuna movement according to the size of fish and the habitat index


Figure 8. Change in advection according to the gradient of habitat and the size of the fish without consideration of habitat values (left) and change in advection for a skipjack of $\sim 50 \mathrm{~cm}$ ( 5 quarter) according to habitat and habitat gradient (right).

## Skipjack population

The skipjack tuna population in SEPODYM is age-structured to account for growth and gear selectivity. Growth and mortality-at- age estimates are those estimated from MULTIFAN-CL analyses (Hampton 2002). The total level of recruitment (or spawning) is adjusted, so that the stock biomass estimates are roughly equal to those obtained independently with MULTIFAN-CL estimates. While MULTIFAN-CL produces recruitment and biomass estimates from robust statistical methods, SEPODYM recruitment and biomass are predicted only from environmental constraints. Therefore, comparisons of fluctuations in time and by region between these two independent estimates are useful to investigate hypotheses on the mechanisms of recruitment.

## Tuna Fisheries

Skipjack tuna fisheries have been classified into pole-and-line and purse seine fisheries, the latter being sub-classified by set type categories: unassociated schools, and schools associated with log, fish aggregation device (FAD), or animals (dolphin, whales, whale shark...). Each fishery has separate catchability coefficients and age-based selectivity function (Fig. 8). The selectivity functions are adjusted to obtain predicted length frequency distributions of catch in agreement with the observed
distribution. Fishing effort of each feet vary by month and in space, with a one degree square resolution except for the Philippine and Indonesia fleets that provide data aggregated by five degree square, and year. The catchability coefficients are scaled to obtain estimated catches at the same level as observed catches. Results of the simulation are compared to observed fishing data by fleets, such as total monthly catch, spatial distribution of catch, and distribution of length frequencies.


Figure 9. Selectivity by fishery used in the present application of sepodym to skipjack population and fisheries (PLINE: pole-and-line, PS: purse seine, ANI: animal, UNA: unassociated, LOG: log, FAD: fish aggregation device).

## Application to skipjack

Total recruitment (biomass of fish at age one quarter) and biomass estimates for the six regions used in MULTIFAN-CL skipjack application (Fig. 5) are extracted from the SEPODYM prediction to be compared with the MULTIFAN -CL estimates. The value of the coefficient $\alpha$ in the spawning habitat affects the range of fluctuation in the recruitment (see Lehodey 2001). As the value of $\alpha$ increases, areas characterized by high primary production have higher positive impacts on recruitment. However, higher value of $\alpha$ also increases the patchy distribution of the overall distribution of juveniles. This may be realistic, but if spatial distribution in primary production or movements of young and adult tuna are not well described in the model, the correlation between predicted and observed catch will decrease compared to a simulation with more diffuse and homogeneous distribution of the recruitment.

Total biomass of skipjack population and of skipjack at age one quarter (recruitment) predicted by the statistical model MULTIFAN-CL and the environmental model SEPODYM are compared in Fig. 10. Both series have high recruitment and biomass after the main El Niño events of 1972-73, 1977-78, 1982-83, 1987-88 and 1991-92, and conversely low levels associated with the two La Niña events of 1975 and 1989.

Comparison of recruitment estimates by regions defined for MULTIFAN-CL application show similar level of recruitment for both model predictions in regions 5 and 6 that provide most of the total recruitment (Fig. 11). The variability of recruitment is stronger in region 6, likely associated to the ENSO-related displacement of the convergence front between the warm pool and the cold tongue. The level of recruitment is very low in region 4 for the SEPODYM prediction. In region 1 and 2 the series shows similar variations in the seasonal peaks but the SEPODYM recruitments are lower by a factor of 5 and 10 in region 1 and 2 respectively. The difference increases to a factor 30 in region 3 . A very plausible explanation is the lack of resolution of the Kuroshio and its extension along latitude $\sim 35 \mathrm{~N}$ as the strong current likely transport the juvenile skipjack in the north east Pacific (i.e., region 2 and 3). Detailed sea surface temperature data show that warm eddies with $\mathrm{SST}>28^{\circ} \mathrm{C}$ move along the Kuroshio extension in summer north of $30^{\circ} \mathrm{N}$. This cannot be reproduced by the model and has direct consequences on the recruitment given the temperature function used (Fig. 6)

The differences between both model series are much lower when comparing predicted biomass (Fig. 12), suggesting possible movement of tuna from areas outside of regions 1 to 6 . For example, this is likely the case with fish coming from the western Pacific area east of $110^{\circ} \mathrm{E}$ and moving into region 1 to 3 along a band of favorable habitat following the Kuroshio current.



Figure 10. Comparison of skipjack recruitment (total biomass of fish of age 1 quarter) and total biomass estimates from MULTIFAN-CL (thick curve) and SEPODYM (thin curve) in the WCPO (sum of 6 regions shown on Figure 8).

The predicted catch length frequency distributions present a general agreement with the observation for pole-and-line, FAD and log fisheries, indicating that selectivity coefficients are reasonably defined (Fig. 13). Sets on unassociated schools select large fish ( $>40 \mathrm{~cm}$ ) and despite a strong selectivity imposed for small sizes, there is a shift in the size of predicted catch. There is no available length frequencies for sets on schools associated with animals and its selectivity function was considered similar to the log fishery. The purse seine sets associated to $\log$ or FAD select the smallest fish. These sets on unassociated schools have also the highest catchability coefficient, followed by sets on FADs and logs. The pole-and-line fishery has an intermediate coefficient and the purse seine set associated to animals a low coefficient. However, animal associated sets are mainly from the eastern Pacific and most often correspond to sets targeting yellowfin rather than skipjack tuna.

The total predicted catch follow the observed catch fairly well for the tropical fisheries, that is purse seine fisheries (Fig. 14). The fisheries have been described on the basis of very broad criteria. A better description will require breaking up the present fisheries into their tropical and sub-tropical components, i.e., Japan pole-and-line and offshore purse seine fleet, and into western and eastern components. This should facilitate the analysis, but also likely correspond to different catchability, e.g., skipjack are likely more vulnerable in the Kuroshio extension when they are "trapped" in warm eddies. The domestic fleets from the Philippines and Indonesia that use a mixing of different gears should be also detailed.

Spatial correlations between predicted and observed catch (Fig. 15) present a clear seasonal pattern for the pole-and-line fleet that reflects the inability of the model to capture the dynamics of the Kuroshio
extension. Otherwise, spatial correlations for other fisheries are fairly good and $r$ values fluctuate around an average of 0.6 to 0.7 .

## Conclusion

New developments in the modelling of forage result in encouraging and more realistic predictions than in the previous version. However, additional analyses are needed to validate and refine the parameterization of temperature functions. With the consideration of the size for modelling tuna movements, these changes together improve the spatial dynamics of the skipjack population and allowed to increase the magnitude of fluctuation in the recruitment to approach the level of fluctuation predicted by the statistical model MULTIFAN-CL, and without decreasing the level of correlation between predicted and observed catch. Further improvements of the spatial dynamics require an increasing resolution in regions with strong dynamics such as the Kuroshio region and maybe the Coral and Tasman Seas. Predicted fields of physical-biogeochemical coupled models need to be investigated in detail, especially over the recent period covering the 1997-98 El Niño.

These results do not change the previous conclusion on the impact of the ENSO variability. There is a positive (negative) effect of El Niño (La Niña) events on the recruitment that is propagated into the stock in the following two-three years. The mechanisms suggested by this modelling are an extension of the temperature spawning habitat combined with an increase of primary production in the western central Pacific during El Niño conditions. The spawning habitat based on satellite derived data (SST, chlorophyll) associated with a high resolution physical model could be used to predict potential "high spots"of spawning and could help in the preparation of research cruises.

After the peak of biomass and catch related to the strong 1997-98 El Niño event, the last La Niña episode of 1998-2001 should lead to a decrease of the skipjack stock biomass in the next two years.





Figure 11. Comparison of skipjack recruitment from MULTIFAN-CL (thick curve) and SEPODYM (thin curve) for the 6 regions defined for Multifan CL analysis.


Figure 12. Comparison of skipjack total biomass from MULTIFAN -CL (thick curve) and SEPODYM (thin curve) for the 6 regions defined for Multifan CL analysis.


Figure 13. Observed (thick curve) and predicted (thin curve) length frequencies distribution of skipjack catch by fishery (PL: pole-and-line, PS: purse seine, Ani: animal, UNA: unassociated, LOG: $\log$, FAD: fish aggregation device).






Figure 14. Total observed (thick curve) and predicted (thin curve) skipjack monthly catch by fishery (metric tonnes).


Figure 15. Monthly spatial (one degree square resolution) correlation coefficients (crosses) between observed and predicted skipjack catch for the five fisheries. The bars give the number of observations for each month.

## Reference List

Bertignac,M., Lehodey,P., and Hampton,J. 1998. A spatial population dynamics simulation model of tropical tunas using a habitat index based on environmental parameters. Fish.Oceanogr. 7: 326335.

Chai,F., Dugdale,R.C., Peng,T.-H., and Barber,R.T. 2002. One Dimensional Ecosystem Model of the Equatorial Pacific Upwelling System, Part I: Model Development and Silicon and Nitrogen Cycle. Deep Sea Research II.

Dugdale R.C., Barber F., Chai F., Peng T.H., Wilkerson F.P. , 2002. One dimensional ecosystem model of the equatorial Pacific upwelling system, Part II: Sensitivity analysis and comparison with JGOFS EqPac DAta. Deep Sea Res. II: 49 (13-14), 2746-2762
Hampton J., 2002. Stock assessment of skipjack tuna in the western and central Pacific Ocean. $15^{\text {th }}$ SCTB, SPC, Noumea, New Caledonia. Working Paper SKJ-1.

Heath M.R., Zenitani H., Watanabe Y., Kimura R., Ishida M. 1998. Modelling the dispersal of larval Japanese sardine, Srdinops melanosticus, by the Kuroshio current in 1993 and 1994. Fish.Oceanogr. 7: 335-347.

Lehodey,P., Bertignac,M., Hampton,J., Lewis,A., and Picaut,J. 1997. El Nino Southern Oscillation and tuna in the western Pacific. Nature 389: 715-718.
Lehodey,P., Andre,J.-M., Bertignac,M., Hampton,J., Stoens,A., Menkes,C., Memery,L., and Grima,N. 1998. Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical bio-geochemical model. Fish.Oceanogr. 7: 317-325.

Lehodey, P. 2000. Impacts of the El Niño Southern Oscillation on tuna populations and fisheries in the tropical Pacific Ocean. Secretariat of the Pacific Community No. RG-1.

Lehodey,P. 2001. The pelagic ecosystem of the tropical Pacific Ocean: Dynamic spatial modelling and biological consequences of ENSO. Prog.Oceanog., 30 pp.
Li, X.; Chao, Y.; McWilliams, J.C.; Fu, L-L. 2001. A Comparison of Two VerticatMixing Schemes in a Pacific Ocean General Circulation Model. Journal of Climate, 14 (7): 1377-1398

Murtugudde,R.G., Signorini,S.R., Christian,J.R., Busalacchi,A.J., McClain,C.R., and Picaut,J. 1999. Ocean color variability of the tropical Indo-Pacific Basin observed by SeaWiFS during 19771998. J.Geophys.Res. 104: 18351-18366.

Polovina, J. J., E. Howell, D. R. Kobayashi, and M. P. Seki, 2001, "The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources," Prog. Oceanog. 49, 469-483.
Sibert,J.R., Hampton,J., Fournier,D.A., and Bills,P.J. 1999. An advection-diffusion-reaction model for the estimation of fish movement parameters from tagging data, with application to skipjack tuna (Katsuwonus pelamis). Can.J.Fish.Aqu.Sci. 56: 925-938.

Stoens,A., Menkes,C., Radenac,M.-H., Dandonneau,Y., Grima,N., Eldin,G., Memery,L., Navarette,C., Andre,J.-M., Moutin,T., and Raimbault,P. 1999. The coupled physicalnew production system in the equatorial Pacific during the 1992-95 El Niño. J.Geophys.Res. 104: 3323-3339.
Sugimoto T., Tadokoro K., 1998. Inter-decadal variations of plankton biomass and physical environment in the North Pacific. Fish.Oceanogr. 7: 289-300
Whitehead, P.J.P., G.J. Nelson and T. Wongratana, 1988. FAO species catalogue. Vol. 7. Clupeoid fishes of the world (Suborder Clupeoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Part 2 - Engraulididae. FAO Fish. Synop. 7(125)Pt. 2:579 p.

