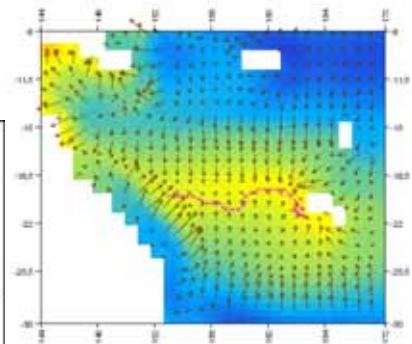
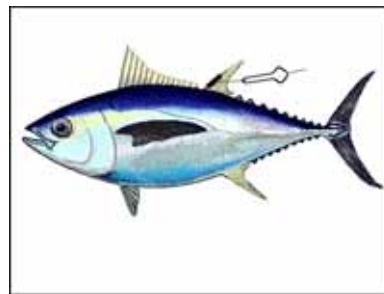
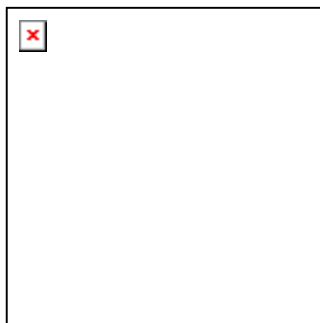




The influence of the environment on horizontal and vertical bigeye tuna movements investigated by analysis of archival tag records and ecosystem model outputs



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Introduction

The purpose of this work is to investigate the influence of the environment on bigeye tuna movements in order to develop a rule-based IBM, where fish will be able to ‘swim through’ environmental data for the simulation of spatial dynamics from individual to population scale. One of the main reasons for developing individual-based models is to investigate individual variability and its potential significance for population dynamics (Huston et al. 1988; Grimm 1999).

The SEAPODYM model developed by Lehodey (2004) requires the parameterisation of fish behaviour in relation to environmental variability, which may be more accurately achieved by developing rule-based I/ABMs based on archival tag data. This project is funded by the Pelagic Fisheries Research Program (University of Hawaii at Manoa) as part of the *Mixed Resolution Models for Individual to Population Scale Spatial Dynamics* project.

Data available

Two types of data were available (Fig 1) :

- *archival tag records* from the WCPO : records from 17 “classic” archival tags deployed in the Coral Sea between 1999 and 2001 (47 to 1441 days at liberty) during a joint CSIRO/SPC project (Clear et al. 2005; Evans et al. 2005) and from 7 “pop-up” (PSAT) archival tags deployed by SPC in the waters surrounding Papua New Guinea, New Caledonia and Tonga between 2002 and 2005 (13 to 109 days of recording). Time and space scales were not the same for PSAT records (data averaged over 1 to 6 hours and defined depth layers) as for AT records (4 minutes time step ; depth in meters).
- *ocean model outputs*, including space-time forage biomass estimations from SEAPODYM model developed by Patrick Lehodey (Lehodey, 2004). The initial scale for SEAPODYM outputs (1 month, 1° in latitude/longitude, 2 layers on the vertical) was improved in 2005 (10 days, 0.5° in latitude/longitude, 3 layers on the vertical : 0-200 m, 200-500 m and >500 m) (Lehodey, 2005).

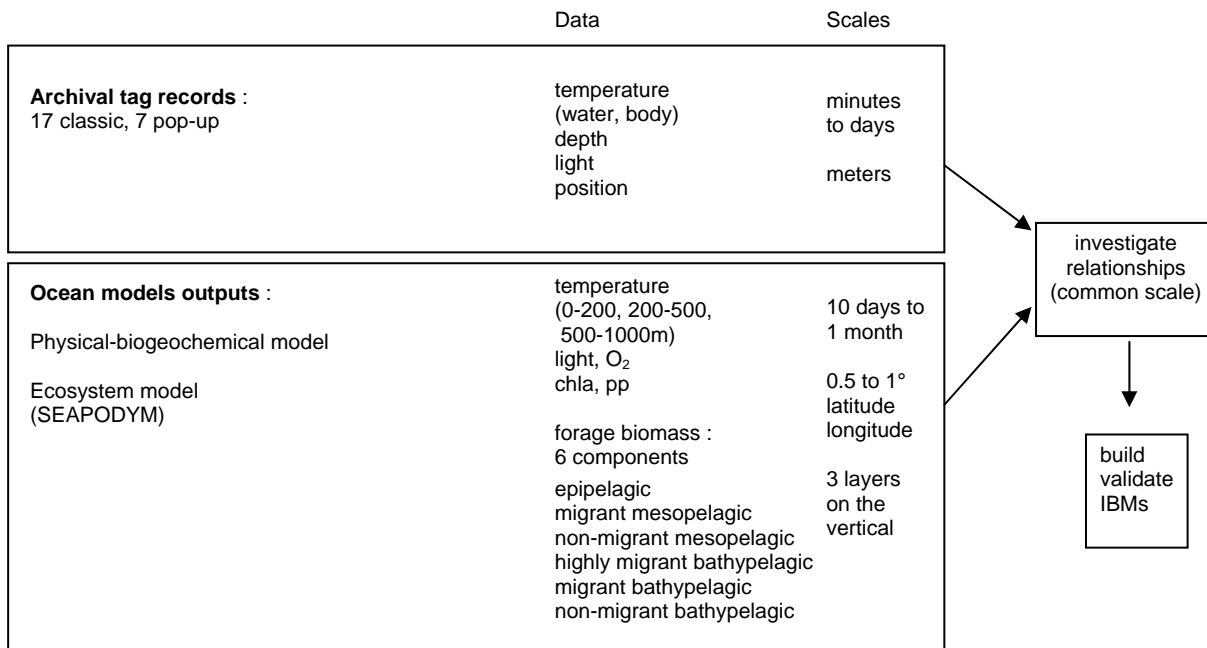


Figure 1 : data, scales and method

The difference in scales between individual tag records and ocean model outputs represents a challenge in the objective of developing models for tuna movements. Therefore it was decided to first *investigate the relationships between tagging and model data* on a common scale. The results of this exploratory analysis will be used to develop a rule-based IBM, in order to validate the parameterisation of fish behaviour in relation to environmental variability used in SEAPODYM (Lehodey, 2004) and to validate more mechanistic (i.e. physiology-based) IBMs for tuna behaviour (Kirby *et al.*, 2003).

Horizontal movements

Horizontal movements were investigated on a monthly scale then on a 10-day scale. Light records from the pop-up archival tags were processed using Wildlife Computers ‘Global Position Estimator’ software to estimate longitude and latitude. The horizontal movements between release and pop-up locations (Fig. 2) could not be estimated, due to the low quality of the records.

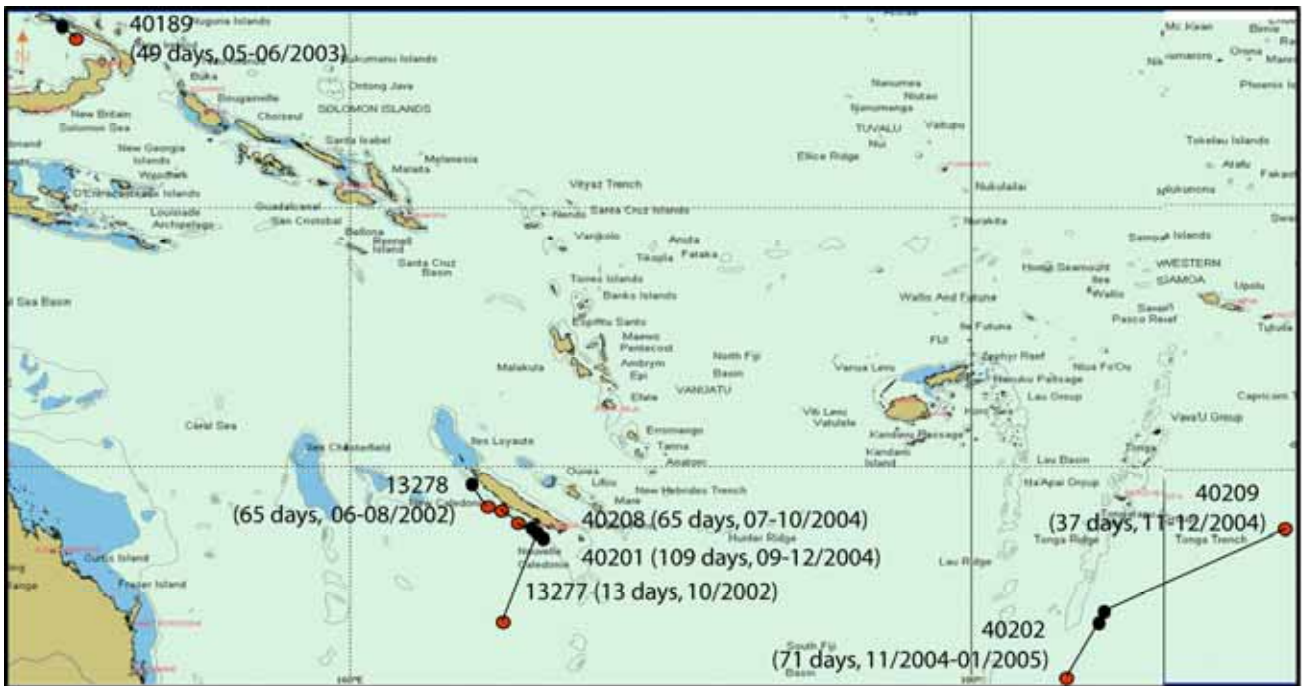


Figure 2 : release locations (black dots), pop-up locations (red dots) and number of recording days for 7 PSAT archival tags deployed on bigeye tunas by SPC in the WCPO between 2002 and 2005.

Light records from the archival tags released in the Coral Sea (Clear et al. 2005) were processed by CSIRO using Wildlife Computers ‘Global Position Estimator’ software to estimate longitude and latitude. Most probable horizontal movements were then estimated from the geolocation data using Kalman filter analysis (Kftrack R Package by J. Sibert and A. Nielsen; Sibert *et al.* 2003). While many individuals show a high degree of residency in the NW Coral Sea waters (Clear et al; 2005), two individual tag records clearly exhibit eastward migration to New Caledonian waters (Fig. 2) at the same period of the year (Oct–Apr). The monthly evolution of predicted sea surface temperature and forage biomass from Jan 1999 to Dec 2002 in the area delimited by the supposed migration route (148°E–165°E, 16°S–22°S; Fig. 3) suggest that this is a time of seasonal warming and peak biomass of epipelagic and migrant mesopelagic forage.

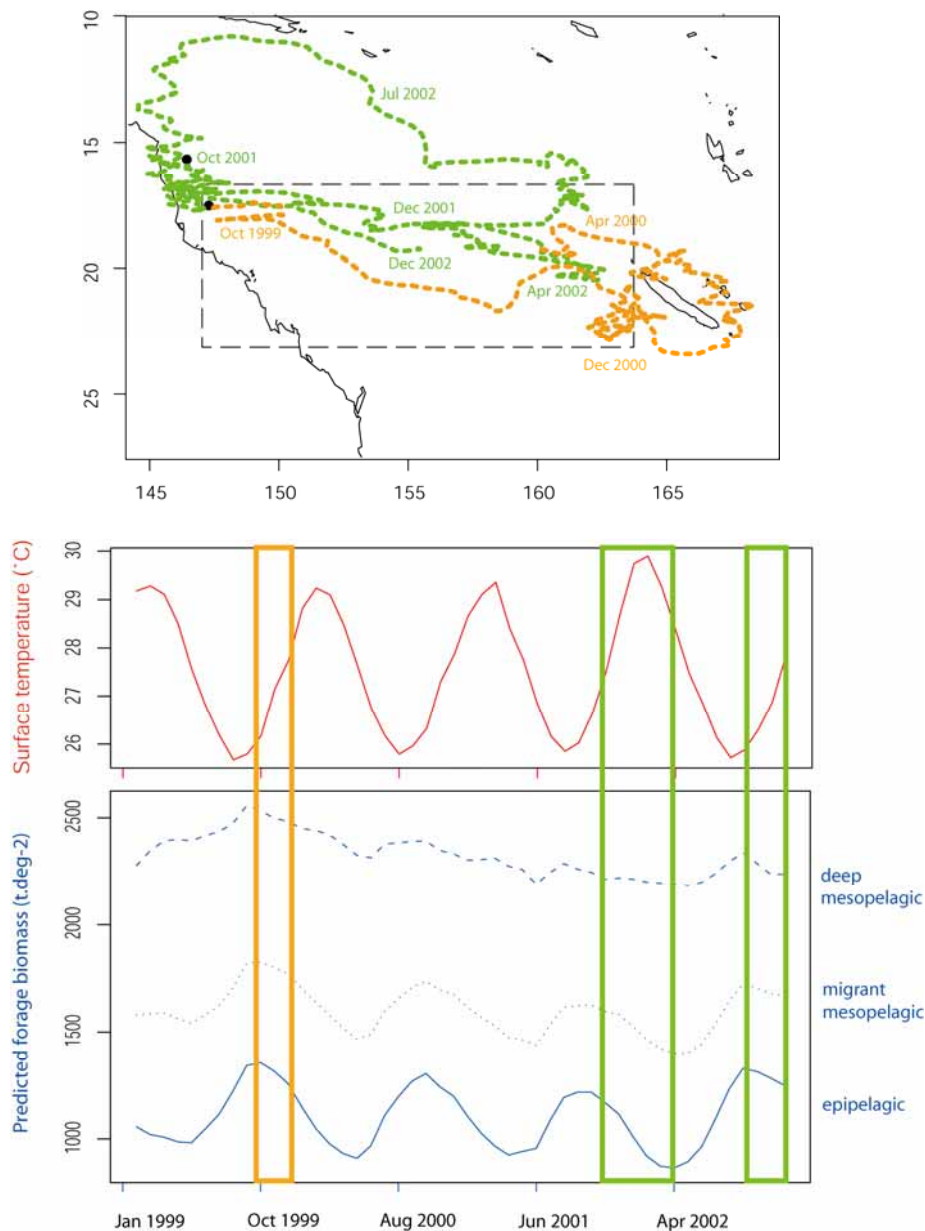


Figure 3 : Migration route of two bigeye tunas and seasonal evolution of environmental variables. Top: most probable tracks for 2 bigeye tagged in Oct 1999 and 2001 in the Coral Sea (orange and green dotted lines). Dashed rectangle: area defined for the extraction of environmental variables. Bottom: Monthly SST and biomass of 3 forage components (epipelagic, migrant mesopelagic, deep mesopelagic) from Jan 1999 to Dec 2002. Rectangles (orange and green): months with tuna migration through this area.

A first application of the coupling between the individual tag records and environmental data estimated along their tracks was the comparison of sea surface temperatures at a finer scale. Fig. 4 shows a general coherence between predicted monthly temperature and temperatures recorded by archival tags. Discrepancies can be attributed to geolocation errors. Latitude, which is subject to errors of several degrees (Sibert *et al.* 2003) was adjusted so as to minimize these discrepancies (example on Fig. 4).

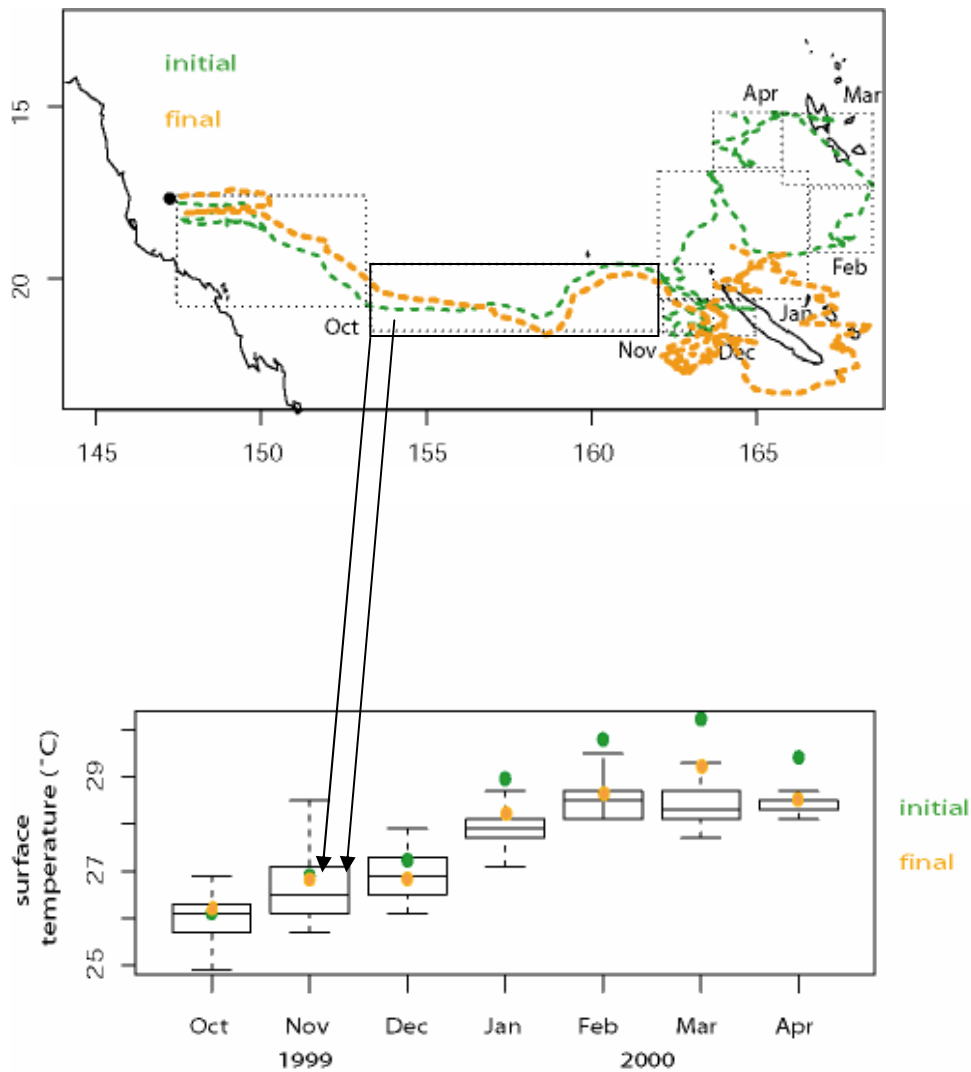
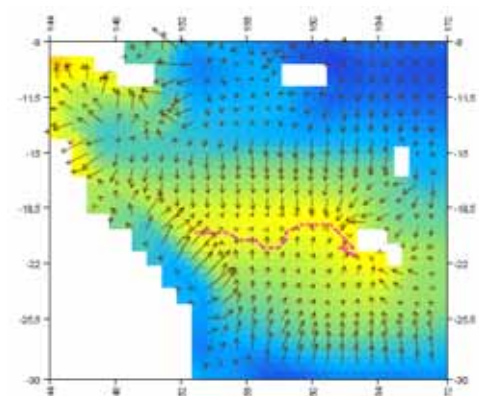


Figure 4 : Comparison between surface temperatures recorded by a tag (boxplot) along its initially estimated track (green dotted line) and extracted from the ocean model (green point = space-time average). Correction of latitude values (orange dotted line = corrected track) in order to reduce the discrepancies between tag and model temperature values (orange points).

A second application of the coupling between the individual tag records and environmental data estimated along their tracks was the validation of ‘bigeye habitat’ defined in SEAPODYM (Fig.5) as a function of temperature and forage biomass. On a monthly scale, a general coherence was between some tracks and the hypothesized habitat. Further parameterisation is needed to simulate feeding and reproductive behaviour and extend these results to more individuals and to the year cycle.

Figure 5 : Elements for the validation of ‘bigeye habitat’ in SEAPODYM (Lehodey 2004)



Vertical movements

Vertical movements were also investigated. Bigeye tunas exhibited four types of vertical behaviour (Fig. 6) : the ‘classic’ or W-shaped type with typical depths of 300-500 m during the day and 0-200 m during the night (74 % of total time), the ‘mixed’ type with only short dives under 200 m during the day (24 %), the ‘surface’ type with depth continuously <100 m during day and night (1 % of total) and the ‘deep dive’ type consisting of short-duration dives <600 m (1 %).

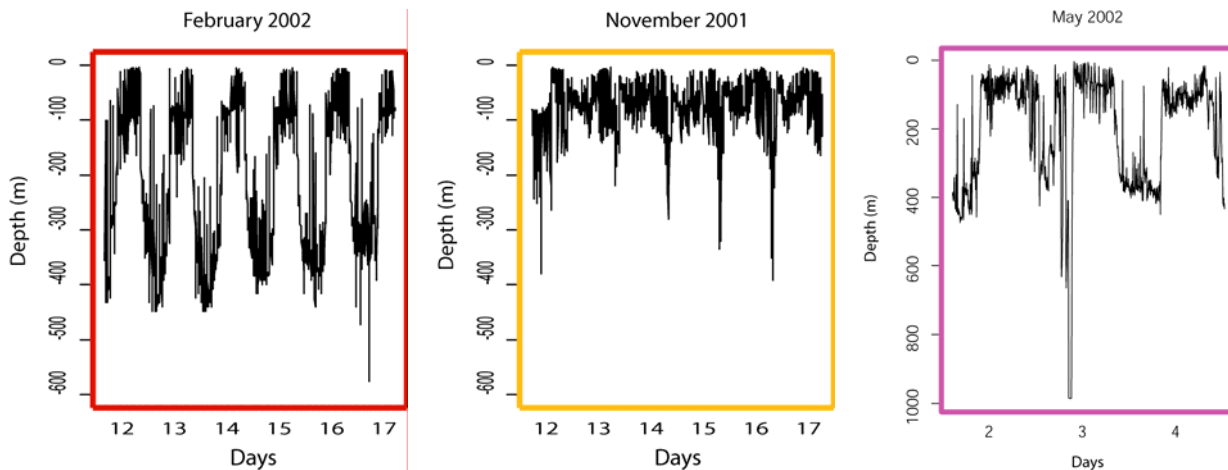
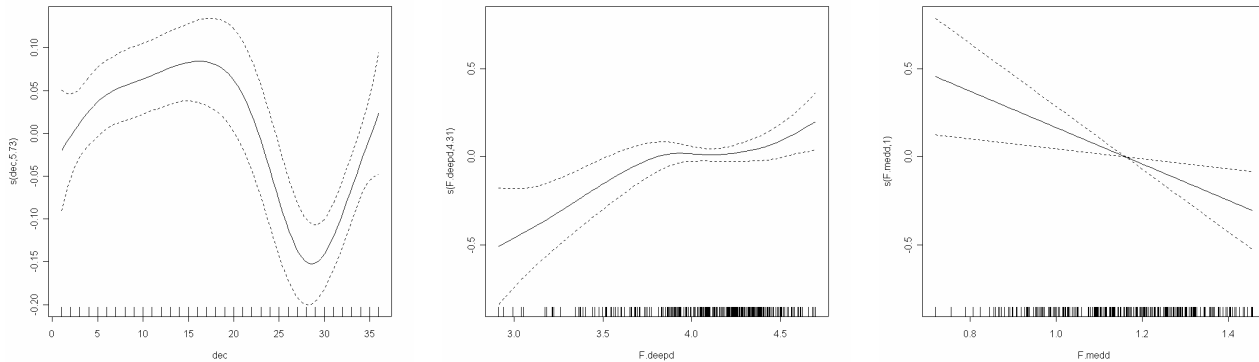


Figure 6 : examples of ‘classic’ (left), ‘mixed’ (middle) and ‘deep dive’ (right) vertical behaviour.

The relationships between the type of behaviour and the environment encountered along the tracks were investigated using the same data extraction procedure as for horizontal data. After the examination of a series of possible variables for vertical behaviour (i.e. mean depth during the day/night/both, depth variance during the day/night/both, percentage of time spent within different depth ranges during the day/night/both), average depth during the day and proportion of time spent above 200 m were considered as good descriptive variables of the major behavioural types (‘classic’ and ‘mixed’), the latter allowing the inclusion of PSAT data in the analyses.

Generalized Additive Models were built and examined using a procedure of stepwise selection of covariates. The dependent variable (or variable which variations are to explain) was the average depth during the day during a 10-day archival tag record. The covariates were time (in 10-day periods), temperature in the three layers (0-200 m, 200-500 m, >500 m) during this period, dissolved oxygen concentration in the three layers, primary production over the water column and forage biomass (i.e. sum of the different forage components) estimated during the day for the three layers. The covariates were ranked and selected according to their significance and predictive power of the models including them.

The ‘best’ model according to these criteria was a three-covariate model (Fig. 7).



Formula:

$mdday \sim s(F.deepd) + s(time) + s(F.meddd)$

Approximate significance of smooth terms:

	edf	chi.sq	p-value
s(time)	7.401	75.56	8.0485e-12
s(F.deepd)	5.914	47.837	5.5682e-08
s(F.meddd)	1	3.8352	0.051199

R-sq.(adj) = 0.257 Deviance explained = 29.4%
 GCV score = 2736.7 Scale est. = 2592.2 n = 290

Figure 7 : summary of ‘best’ GAM selected (bottom). Plots for the 3 selected covariates : ‘time’ (10-day period), ‘forage biomass in the deep layer (>500m) during the day’ and ‘forage biomass in the middle layer (200-500m) during the day’ (top).

Time (in 10-day periods) was the most significant covariate, which shows the seasonal variation in vertical behaviour (Fig. 7), with a peak in August-November (time steps 22 to 33).

Average depth during the day was positively related to estimated forage biomass in the deep layer (>500m) and negatively related to estimated forage biomass in the ‘middle’ layer (200-500m). This suggests rather logically that bigeye tunas, classically swimming at depths 200-500 m during the day, would dive deeper as bathypelagic forage biomass increases and mesopelagic biomass decreases.

There was a clear seasonal trend in the vertical behaviour during the day, in spite of important individual variability (Evans et al. 2005). Average depth during the day was closer to the surface from August to November (Fig. 8). A higher proportion of daytime was spent in surface waters during these months by nearly all bigeye tuna tagged in the Coral Sea (Fig. 9a). The PSAT archival tag records from New Caledonia and Tonga areas suggest the same kind of seasonal shift in depth preferences (Fig. 9b). A higher proportion of time was spent in deeper waters at night during the same spring period by bigeye tuna tagged both in the Coral Sea and in NC and Tonga waters (not illustrated).

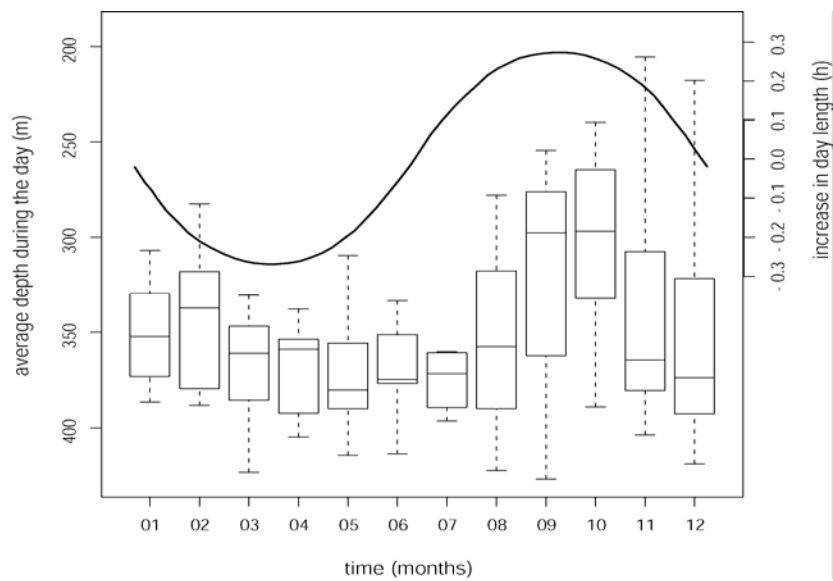


Figure 8 : Average depth during the day by month (boxplots) recorded by archival tags released in the Coral Sea and gradient of day length at latitude 25°S during the year (solid line).

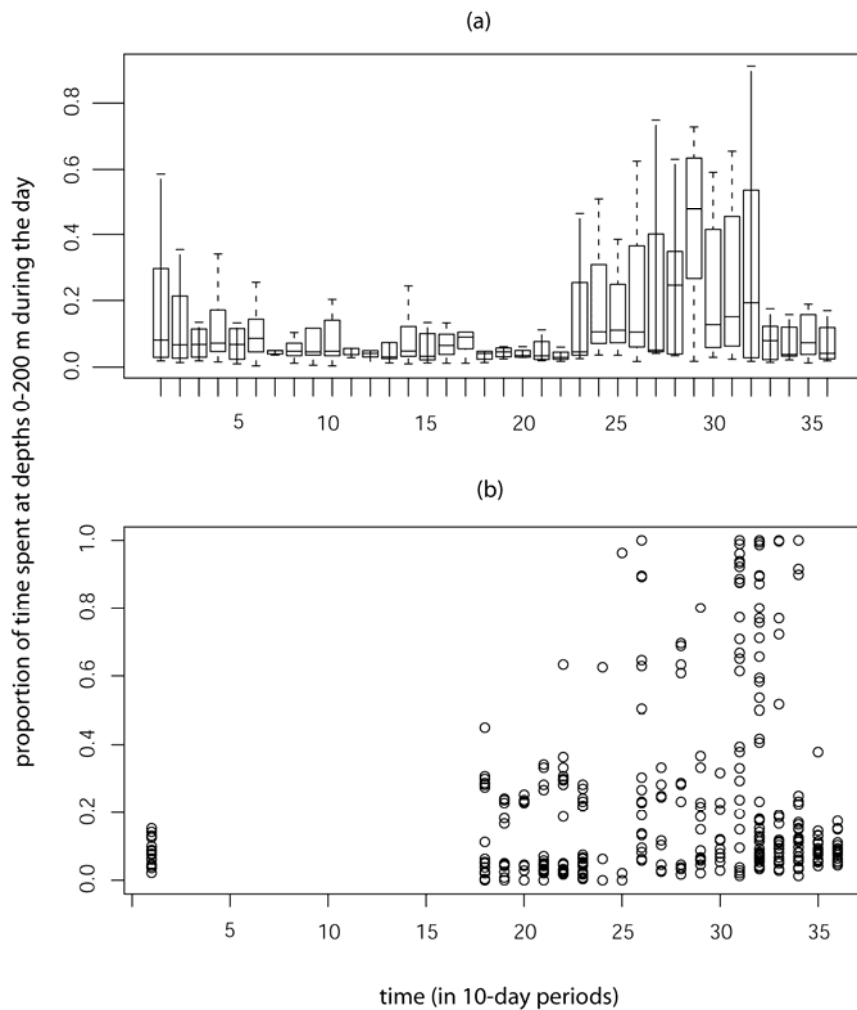


Figure 9 : Proportion of time spent at depths 0-200 m during the day by 10-day periods (from January to December) recorded by archival tags released in the Coral Sea (a) and by PSAT archival tags (b) in waters around New Caledonia and Tonga.

An analysis of the environment estimated from SEAPODYM outputs corresponding to the 10-day geolocation areas of archival tags released in the Coral Sea (same data extraction procedure as for horizontal data) showed that this shift in vertical behaviour corresponds to the period of :

- maximum increase in day length (Fig. 7)
- warming of the surface layer (Fig. 10)
- drop in primary production after a peak in July (Fig. 10)
- peak in forage biomass in the surface layer (Fig.10)
- peak then drop in forage biomass in the layer 200-500 m (Fig. 10)

In the waters around New Caledonia and Tonga (area 160 E-170 W, 20 S-30 S), this period also corresponds (Fig. 10) to a peak in the average forage biomass during the day in the surface layer (0-200 m) estimated from SEAPODYM outputs and to a secondary peak the average forage biomass during the day in the intermediate layer (200-500 m).

In order to put some statistical hierarchy in these factors, a GAM model was built using a procedure of stepwise selection of environmental covariates, excluding time (Fig. 11). The proportion of time spent in the surface layer during the day increased most significantly in relation to the forage biomass in the surface layer during the day (Fig. 11) and to the increase in temperature.

The peak in forage biomass in the upper layer is mainly due to a spring increase in epipelagic forage biomass, particularly obvious in the NW Coral Sea (not illustrated). The simulation results are coherent with some observations, *e.g.* the aggregations of bigeye tunas observed in surface waters of this area during the spring months in association with spawning concentrations of 'mesopelagic migrant' lantern fish *Diaphus sp.* (Mc Pherson, 1988). The higher proportion of time spent in surface waters during the day and in deeper waters during the night may be related to such prey aggregations during the spring months.

It is however difficult to distinguish the roles of feeding and reproduction in the seasonal shift in vertical behaviour during the day and the night. Indeed most of the tagged fish had reached size at maturity (Clear et al. 2005) at the time of recapture and spawning activity (catches of ripe females) has been reported in the Coral Sea from August to December (Farley et al., 2003). Spawning has been observed in the Pacific during the first half of the night (Nikaido et al. 1991), while tag records suggest deeper dives would mainly occur during the second part of the night (not illustrated).

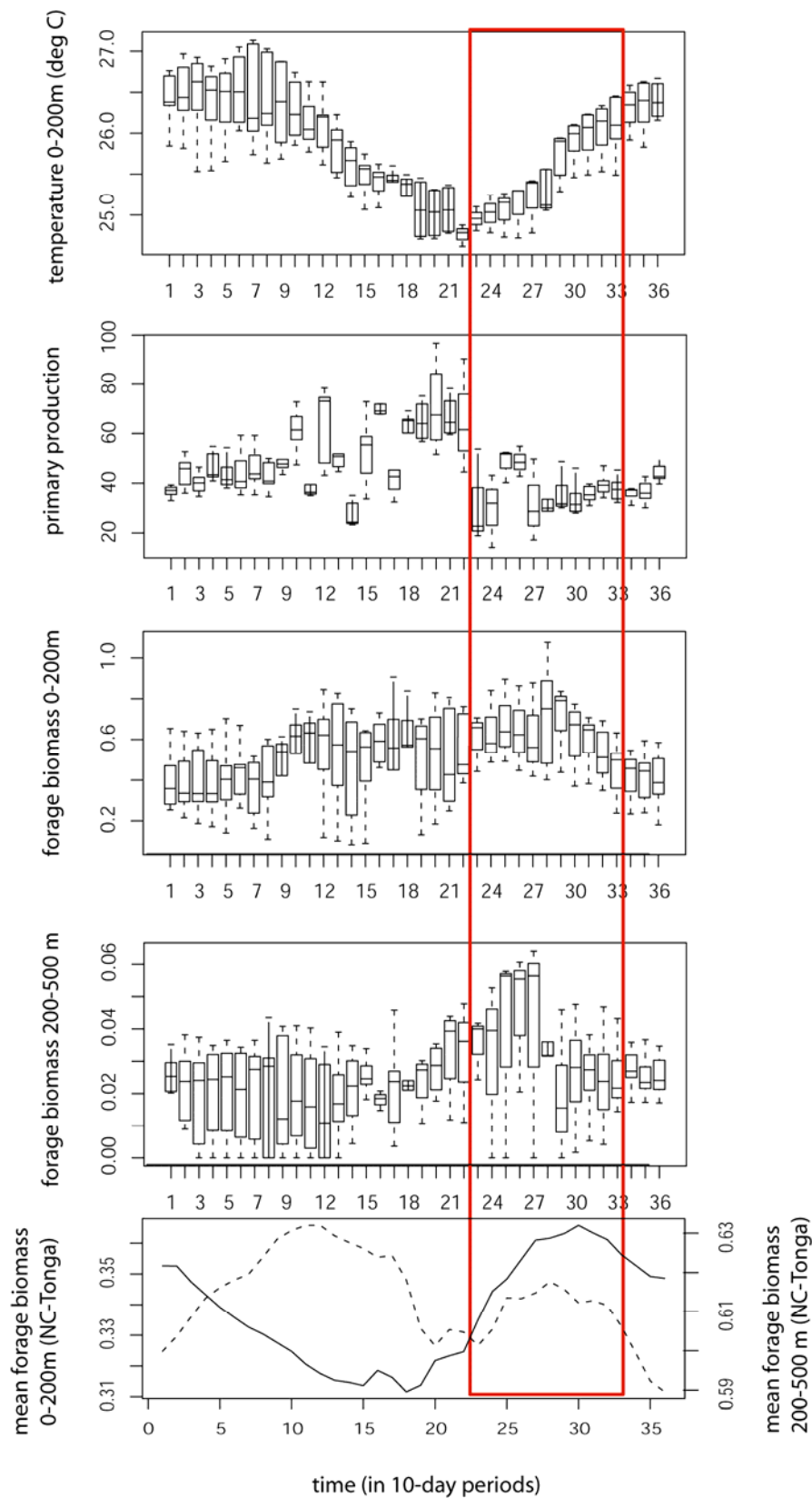


Figure 10 : Top : Evolution (boxplots, from January to December, time in 10-day periods) of temperature in the surface layer (0-200 m), primary production, forage biomass in the surface layer (0-200 m) and in the intermediate layer (200-500 m) estimated from SEAPODYM outputs corresponding to the 10-day geolocation areas of archival tags released in the Coral Sea. The red rectangle corresponds to the period of higher proportion of time spent in surface waters by bigeye tuna (cf. Fig. 9a). Bottom : evolution of average forage biomass in the surface layer (0-200 m, solid line) and in the intermediate layer (200-500 m, dotted line) estimated from SEAPODYM outputs corresponding to the waters around New Caledonia and Tonga (area 160 E-170 W, 20 S-30 S) from 1999 to 2002 .

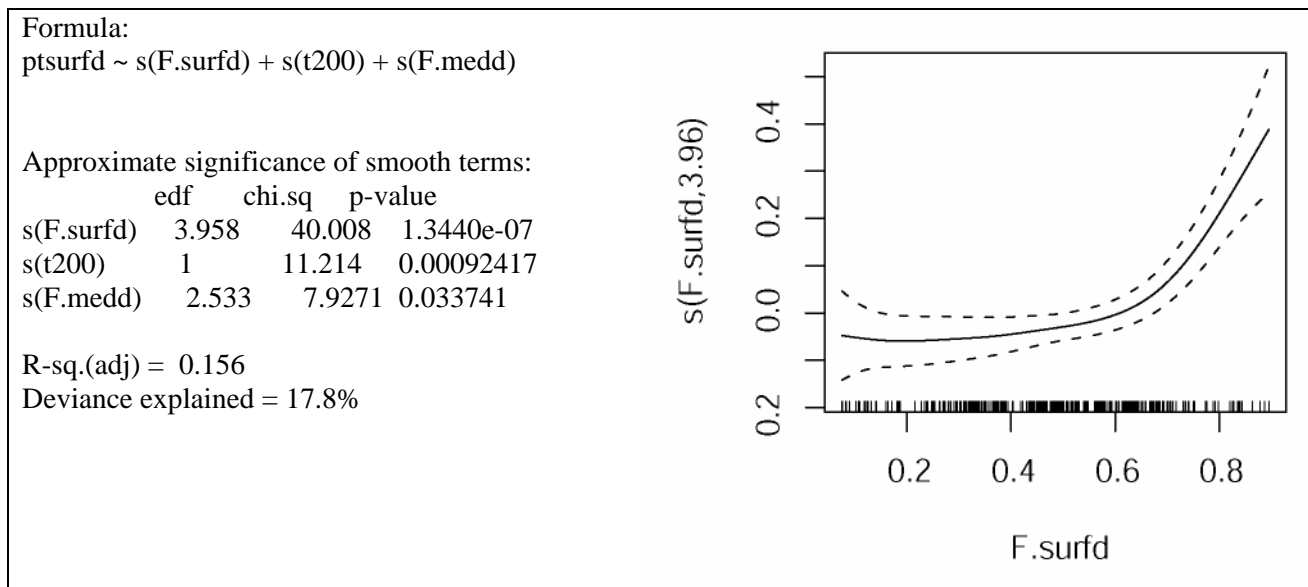


Figure 11 : Generalized Additive Model summary (left). Plots for the first covariate 'forage biomass in the surface layer (<200m) during the day' (right).

These results suggest two types of vertical behaviour in relation to environment :

- feeding behaviour observed all year round, in which the dive depth during the day would be related to the estimated biomass of bathypelagic (and mesopelagic) forage.
- feeding and reproductive behaviour observed from August to November, in which tunas would target seasonal forage biomass concentrations, especially in warmer surface waters during the day.

Several critical points and perspectives can be emphasized :

- the lack of precision of geolocation estimates, especially latitude, remains critical in particular for PSAT data. It is a limitation of the spatial accuracy of the coupling between tag records and environmental data extracted from SEAPODYM. It can be improved though by latitude correction procedures based on the reduction of the difference between observed (tag) and estimated (model) temperatures (see above and Clear et al. 2005).
- the gap in space-time scales between tag records and model outputs has been reduced (SEAPODYM outputs at the new scale of 10 days and 0.5 °). The development of a mixed-resolution framework should be a further step in this objective.
- the limited amount of deviance explained by the GAMs, which can be seen as a result of the two previous points, limited sample size, high individual variability and effect of a number of processes (e.g. physiological) not included in the model.

These results constitute a first stage towards the definition of a rule-based IBM of bigeye tuna movements in relation to their environment. The vertical behaviours highlighted will be used to define habitat qualities possibly determining horizontal movements and for the validation of the parameterization of bigeye habitat in SEAPODYM, for simulation purposes on a 10-day scale.

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