Modelling the yellowfin tuna (*Thunnus albacares*) vertical distribution using sonic tagging results and local environmental parameters

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Abstract

The diurnal vertical behaviour of yellowfin tuna observed from sonic tagging experiments in the western Indian Ocean (Comoros archipelago) is compared with the vertical profiles of temperature and dissolved oxygen concentration. Two different behavioural situations: off-FAD and FAD-associated yellowfin tuna, are characterized by the relationships between swimming depth and vertical structure of temperature and dissolved oxygen concentration (*i.e.* depth and thickness of the mixed layer, of the thermocline layer and of the oxycline) observed in the tracking area. Gradients of both parameters are shown to be the key factors which determine the vertical swimming behaviour. From an analysis carried out on the whole oceanographic data set of the Western Indian Ocean, oxycline is found to match with the depth of the $4.2\text{-}4.3\,\mathrm{ml.l^{-1}}$ dissolved oxygen concentration.
Vertical distributions of yellowfin tuna, for both off-FAD and FAD-associated situations, are modelled by using normal-derived distributions. These models indicate the probability of the presence of yellowfin tuna, related to the vertical profiles of temperature and dissolved oxygen concentration. A single mode distribution is fitted to describe the FAD-associated situation, and a bi-modal one for the off-FAD situation. Positions of the modes are determined by the relationship between the vertical swimming behaviour and the position of either maximum gradient of temperature or dissolved oxygen concentration. An iterative calculation of normal distribution standard error is conducted to adjust the shape of the curve to cover the entire layer in which yellowfin tuna is considered to be present. Both models were applied in a remote area, east of the Seychelles, where purse seine catches are important. The predicted vertical distribution seems to be realistic and matches the observations given by echosound pictures of tuna schools obtained in the same area by purse seiners.

Keywords: Yellowfin tuna, tuna, *Thunnus albacares*, modelling, prediction, vertical distribution, sonic tagging, environment, fish aggregating devices (FADs), Indian Ocean.

Modélisation de la distribution verticale de l'albacore (Thunnus albacares) *à partir de données de marquage acoustique et de paramètres locaux d'environnement.*

Résumé

Les déplacements verticaux diurnes de trois albacores, observés à partir de marquages acoustiques réalisés dans l'océan Indien occidental (archipel des Comores), sont mis en parallèle avec la répartition verticale de la température et de la concentration en oxygène dissous. Deux types de comportements, albacores associés à un Dispositif de Concentration de Poisson (DCP) et albacores non associés à un DCP, peuvent être distingués par les relations entre les profondeurs de nage et la structure verticale de la température et de l'oxygène dissous (épaisseur de la couche homogène, de la thermocline et de l'oxycline) observées dans la zone des marquages. Les gradients de température et de la concentration en oxygène dissous se révèlent être les facteurs essentiels qui déterminent les déplacements verticaux des albacores. Un examen des données océanographiques collectées dans l'ensemble de l'océan Indien tropical occidental (10°N-20°S, 40°E-80°E) révèle que la profondeur d'immersion de l'oxycline correspond très largement à celle où des valeurs de concentration en oxygène dissous de 4,2 à 4,3 ml/l sont observées.

La répartition verticale des albacores dans chacune des deux situations (associé à DCP et hors DCP) est modélisée au moyen de distributions dérivées de la loi normale. Ces deux modèles donnent la probabilité de présence de l'albacore à diverses profondeurs en fonction d'une structure verticale donnée de température et de concentration en oxygène dissous. Une distribution uni-modale est utilisée pour décrire la répartition verticale des albacores associés à un DCP tandis que celle des albacores non associés (bancs libres) est de forme bi-modale. La position des différents modes est déterminée par les relations entre les déplacements verticaux observés des albacores et l'immersion du gradient maximum de température ou d'oxygène dissous. Un calcul itératif de l'écart-type des distributions est effectué pour ajuster la forme des distributions calculées à celle des distributions verticales observées; cette procédure permet de bien prendre en compte l'ensemble de la couche d'eau dans laquelle les albacores ont été observés par marquage acoustique. Les deux modèles sont appliqués à une zone éloignée, située à l'est des îles Seychelles, où les captures d'albacore faites par les thoniers senneurs sont très importantes. Les répartitions verticales prédites par les modèles apparaissent réalistes car elles correspondent bien aux enregistrements sonar obtenus par des senneurs dans la zone exacte d'application des modèles.

Mots-clés : Albacore, thons, *Thunnus albacares*, modélisation, prédiction, répartition verticale, marquage acoustique, environnement, dispositifs de concentration de poissons (DCP), océan Indien.

FOREWORD

Due to the small number of fishes available and used in the present paper (three yellowfin tuna from the Comoros Islands area), it could *a priori* seem hazardous and unsuitable to undertake any mathematical work, mainly for modelling purposes. This argument was taken into account and a sophisticated statistical adjustment of a model was judged unworthy. Thus the word "modelling" seems inappropriate to describe the rough adjustment of a normal distribution to the observed tracking data, which is presented here. A careful examination of the intrinsic nature of the observations made (sonic tracking) and the general consistency of the observations made (in the present work and in previous studies quoted in this study) on tracked fishes and on schooling fishes as well, tends to indicate the results obtained from a small number of tracked fish are significant and realistic. Moreover the validation of the predictions given by the proposed model tends to confirm the consistency of the work. But the most sceptical reader should at least appreciate the originality of the method (modelling) which allows us to use jointly, for the first time, tracking data, environmental parameters and the most recent knowledge on physiological requirements of tropical tuna. This so-called "modelling" could then be considered as a promising new way of processing the tracking data because of its potential interest to forecast the catchability of yellowfin tuna all over the tropical oceans.

INTRODUCTION

The influence of the environment on the vulnerability of tropical tuna to fishing gear has been recognized for a long time and several more-or-less empirical attempts were made to predict this vulnerability (Sharp, 1978; Evans, Maclain and Bauer, 1981). On the other hand, several tracking experiments were performed to assess the behaviour of tuna (Yuen, 1970; Yonemori, 1982; Carey and Olson, 1982; Cayré and Chabanne, 1986; Holland *et al.*, 1990; Cayré, 1991) but this work remains mostly descriptive of the behaviour. Recent work on the physiology of tropical tuna (Bushnell, Brill and Bourke, 1990; Bushnell and Brill, 1992) confirms and measures the sensitivity of these species to the water temperature and oxygen concentration; these parameters are pointed out as key factors for the life of tropical tunas.

The objectives of this study are (1) to model a relationship between the vertical movements of yellowfin and the vertical structure of temperature and oxygen gradients in the ocean and (2) to predict the depth of maximum probability of presence of yellowfin tuna that can explain the observed variation in the catchability of yellowfin tuna by purse seiners.

A first analysis (Marsac, 1992) was made from tracking data collected only in the Pacific Ocean (Hawaii and Tahiti) and applied in the Indian Ocean. The vertical distribution of tuna was calculated within continguous 1°C thermal layers. In this paper, the effect of the thermal gradient was not directly considered and a discrete type model was proposed to estimate a theoretical distribution of fish for oxygen values greater than 1.5 ml/l (considered as the lethal concentration) for yellowfin tuna. In the present paper, the method is more directly based on gradients of both temperature and oxygen, to delimit larger layers where normal-shaped models are calculated.

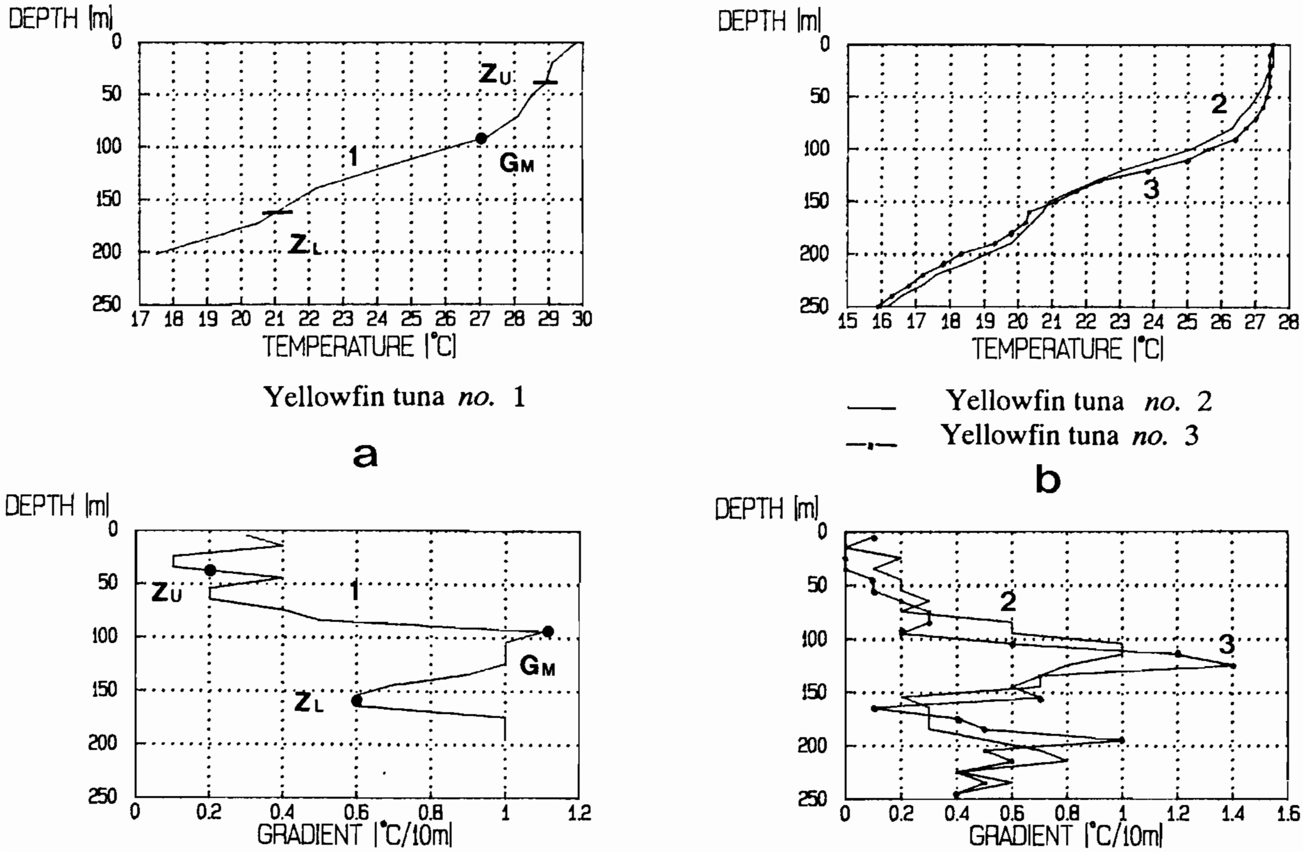


Figure 1. — Temperature and vertical gradient profile plotted by 10 m depth strata observed, (*a*) during the off-FAD tracking of yellowfin tuna No. 1 and (*b*) during the FAD-associated trackings of yellowfin tuna No. 2 and 3. As an example, upper (Z_u) and lower (Z_L) limits of the thermocline as well as the position of the maximum vertical thermal gradient (G_m) are indicated on figure 1 *a*.

METHODS AND DATA

Tracking Data

Three yellowfin tuna were tracked during the Regional Tuna Project (Indian Ocean Commission) in the area of the Comoros Islands (Cayré, 1991). Two of them remained in the vicinity of fish aggregating devices (FADs), and the third one moved away just after it was tagged. Thus it is possible to separate two types of tracking: "**FAD-associated**" fish tracking and "**off-FAD**" fish tracking, *i.e.* free-swimming school fish (*table* 1).

For the present analysis, only the diurnal portion of the tracking data was used, because this study is aimed to predict the catchability of yellowfin tuna mainly harvested during the diurnal period by surface fisheries.

The three fish sampled can be considered as a homogeneous group since their size (from 73 to 105 cm fork length) was under the mean first size at maturity which was estimated to be between 110 and 115 cm (fork length) in the western Indian Ocean (Hassani and Stequert, 1991). Comparison between the swimming depths of the tracked fish and depth of schools detected by echosounding showed that these fish were schooling (Cayré, 1991). This tends to support the assumption that the behaviour of the tracked fish represents the behaviour of the schools in which they were swimming.

Table 1. — Summary of trackings of yellowfin tuna in Comoros Islands area in 1989.

Tracking type	Off-FAD	FAD-associated	
Fish No.	1	2	3
Length (F_L)	80 cm	105 cm	73 cm
Tagging:			
Date	April 18, 1989	May 14, 1989	May 17, 1989
Time (TU + 3)	13.05	6.06	6.18
Position	12°07,8S 44°25,6E	12°06,2S 44°20,6E	12°06,8S 44°20,9E
Duration of track	22hrs.	24hrs. 04	13hrs. 07

Oceanographic data

The basic information came from the temperature versus depth profiles measured during the tracking

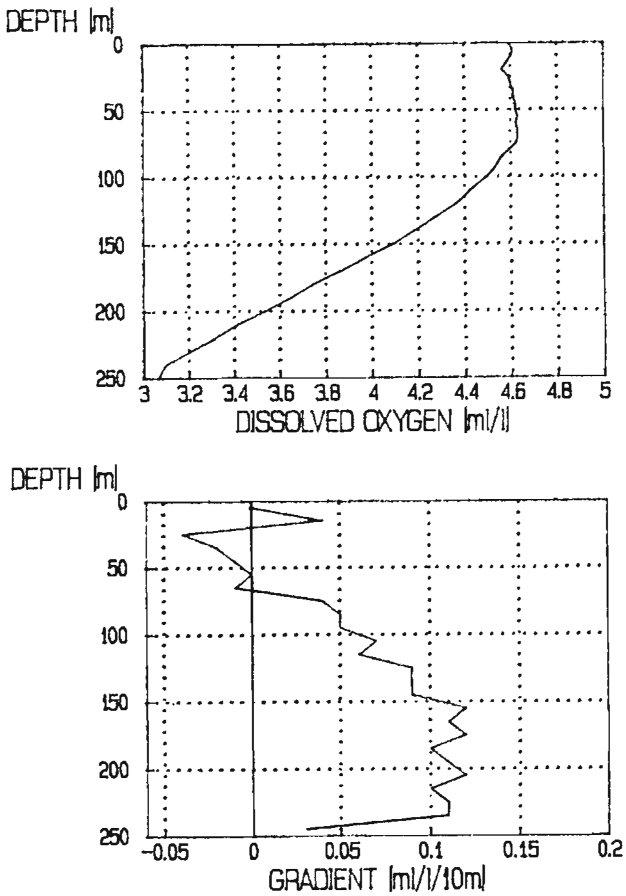


Figure 2. – Dissolved oxygen concentration profile and vertical gradient value by 10 m depth strata in the tracking area (Comoros Islands).

experiments with a probe. The vertical thermal gradients were calculated from these profiles (*figs.* 1 *a* and 1 *b*).

Dissolved oxygen concentration profile, calculated in the tracking area for the second quarter of the year (*fig.* 2), was extracted from an hydrological data base which was set up during the Regional Tuna Project (Marsac, 1990) from a compilation of 3 586 oceanographic stations carried out between 1906 and 1987 in the western Indian Ocean. In order to apply the model proposed in this paper to remote areas of the Indian Ocean, temperature profiles corresponding to these areas were extracted from the TOGA (Tropical Ocean and Global Atmosphere) data base.

RESULTS

Swimming depth and vertical thermal structure

The swimming depth of the tracked fishes was recorded every 20 seconds.

The vertical movements of the off-FAD (*fig.* 3) and of the FAD associated yellowfin tuna (*fig.* 4) were plotted after smoothing of the basic data by a 21-term moving average.

The upper limit of the thermocline Z_U (*i.e.* depth of the mixed layer) is defined as the depth of the SST-1°C isotherm.

The lower limit of the thermocline Z_L is defined as the depth where the first minimum of temperature gradient is found. For example in April 1989 (*fig.* 1 *a*) the thermocline ranged between 40 and 160 m. In May (*fig.* 1 *b*) the limits of the thermocline were 80 and 150 m.

These boundaries and the depth of the maximum vertical thermal gradient G_M observed within the thermocline are superimposed on the plot of the observed vertical movements of the tracked yellowfin tuna (*fig.* 3 and 4).

A marked difference in the behaviour of the two types of tracking (FAD associated and off-FAD fishes) can be observed (*figs.* 3 and 4).

The off-FAD tracked fish (*fig.* 3) remains swimming within the thermocline, with a mean swimming depth of 84 m close to the maximum thermal gradient depth (95 m) of the thermocline. However, the significance of this mean swimming depth may be doubtful due to the great variability in the observed vertical movements. On the other hand the FAD associated fish (*fig.* 4) were swimming in the upper part of the thermocline and within the mixed layer, 35 m above the maximum gradient depth (120 m).

These characteristics are summarized in *table* 2 where the figures calculated from Hawaii tracking experiments (off-FAD fishes: Holland, Brill and Chang, 1990) and Tahiti trackings (FAD associated fish: Cayré and Chabanne, 1986) are included for comparison. Results published by Carey and Olson (1982) and Yonemori (1982) were unfortunately not presented in the appropriate manner to be quantified and used in this study. A fair amount of similarity of the behaviour related to the maximum gradient depth can be observed within each type of tracking (off-FAD and FAD-associated) whatever the tracking area.

These observations can be quantified through a correlation analysis using a non-parametric test (*table* 3).

From this table one can see the off-FAD tracked yellowfin tuna has a "preferred" swimming depth significantly closer to and above the maximum thermal gradient depth, than what is observed for the FAD-associated fish.

Swimming depth and vertical dissolved oxygen profile

Oxygen concentration is recognized as a factor limiting the habitat of yellowfin tuna. The lethal concentration for this species was estimated to be

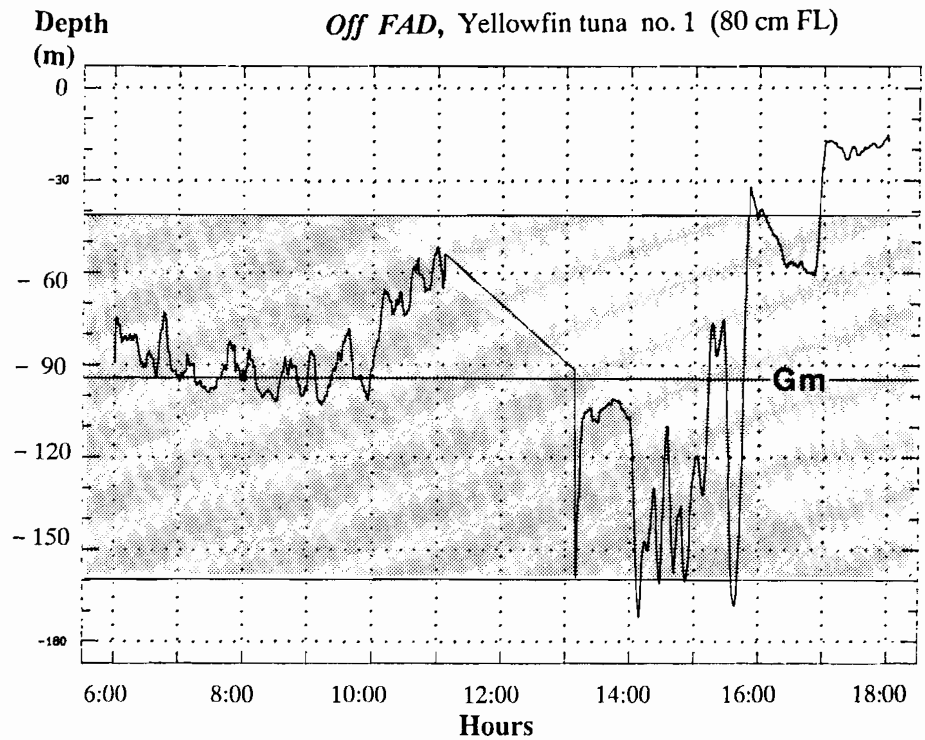


Figure 3. Vertical movements of the off-FAD yellowfin tuna No. 1, thermocline layer (shaded) and maximum thermal gradient (G_m). From 11:00 a.m. to 13:00 p.m. the tracked fish was temporarily lost.

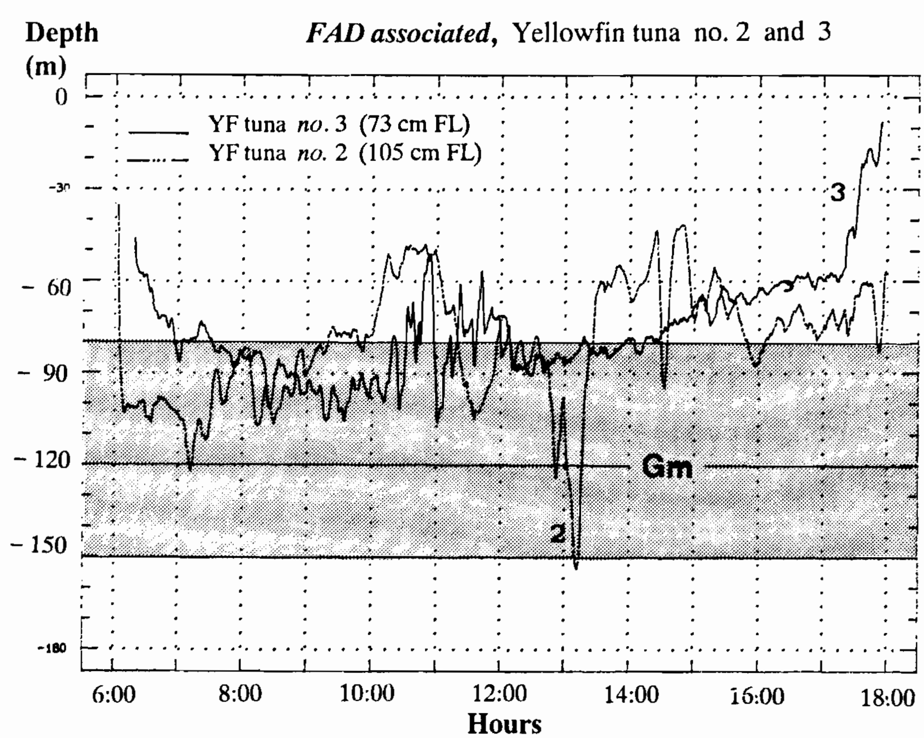


Figure 4. – Vertical movements of the FAD-associated yellowfin tuna No. 2 and 3, thermocline layer (shaded) and maximum thermal gradient (G_m).

Table 2. – Relative frequency of the time spent at different depth strata according to the depth of the maximum gradient of temperature ($Z_{G\,max}$)

Off-FAD trackings

Track	$Z_{G\,max}$	$Z_{G\,max}$ ± 20 m	$Z_{G\,max}$ ± 10 m	Mean Swimming depth
Fish No. 1	95 m	75-115 m 50.0%	85-105 m 36.8%	84 m
Hawaii	50 m	30- 70 m 33.3%	40- 60 m 16.7%	

FAD trackings

Track	$Z_{G\,max}$	$Z_{G\,max}$ ± 20 m	$Z_{G\,max}$ ± 10 m	Mean Swimming depth
Fish No. 2	120 m	100-140 m 16.9%	110-130 m 4.8%	80 m
Fish No. 3	120 m	100-140 m 6.9%	110-130 m 3.1%	76 m
Tahiti		120-160 m 15.9%	130-150 m 7.9%	

Table 3. – Rank correlation (Spearman's coefficient) between the relative frequency of time spent by 10 m depth strata and the vertical thermal gradient calculated in each stratum and for each of the 3 yellowfin tunas.

The lag represents the shift of one series of data versus the other one. The lag values correspond to the location of the maximum presence of yellowfin tuna above the depth of the maximum gradient.

Lag (by 10 m strata)	Off-FAD Tuna No. 1	FAD associated Tuna No. 2	FAD associated Tuna No. 3
0	0.164	0.157	0.043
10	0.282	0.287	0.292
20	0.605*	0.465*	0.575*
30	0.820**	0.540**	0.767**
40	0.516	0.656**	0.841**
50	0.357	0.605**	0.500
60	0.085	0.452	0.227
Maximum value of the observed gradient	1.1	1.1	1.1
Depth of the maximum gradient	95 m	120 m	120 m

* Significant to the 5% level.

** Highly significant to the 1% level.

2.1 $ml.O_2.l^{-1}$, but it appears that they are sensitive (decreasing of heart rate) to reduced ambient oxygen values between 4.3 and 3.6 $ml.O_2.l^{-1}$ (Bushnell, Brill and Bourke, 1990; Bushnell and Brill, 1992). The oxygen concentration observed in the area (*fig.* 2) is always well over the lethal limit, but the 4.0 $ml.O_2.l^{-1}$ value occurs at a depth of 160 m. It

Table 4. – Ratios between the depths of different oxygen concentration values (from 3.6 to 4.4 $ml.O_2.L^{-1}$) and the corresponding depths of maximum oxygen gradient (oxycline) as observed from hydrological stations in the western Indian Ocean.

Oxygen ($ml.l^{-1}$)	3.6	3.8	4.0	4.2	4.4
Nombre of stations	549	605	657	719	766
Mean ratio	1.34	1.29	1.19	1.05	0.84
Standard error	0.021	0.022	0.019	0.014	0.006

is noteworthy that almost the whole vertical distributions off-FAD (*fig.* 5) and of FAD-associated (*fig.* 6) tracked yellowfin are included between the surface and the 160 m depth. Moreover, the depth of 160 m corresponds to the depth where the first maximum vertical gradient of oxygen concentration (*i.e.* oxycline) is observed (*figs.* 5 and 6). This observation is consistent with the experimental results obtained on yellowfin tuna in restrained conditions which showed that the species "appeared to respond to the rate of change as to the absolute change" in oxygen concentration (Bushnell, Brill and Bourke, 1990). Thus the depth of the oxycline will be further considered as a limiting factor of the presence of yellowfin tuna when the maximum gradient (*i.e.* oxycline depth) occurs at depths where oxygen concentration values are between 4.3 and 3.6 $ml.O_2.l^{-1}$.

This apparent close relationship between oxycline and the 3.6-4.3 $ml.O_2.l^{-1}$ concentration range was checked in a wider area in the Indian Ocean (10°N-20°S and 35°E-80°E). The analysis was carried out on the whole hydrological data base (Marsac, 1990) without any consideration regarding seasons or subareas. The ratios between the depth of the 3.6, 3.8, 4.0, 4.2 and 4.4 $ml.O_2.l^{-1}$ and the depth of maximum oxygen gradient were calculated (*table* 4). It appears that, as a whole, oxycline position corresponds to a 4.2-4.3 $ml.O_2.l^{-1}$. It is noteworthy that this correlation which was suggested by observations in a restricted area (Comoros Islands) remains valid on a wider geographical scale.

This general coherence in the relationships between physical parameters allows application of the tracking results obtained in the Comoros Islands area to any other area of the western Indian Ocean within the area mentioned above (10°N-20°S and 35°E-80°E).

Modelling the vertical distribution of yellowfin tuna

Two modes can be observed in the vertical distribution of off-FAD fishes (*fig.* 5*a*). A first peak is located within the mixed layer (0-40 m) and a second

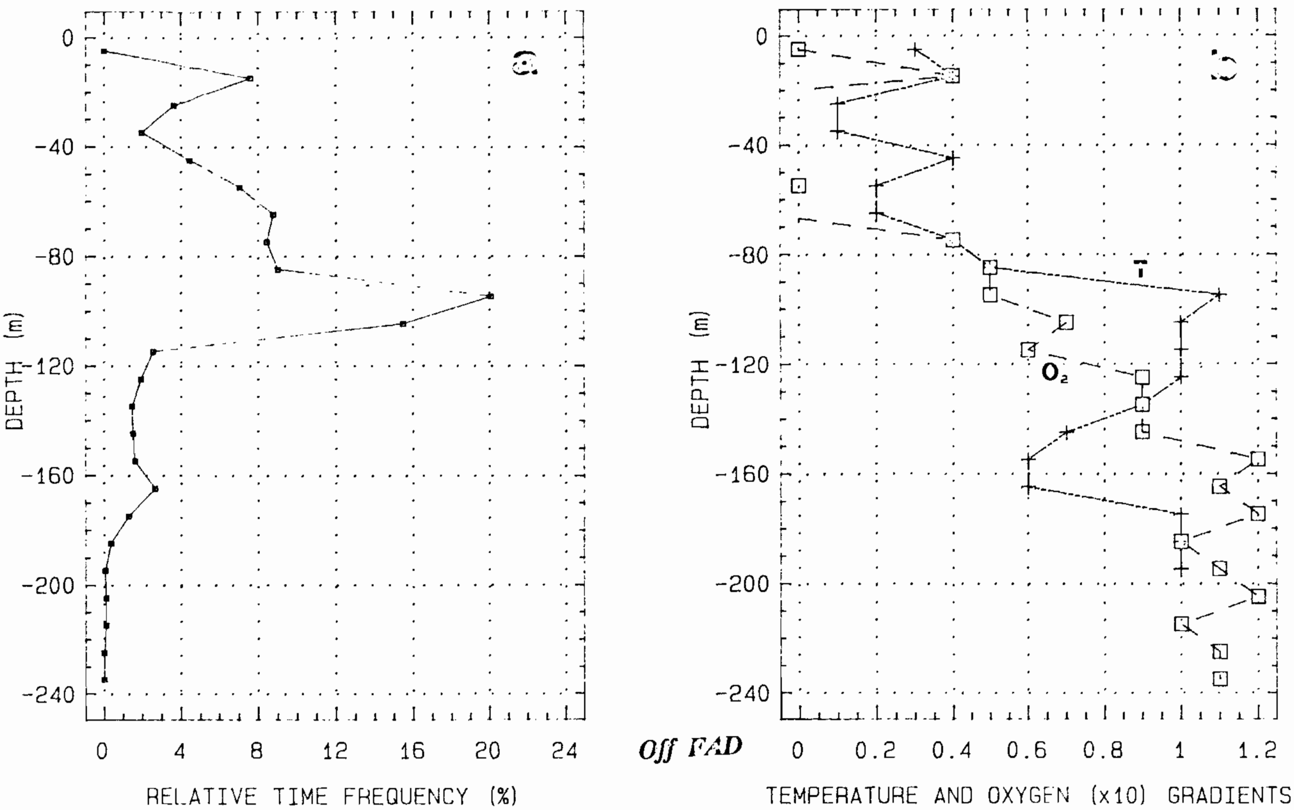


Figure 5. — (*a*) Vertical distribution of the off-FAD yellowfin tuna and (*b*) vertical gradients of temperature and dissolved oxygen concentration. Negative values of the oxygen concentration gradient observed from 20 m to 60 m were not plotted.

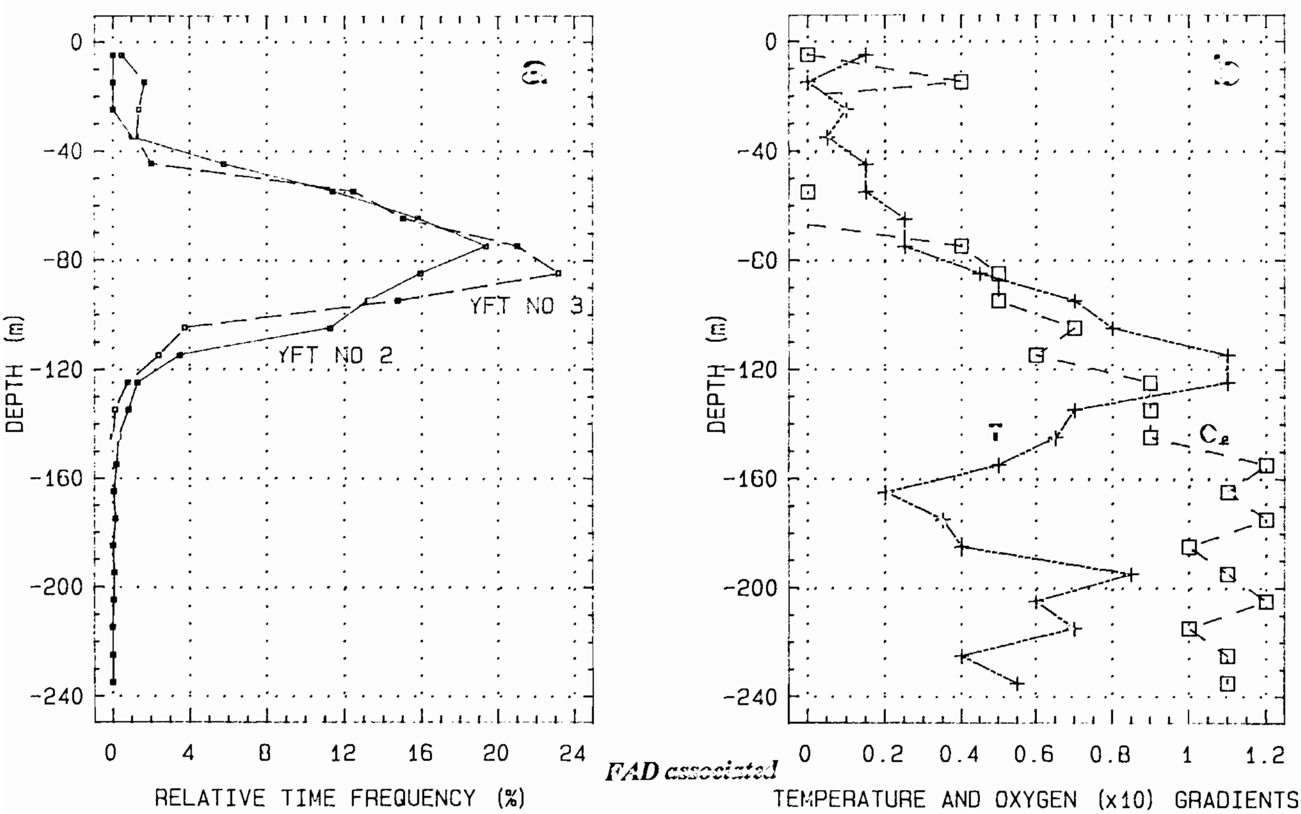


Figure 6. — (*a*) Vertical distribution of the FAD-associated yellowfin tuna and (*b*) vertical gradients of temperature and dissolved oxygen concentration.

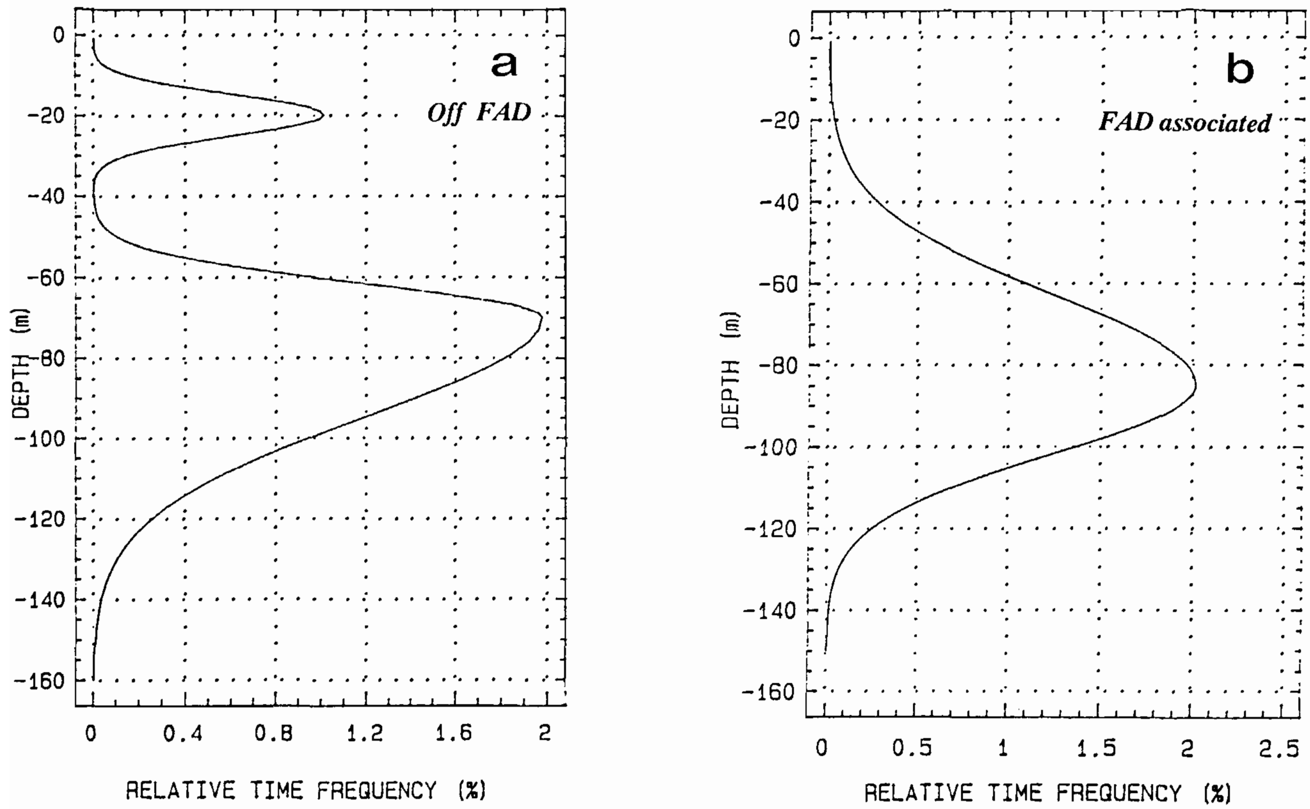


Figure 7. — Vertical distribution of yellowfin tuna calculated by the model with the tracking data obtained in Comoros Islands for (*a*) off-FAD and (*b*) FAD-associated situations.

one within the thermocline layer (40-160 m). Moreover a single mode appears in the FAD-associated fishes' distribution (*fig.* 6 *a*).

Due to this basic difference, off-FAD and FAD-associated observations will be considered separately for modelling. Normal distributions are used to describe these two types of vertical distribution (off-FAD and FAD-associated situation).

The normal distribution is defined by:

$$f(x)=\frac{1}{\sqrt{2\pi\sigma}}\cdot e^{-(x-\mu)^2/2\sigma^2} \quad (1)$$

with $E(x)=y$ and $\operatorname{var}(x)=\sigma^2$
From our data, the expression will be

$$f(Z)=\frac{1}{\sqrt{2\pi s}}\cdot e^{-(Z-m)^2/2s^2} \quad (2)$$

where Z is depth (in metres), m is estimated mean and s is estimated standard deviation.

Off-FAD situation (*fig.* 7 *a*)

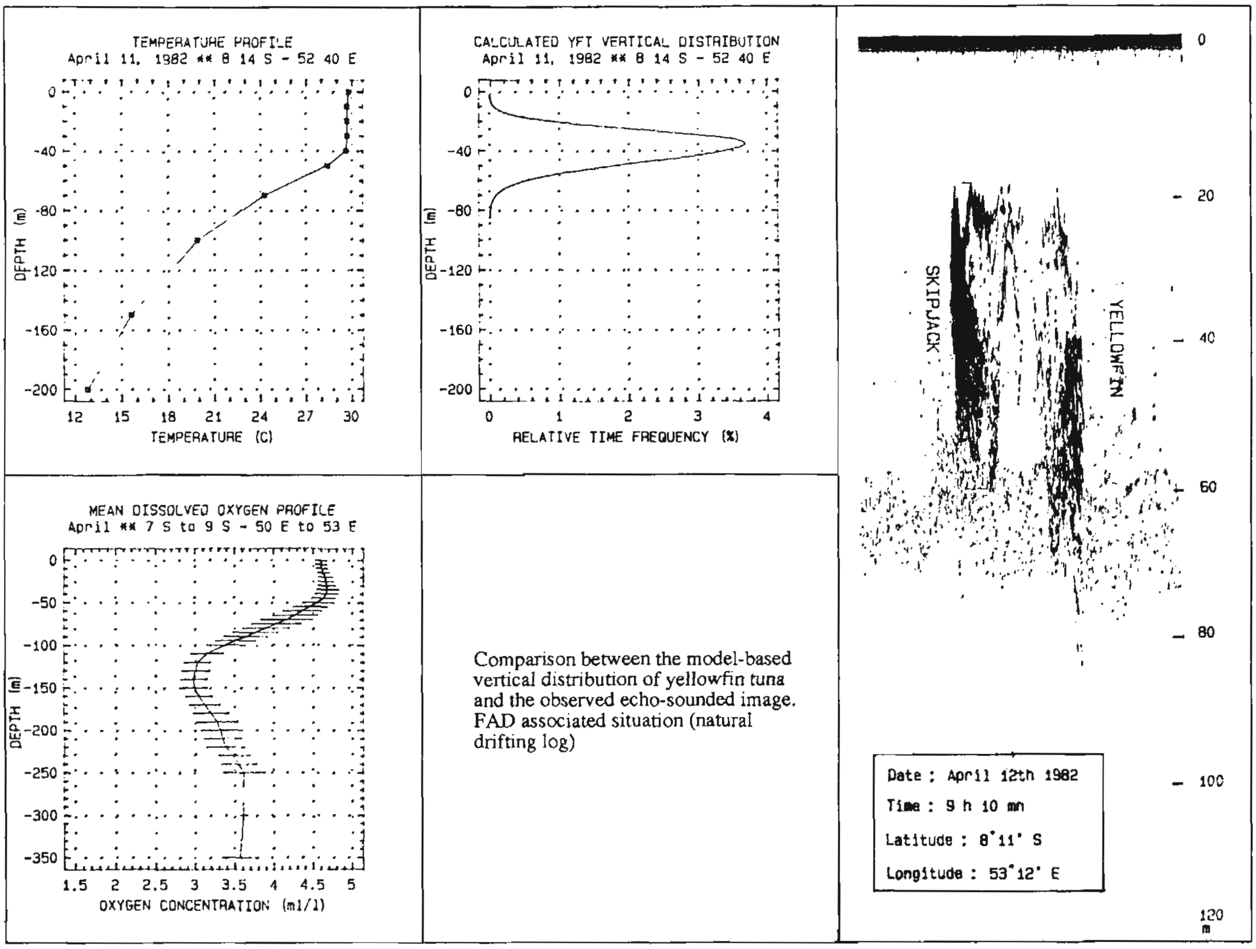
The model is built up following the following successive steps.

— Estimation of the mixed-layer boundaries, Z_U and Z_L, from the vertical profiles of temperature: 0-40 m (*fig.* 1 *a*).

— A normal distribution, centred at the mid point of the mixed layer (20 m) is calculated. The standard deviation is adjusted by an iterative process in order to enable the final calculated distribution to cover the whole considered layer (0-40 m); thus the 2.5% probability limits of the curve are set at each previously defined Z_U and Z_L: 0 and 40 m in the present case.

— Estimation of the thermocline boundaries Z_{U2} and Z_{L2} (40-160 m), as well as the depth where the first maximum thermal gradient value is observed (95 m, *fig.* 1 *a*).

— According to the results expressed in *table* 3, the normal distribution calculated in the thermocline layer will be centred at 25 m above the maximum thermal gradient depth: $m=95\text{-}25=70$ m. In order to include the upper limit of the thermocline (40 m), a first normal distribution centred at 70 m and extending from 40 m to its symmetrical point (100 m), is adjusted. The standard deviation of the distribution is calculated and adjusted in the same way as described for the mixed layer.



Comparison between the model-based vertical distribution of yellowfin tuna and the observed echo-sounded image. FAD associated situation (natural drifting log)

Figure 8. — Validation of the FAD-associated model by comparison with an echo-sounding record made on a log-associated school.

— From the tracking data it is calculated that 13% of the time is spent within the mixed layer and 82% in the thermocline. Both normal distribution functions will be adjusted so as to reflect this pattern.

Due to the observed depth of the maximum gradient of temperature, the previously calculated normal distribution does not necessarily cover the entire considered layer (e. g. 40-160 m). In order to include the whole layer we impose an asymmetrical shape on the previous normal distribution. The mode remains centred at the initially fixed mean value (70 m) but each 1 m by 1 m point of the asymmetrical part of the curve, with its corresponding probability, is shifted along the depth axis.

Two different procedures have to be considered depending on the way asymmetry has to be imposed.

Asymmetry towards the lower part of the layer

This case has to be considered when the mean central depth (Z_m) of the normal distribution is closer to the upper depth (Z_u) than to the lower depth (Z_L) of the considered layer. In this case each successive point of the deeper mid-part of the normal distribution (from Z_m to Z_0) has to be shifted. To shift these points we will recalculate the increment (originally fixed to 1 m) of the successive points of the normal distribution. The new increment (Z) will be:

$$Z = (Z_L - Z_m)/(Z_0 - Z_m) \qquad (3)$$

with $Z_0 = Z_m + (Z_m - Z_u)$

where Z_u is upper depth of the layer (e. g. 40 m),

Z_m is mean central depth of the normal distribution (e. g. 60 m),

Z_0 is lower depth limit of the normal distribution before shifted (*e. g.* 80 m) and

Z_L is lower depth of the layer (e. g. 110 m).

As an example, the numbers given between brackets indicate that the considered layer ranges from 40 to 110 m, the distribution is centred at 60 m (mean central depth) and extends from 40 to 80 m. Each successive point of the curve between 61 and 80 m (*i. e.* 61, 62, 63, etc.) is then shifted along the depth

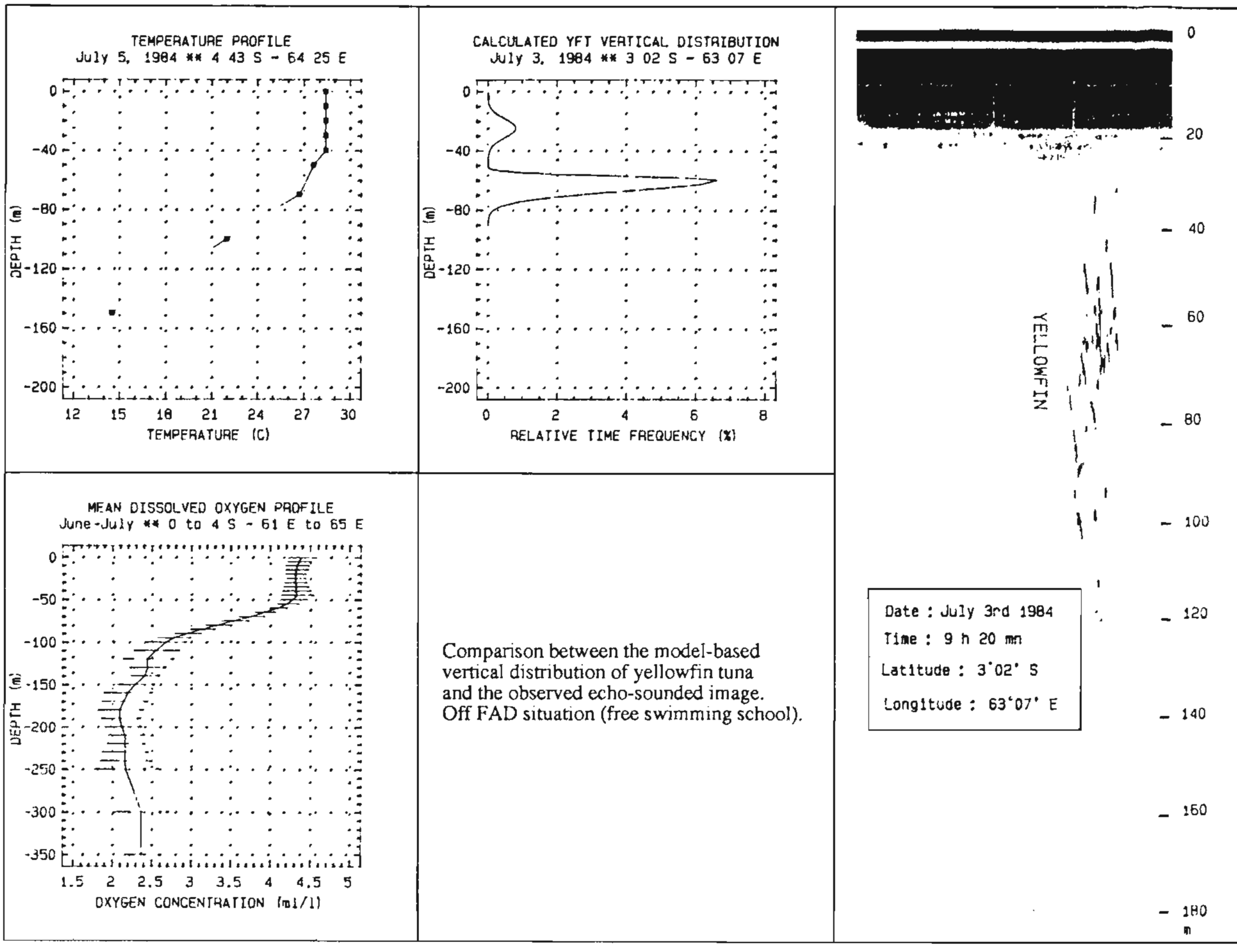


Figure 9. — Validation of the off-FAD model by comparison with an echo-sounding record in an off-FAD situation.

axis using a new increment (Z=2.5). So these successive points are shifted to 62.5, 65.0, 67.5, etc.

Asymmetry towards the upper part of the layer

This case has to be considered when the mean central depth (Z_m) of the normal distribution is closer to the lower depth (Z_L) than to the upper depth (Z_u) of the considered layer. In this case each successive point of the shallower mid-part of the normal distribution (from Z_m to Z_u) has to be shifted. The new increment (Z) will be:

$$Z=(Z_m-Z_u)/(Z_m-Z_0) \quad (4)$$

with $Z_0=Z_m-(Z_L-Z_m)$.

For both these cases of asymmetry, the probability of each point, previously calculated with the probability function of the curve, remains unchanged and attributed to each corresponding shifted point.

The total surface included under the curve is adjusted in order to keep a total time frequency value of 82% within the thermocline.

As mentioned above, oxycline can be considered as a limiting factor in the Indian Ocean, because oxycline is generally encountered at dissolved oxygen concentrations which affect yellowfin tuna behaviour. From the basic data (tracking and physical parameters) used in the present analysis, 5% of the time was spent by the tracked fish below the oxycline which was found at a depth of 160 m. Since the distribution never extends below the oxycline, this 5% will not be taken into account by the model which will therefore explain 95% of the vertical distribution of juvenile yellowfin tuna.

If oxycline falls at a depth above the lower limit of the thermocline layer, this depth will be considered as the floor of the vertical distribution, *i.e.* as the Z_3 limit of the model.

FAD-associated situation (*fig.* 7 *b*)

To describe the vertical distribution of FAD-associated yellowfin tuna (*fig.* 6 *a*), a single normal curve

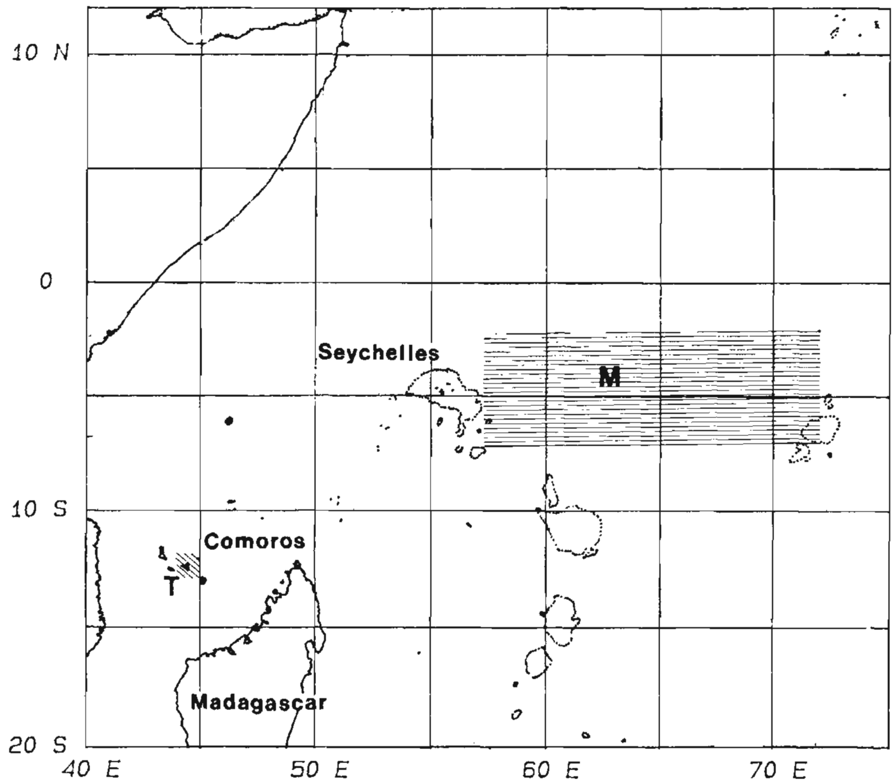


Figure 10. – Location of tracking area (T) and area selected for application of the models (M).

Table 5. – Mean catch and CPUE by year for yellowfin tuna, in the eastern Seychelles area (2°S-7°S/57°E-72°E) and in the whole fishery (15°N-25°S/35°E-75°E). Period: 1987-1990, French and Spanish fleets combined.

Area	Catch		CPUE
	(Mt)	(%)	
Whole fishery	88 102	100	9.3
East Seychelles	25 480	29	10.0

is adjusted in the same way as previously described for off-FAD situation.

The boundaries Z_u (= 0 m) and Z_L (= 150 m) of the distribution correspond to the surface (Z_u) and to the lower limit of the thermocline layer (Z_L). According to the results expressed in *table* 3, the first calculated normal distribution will be centred at 35 m above the maximum thermal gradient: $m = 120\text{-}35 = 85$ m.

The standard deviation of the distribution is calculated and the curve adjusted (*fig.* 7 *b*) as previously described for off-FAD situation. This model describes 100% of the observed vertical distribution of the tracked juvenile yellowfin tuna.

Validation

The main objective of this model is to predict the vertical distribution of yellowfin tuna in any area where accurate temperature and oxygen profiles are available. Therefore, before making such an application in a selected area, a comparison between the model-based distribution and direct observation provided by an echo sounder image is attempted to estimate the reliability of the model.

We obtained a set of echo-sounder images recorded by purse seiners prior to yellowfin tuna catch. These images were gathered from selected time and space strata where reliable vertical temperature and dissolved oxygen profiles were available. The two situations (off FAD and FAD-associated) were considered and corresponding images were obtained respectively in two sites: 3°02'S and 63°07'E on 3 July 1984 (off-FAD situation), and 8°11'S and 53°12'E on 12 April 1982 (log-associated school). The vertical temperature profiles corresponding to these 2 situations were selected from the data base in order to be as close as possible to the location of both situations (respectively 28 and 127 nautical miles) and were collected

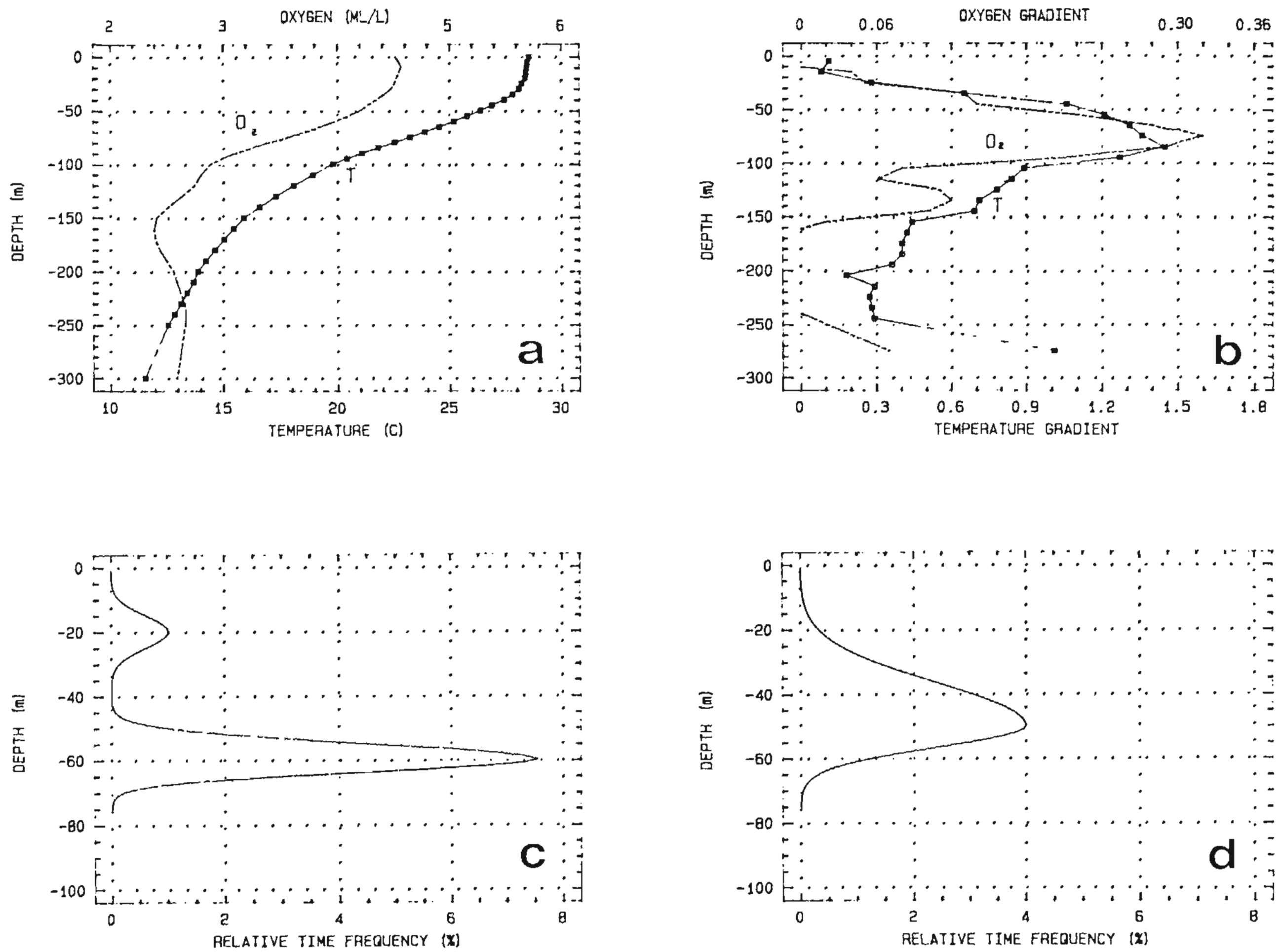


Figure 11. – Modelling of the vertical distribution of yellowfin tuna in a selected area East of the Seychelles Islands: 2°S-7°S, 57°E-72°E, in January and February: (*a*) mean vertical profiles of temperature and dissolved oxygen concentration, (*b*) temperature and oxygen gradients by 10 m strata, (*c*) vertical distribution of yellowfin tuna calculated following the off-FAD model, (*d*) vertical distribution of yellowfin tuna calculated following the FAD-associated model.

within a time lag of less than 2 days. The different depth layers used by the models were defined from these profiles. With respect to oxygen, the data selection was carried out on a wider time-space scale (maximum time-space strata of 4×4 degrees and 15 days) due to the infrequency of oxygen concentration observations available in the area of both sites. The models are then calculated from these physical parameters.

In the FAD-associated situation (*fig.* 8), vertical distribution predicted by the model matches quite well with the echo-sounder observation. Both indicate that yellowfin tuna are distributed between 20 and 70 m.

In the off-FAD situation (*fig.* 9) the model predicts a maximum abundance of fish between 60 and 70 m depth. A similar depth of maximum abundance can be observed on the echo-sounder image. However, due to the depth of the oxycline (90 m), the tuna which can be observed in deeper layers (90 to 110 m, as shown by the echo sounder) are not considered by the model.

The vertical distribution given by the model, using the local temperature and oxygen data, seems reliable in the FAD-associated situation, but some discrepancies may occur in the off-FAD situation. This could be due to the fact that the latter refers to free-swimming schools which include large yellowfin tuna. These fishes are mostly mature and their ecophysiological requirements (vs. temperature and oxygen) differ from those of juvenile yellowfin tuna on which the present analysis is based.

On the other hand, the FAD attracts generally small fish (Hallier, 1991) which belong to the same size group as those used to build the present model.

Therefore, we can expect better model reliability in this situation.

Application in other areas

The area extending between the Seychelles and the Chagos archipelago (2°S-7°S/57°E-72°E) is exploited mostly by purse seiners during the first quarter of the year (*fig.* 10), where yellowfin is the dominant species in the catches. On an annual basis, yellowfin catch in this area represents 29% of the total catch of yellowfin tuna in the western Indian Ocean (*table* 5).

The two models were applied in this area in January and February. The oceanographical data base was used to produce the vertical profiles of temperature, dissolved oxygen and their gradients (*fig.* 11).

The mixed layer extended from 0 to 40 m, and the thermocline layer from 40 to 110 m (*fig.* 11 *a*). The depth of the oxycline (75 m) was located above the maximum thermal gradient (85 m), and therefore would be considered as the factor limiting the vertical distribution (*fig.* 11 *b*).

As a consequence, the deeper layer of the off-FAD model would extend from 40 to 75 m; in the FAD-associated model the single layer considered in the model would extend from 0 to 75 m.

The vertical distribution of yellowfin tuna calculated by the two models (*figs.* 11 *a* and *b*), highlights and illustrates the differences of behaviour observed from the sonic tracking experiments.

The model makes it possible to estimate the potential vulnerability of the yellowfin tuna to the purse seine and can explain the differences observed among fishing areas. For instance, the off-FAD model indicates that between the Seychelles and Chagos, 95% of the yellowfin tuna distribution is comprised within the top 75 m (*fig.* 11 *a*), and that in the Comoros Islands only 44% of the distribution is included in the same layer (*fig.* 7 *a*). The on-FAD model indicates that 69% of the yellowfin tuna are distributed between 0 and 50 m in the Seychelles area (*fig.* 11 *b*), and only 7% are found in the same layer in the Comoros area (*fig.* 7 *b*). Therefore, the nets should have a better efficiency on both log-associated schools and free schools in the Seychelles than in the Comoros area.

DISCUSSION - CONCLUSION

In this paper, several main features of the vertical swimming behaviour of young yellowfin tuna (FL < 110 cm) are pointed out with respect to the physical environment. In agreement with the Bushnell, Brill and Bourke (1990) physiological experiments using yellowfin tuna in restrained conditions, this study tends to strengthen the idea that gradients of temperature and dissolved oxygen have a greater effect on the behaviour than the absolute values reached by each parameter. However, the gradients must be found within a range of absolute values of these parameters. It was shown that in any part of the tropical western Indian Ocean, there is a strong and striking correlation between the depth of the oxycline and the 3.6-4.2 $ml.O_2.l^{-1}$ concentration values. Furthermore these values of concentration can be considered as a threshold where the general activity of yellowfin tuna starts to be affected. The link between these results highlights the strong relationship between the behaviour of yellowfin tuna and their environment.

Therefore, it appears from this work that the vertical distributions of only two physical parameters (temperature and dissolved oxygen) explain the vertical distribution of yellowfin tuna. Modelling the relationship between these basic oceanographic factors and the behaviour can be utilized to predict the vulnerability of tuna to surface gear (mostly purse seine) in any area of the western Indian Ocean.

The proposed models are based on normal distributions affected by an asymmetrical adjustment when necessary. The models were determined empirically: no calculated fitting was attempted since data corresponding to only 1 and 2 trackings were available for off-FAD and FAD-associated situations. This approach could be reviewed when more tracking observations become available, and especially by pooling the Indian and Pacific Ocean tracking data sets. Anyway, the application of the discrete model (Marsac, 1992), built from only the Pacific data, to the western Indian fishery matched echo-sounder images well. These results would suggest a worldwide common behaviour of yellowfin tuna due to common physiological requirements. It then appears worthwhile to increase the number of tracking experiments as to cover a wider range of size of the observed fishes and to obtain information within diverse oceanographic conditions. The modelling approach seems to be a promising way to interpret the tracking data and jump from the usual descriptive analysis to more comprehensive and forecasting ones.

Nevertheless, the present model seems reliable as far as immature fish are concerned and this is the case for considering FAD-associated fish; in the off-FAD situation, the presence of large yellowfin tuna which inhabit the deeper layers is not taken into account. As a consequence of being calculated from vertical profiles of temperature and oxygen, the models can be influenced by any phenomenon affecting the vertical structure of the ocean. The surface wind can modify the temperature structure, depending on its speed, its duration and the latitude. Quantifying the response of the upper layers of the ocean to wind burst is tricky. In the equatorial region of the Pacific Ocean the thermocline was deepened by 25 m and SST decreased by 0.3 to 0.4°C within a few days following a wind burst of 12 $m.s^{-1}$ (McPhaden *et al.*, 1988); thus surface wind could have a significant and immediate effect on the fish distribution and on its catchability. Due to technical problems in handling the net, very few catches are made by the purse seiners during winds stronger than 12 $m.s^{-1}$. However, such a wind burst, if strong and lasting long enough, could affect the vertical structure of the upper layer of the ocean for a longer period of time (3 to 6 weeks), extending well after the end of the burst of wind itself and thus having some long-lasting effect on the catchability of tunas. Thus, the current yellowfin tuna distribution model can be used in most of the climatic conditions prevailing in the fishery, except for some potential perstitent wind-burst effects which are not taken into account.

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