

Telemetry applied to behaviour analysis of yellowfin tuna (*Thunnus albacares*, Bonnaterre, 1788) movements in a network of fish aggregating devices

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Abstract

This paper analyses acoustic tagging of 8 yellowfin tunas (*Thunnus albacares*, Bonnaterre, 1788) undertaken around Fish Aggregating Devices (FADs) in La Reunion island (Indian Ocean). Emphasis is laid on the horizontal movements and thus complete previous studies on vertical movements around the same FADs. The first result of the present study deals with the relative dwelling time of yellowfin over the distance to FAD where tagged, in 0.9 km intervals. Distributions of dwelling time are different between day and night. During daytime, the fishes remain in the close vicinity of the FAD (mostly within a 1.8 km radius), whilst a drastic disassociation to the FAD occurs at night. During the day, the attractive influence of the FAD disappears 9.3 km away; this finding leads to the suggestion that a minimum distance of 18 km between neighbouring FADs should be applied in La Reunion to avoid overlapping radii of influence. The second group of results points out the potential use of the vertical and total swimming speeds as indicators of the foraging activity of the fish and of the type of movements (behaviour of tight association to FAD, transit among FADs or offshore migration, away from the area of FADs). The day/night change affects the vertical activity, with large magnitude of vertical movements exhibited at night. The total speed during the offshore movements is estimated about 1.2 m s^{-1} : the shift from a phase of tight association to FAD toward a phase of transit movement is characterised by an increase of the total speed. A typology of the relationships between swimming speed and feeding activity is proposed and discussed.

Introduction

Following previous ultrasonic tagging experiments in the Pacific Ocean (Yuen, 1970; Carey & Olson, 1982; Cayré & Chabanne, 1986; Holland et al., 1990), acoustic tracking of tuna was initiated in the Indian Ocean in 1989, within the framework of a Regional Tuna Project undertaken by the 'Commission de l'Océan Indien'. The experiments aim to improve the knowledge of tuna behaviour that are associated with Fish Aggregating Devices (FADs) and thus explore more efficient ways for the exploitation of these migrating resources. FADs appeared in the early 80's as 'miracle solutions' for making populations of tunas available to small scale fisheries of island developing

countries (Preston, 1982; Buckley, 1986; Marsac & Stequert, 1987; Willmann, 1990; Sims, 1992). Following some success in the Pacific islands, the technique rapidly expanded to other tropical oceans, the south west Indian Ocean in particular. The dynamics of the aggregation needed to be explained, and the high resolution in time and space provided by the acoustic telemetry makes it one of the most powerful tools dealing with this issue.

The first experiments in the Indian Ocean were made in Comoros Islands (Cayré, 1991); then other tracking cruises were carried out in La Reunion and Mauritius around FADs. For long, the analysis of the surveys remained fairly descriptive but, as a greater number of fishes was tagged, advanced studies

became possible, focusing on vertical distribution and the effects of the nearby physical environment of the fish (Cayré & Marsac, 1993).

In this paper, we focus more on the horizontal movements of the yellowfin tunas (*Thunnus albacares*, Bonnaterre 1788) tagged at FADs, but still keeping some reference to the vertical activity. The issues addressed are dual: (1) is there a typical horizontal distribution of the yellowfin around FADs, and any day/night effect affecting this distribution, and (2) can quantitative (swimming speed) and qualitative (type of movement) variables express behavioural changes exhibited by the tunas while at the FAD or departing from it.

Materials and methods

From February 1994 until December 1996, four tagging cruises were carried out in the vicinity of FADs anchored off La Reunion island, in the south-west tropical Indian Ocean (Figure 1). This island is influenced by trade winds almost all the year round, and the experiments were made on the leeward side (the West coast) where better working conditions at sea can be met.

Capture and tagging technique

Fishing, tagging and tracking were conducted from a small chartered vessel (10 m long, big game fishing type). The trips were scheduled during the peak tuna fishing season which stretches barely from December to April in La Reunion. The fish were all caught at FADs, using a trolling technique. When hooked, the tuna was rapidly hauled on board and laid on the tagging cradle. A constant flow of sea water was supplied in the mouth of the animal to keep the gills well oxygenated and humid. The transmitter was attached at the back of the second dorsal fin using two nylon 'tie-wraps' through the dorsal pterygiophores and the muscle (Holland et al., op. cit.; Figure 1). The tagging operation lasted approximately one minute, after which the fish was gently released into the water.

Tracking equipment and strategy

The tracking equipment was manufactured by Vemco™ (Halifax, Nova Scotia, Canada). It comprised the following items:

- pressure sensitive ultrasonic transmitters: those used for tuna were 74 mm long, 16 mm diameter and have a life of nearly 5 d according to the depth reached. The signal can be detected at a range of 600 to 800 m. The weight of the tag in the water represents 1 to 2% of the fish weight.
- a directional hydrophone was mounted on a V-fin depressor towed by the boat.
- a receiver (VR-60) was used for decoding the signals and recording depth data every 15 s.

The survey was a continuous search of the strongest signal intensity, by frequent changes of course. When the fish was rather stationary, the vessel kept moving to maintain proper gliding of the V-fin depressor and optimal detection. The latitudes and longitudes given by GPS were noted in a logbook every 5 min with the corresponding depth of the fish. It was assumed the consecutive positions of the tracking vessel were similar to the positions and horizontal movements of the fish.

Data preparation

The series of depth records were downloaded from the receiver memory and processed to produce swimming depth values by one minute bins. A simple average was calculated when several measurements were available for a given bin. In other cases (loss of signal for a few moments), the non-sampled bins were filled in by linear interpolation between the closest values. When the signal was lost for more than ten minutes, no interpolation was attempted and the bins remained blank. A similar procedure was applied to position data, i.e. an interpolation on a one minute time basis for both latitudes and longitudes.

Estimation of swimming speed

The tracking technique does not allow accurate estimation of the horizontal small scale movements (Cayré & Chabanne, 1986). In the situation of a stationary fish, the movements of the boat tend to magnify the actual movements of the fish, and therefore its swimming speed would be overestimated (case A). Conversely, we should also consider the case of a fish exhibiting quick movements on a very fine scale, with signals being detected properly by an almost motionless vessel. For example, along a five minute straight section made by the vessel at a speed of 7 km h^{-1} (600 m long), the fish can return to the same point after a diversion of up to 500 m away from the vessel's course (a dis-

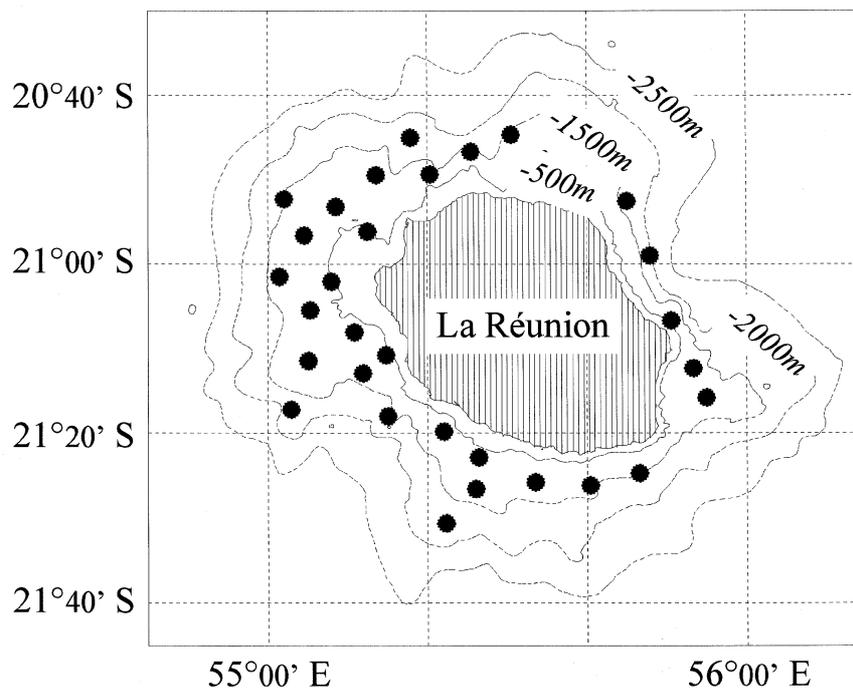


Figure 1. Bathymetric map of the West coast of La Réunion with location of FADs.

tance where the signal is still audible): in such a case, the distance covered by the fish would be twice longer than the boat's one and the swimming speed will be underestimated (case B). Considering more complex movements (sinusoids about the main course), the factor would be greater than 3 (case C). Therefore, caution should be paid in the analysis of very small scale movements, which is particularly the case around FADs. In order to provide a rough order of magnitude of the swimming speed, we used a raising factor of 2 estimated for the intermediate situation (case B) to correct the raw horizontal speed during the phase of association to the FAD.

On the other hand, we can consider that vertical speed (VS) to be properly assessed and can be used without any correction for a comparative analysis. The VS is axis-oriented: negative/positive values corresponding to a downward/upward motion.

A resultant speed (RS) is calculated from the combination (by Pythagorus) of the vertical and raw horizontal speeds. The corrected RS combining the vertical and the corrected horizontal speeds will be applied on FAD sections only.

Behaviour typology

Eight yellowfin tuna tracked during a significant amount of time (> 10 h) are herein considered (Table 1). All the fishes were tagged in the close vicinity of a FAD (300 m radius). Consequently, the FAD of tagging will be considered as the spatial reference from which the movements of every fish are analysed. Therefore, the observations can be classified in 2 phases:

- a phase of tight association to the original FAD of tagging
- a transit phase when the fish leaves the FAD, either to patrol within the area where the FAD network is deployed (FAD-associated behaviour), or to swim offshore, far away from the FADs network area (Offshore-moving behaviour).

All the fishes went through the first phase, at least during the hours following tagging. Later, the tunas tracked diverged in two groups:

- fishes remaining in the coastal area, exhibiting the FAD-associated behaviour (fish no. 1, 2, 3, 5, 7; Table 1);

Table 1. Characteristics of the 8 yellowfin tuna tracking operations.

Fish no.	Fork length (cm)	FAD name	FAD no.	Date	Tracking duration (h)	Moon phase	Type of behaviour
1	110	Le Port	16	Feb 19, 1994	44	Full moon	FAD
2	49	Le Port	16	Feb 23, 1994	21	Full moon	FAD
3	104	St Leu	4	Mar 27, 1995	19	Dark night	FAD
4	95	Stella	5	Mar 29, 1995	24	Dark night	OFFSHORE
5	58	Stella	5	Apr 1, 1995	30	Dark night	FAD
6	70	St Gilles 5M	3	Dec 18, 1995	21	Last quarter	OFFSHORE
7	84	St Gilles 5M	3	Dec 20, 1995	11	Last quarter	FAD
8	76	Etang Salé	25	Dec 3, 1996	30	Dark night	OFFSHORE

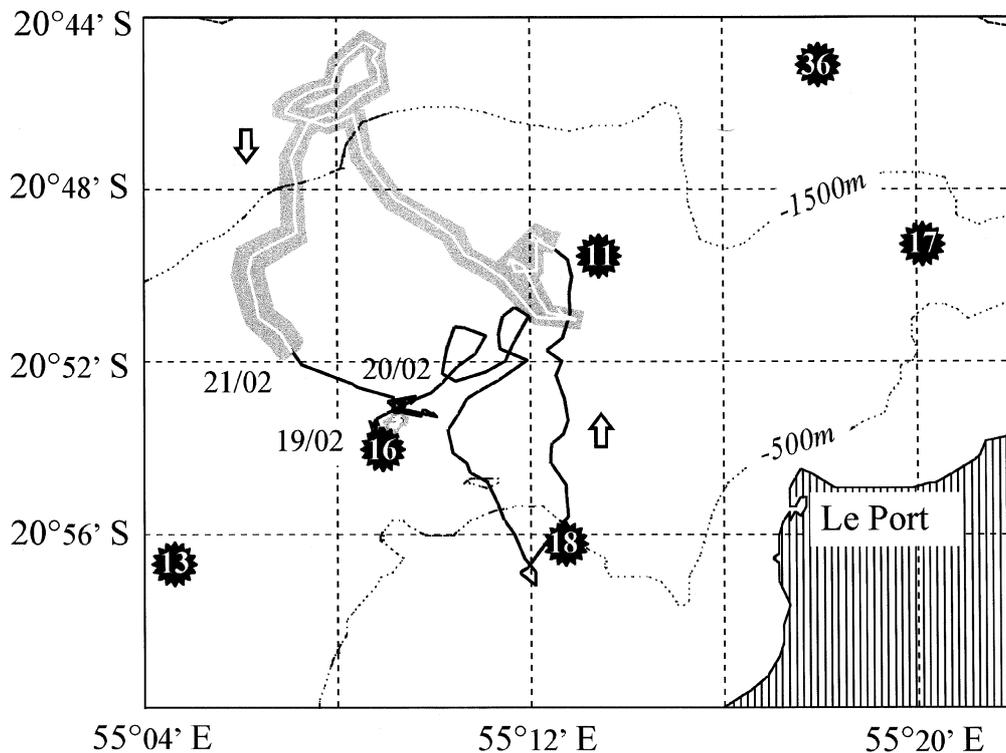


Figure 2. Course of the fish no. 1 (FL 110 cm), Feb. 19 1994, 11:00 to Feb. 21, 6:30.

– fishes escaping from the attraction spheres of the FADs, exhibiting the offshore-moving behaviour (fish no.4, 6, 8; Table 1).

Finally, the moon phase was also considered: in February 1994, the tracks were conducted during full moon nights whilst the other cruises took place in half or new moon nights. This leads to another level of data clustering, according to 3 periods: daytime, moonlight and night time.

Horizontal distribution around FADs

The horizontal distribution of the fish around the FAD is analysed on a linear and unilateral scale, starting at the position of the FAD of tagging. However, a FAD moves about its anchoring location, because of the current and the fact that the mooring line is always longer than the actual depth (the surplus of length versus depth is around 20 to 30% in La Reunion). With a mooring

depth of 500 to 1000 m, the radius of maximal shift can range from 415 to 830 m. As a comparison, an accurate survey of a FAD in Hawaii (Holland et al., op. cit.) shows a 600 m shift radius within 7 h, which is of the same magnitude as our estimate. Cayré & Chabanne (op. cit.) observed a 1700 m shift radius in a depth twice as great as in La Reunion (2000 m), i.e. a similar ratio between actual depth and FAD's shifting area. In view of this uncertainty, we decided to use 926 m (0.5 nautical mile) increments to classify the fish positions, analysing separately daytime (6:00 to 18:00) and night time (19:00 to 5:00) periods. Twilight periods will be considered as well: they denote the transitions between sunset and night and between night and sunrise.

Results

FAD-associated behaviour

- Fish no. 1 (Figure 2). The 44 h track of this tuna is a typical example of strong link with FADs. The fish remained in the close vicinity of the FAD where tagging took place (at 11:00) until midnight. Then, shortly after the moon set (1:00), the animal made a 5 h overnight excursion before moving back toward the FAD immediately after sunrise. Three hours later, the fish left and swam in different directions during 6 h before swimming 6.5 km straightway to another FAD (no. 18) where it stayed for 1 h. Then, it moved almost straightway toward FAD no. 11, crossing the 13 km distance in less than 2 h. The fish visited the FAD very briefly and left at sunset. During the first part of the night, the tuna kept an offshore-oriented course then moved back to the tagging FAD by sunrise, where the track was ended.
- Fish no. 2 (Figure 3). This juvenile tuna was tagged on the same FAD (no. 16) at 14:00. The fish exhibited a similar FAD-associated behaviour during daytime, then swam 7.4 km away during the night. It was lost at dawn then found later (9:00) in the vicinity of the initial FAD where the track ended.
- Fish no. 3 (Figure 4). This tuna was tagged at 11:00 at FAD no. 4, and remained extremely close to the FAD until sunset. The FAD was left at night and the fish took a course to the North, following the 500 m isobath parallel to the coast. Just after dawn, it passed within a few hundred meters of FAD no. 16, but kept straight on, and increased its swimming speed when it was lost.
- Fish no. 5 (Figure 5). Tagged in the morning at the FAD no. 5, this yellowfin tuna remained stuck to it at daytime. The fish finally left the buoy just before sunset for an erratic overnight excursion, at a distance never exceeding 7.4 km from the initial FAD, and passing at less than 3.7 km from another FAD (no. 4). At dawn and during the following hours, the tuna kept a coastward course ending at less than 3.7 km from the shore. At 15:00, when the track was stopped, the fish had reached a third FAD (no. 34).
- Fish no. 7 (Figure 6). The fish was tagged at 18:00 at the FAD no. 3 and departed 4 h later for a night time excursion, patrolling parallel to the coastline above the 300-400 m isobath. The track ended at the FAD no. 4 at dawn the following day.

Offshore moving behaviour

- Fish no. 4 (Figure 7). The fish was tagged at the FAD no. 5. As previously observed in the FAD-associated behaviour tunas, it stayed close to the FAD during daytime, then left the buoy for a straight course to the South, out of the coastal area where FADs are anchored. The track was stopped when the fish was 41 km offshore.
- Fish no. 6 (Figure 8). This tuna was tagged at 17:00 at the FAD no. 3 which was left at sunset while patrolling within a 5.5 km radius from the FAD. At moonrise (quarter moon), the fish departed, kept swimming along the 500 m isobath and passed in the vicinity of another FAD (no. 19). After sunrise, it took a westward course which took it 46.3 km offshore where the track was stopped. It must be noted that, during this daytime excursion, the course was suddenly diverted toward an undersea relief elevation (300 m above the seabed) located 2380 m below the surface (21°06' S–55°10' E).
- Fish no. 8 (Figure 9). The tagging took place at the FAD no. 25, at 17:30 and the fish remained nearby until 21:00. Afterwards, it departed and followed a general offshore movement to the Northwest, without any diversion to FADs at sunrise. However, this track must be analysed with caution because of an anomalous swimming behaviour that could be explained by a lingering death: at 22:15, while patrolling close to the surface, the fish suddenly started to swim deeper, and the depth increased continuously with time until 7:00 when it reached 270 m. According to the time spent in cold waters (more than 2 h below 20 °C without upwards move-

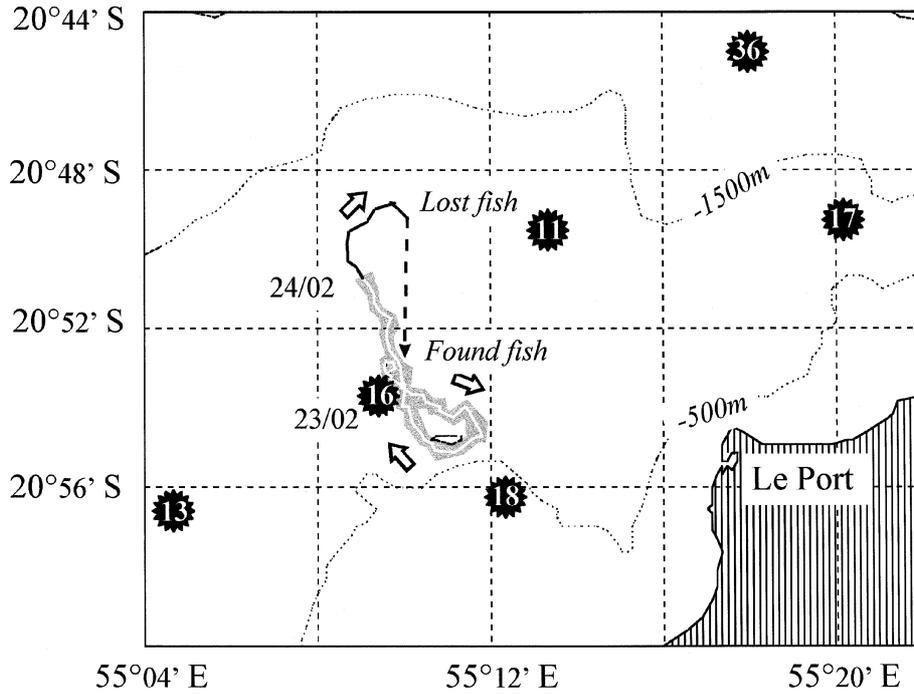


Figure 3. Course of the fish no. 2 (FL 49 cm), Feb. 23 1994, 13:30 to Feb. 24, 10:00.

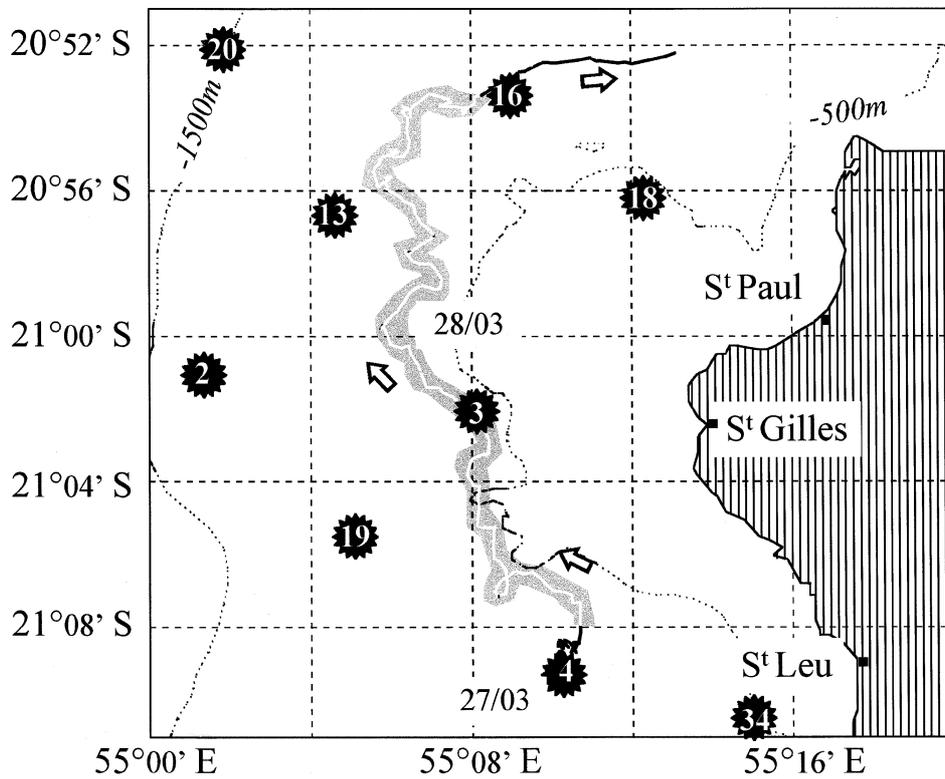


Figure 4. Course of the fish no. 3 (FL 104 cm), Mar. 27 1995, 11:00 to Mar. 28, 7:30.

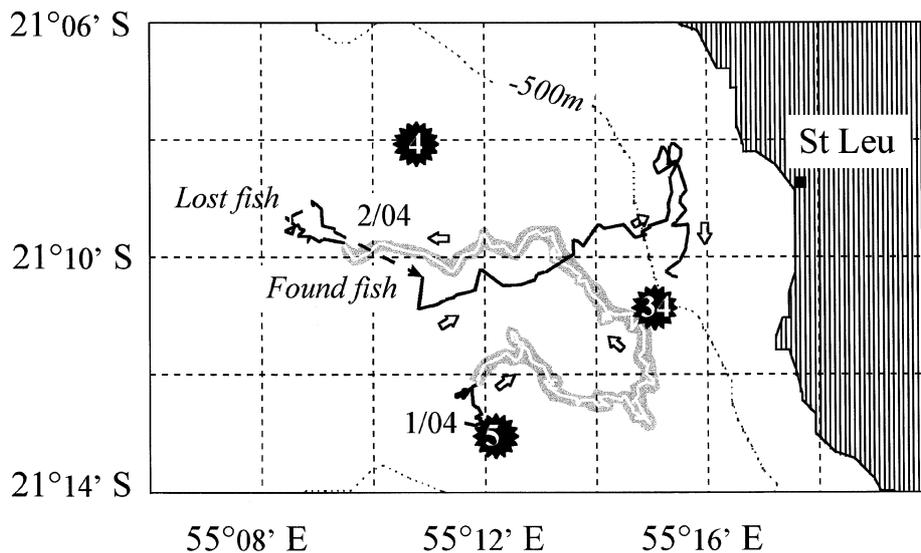


Figure 5. Course of the fish no. 5 (FL 58 cm), Apr. 1 1995, 8:50 to Apr. 2, 14:50.

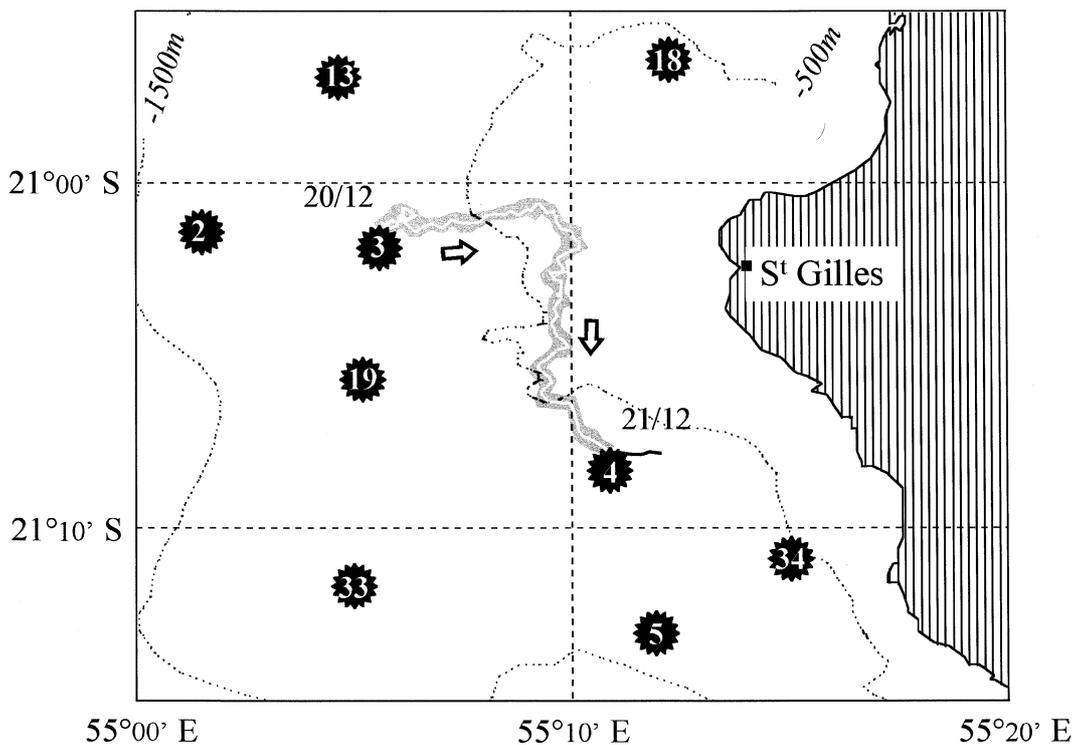


Figure 6. Course of the fish no. 7 (FL 84 cm), Dec. 20 1995, 18:00 to Dec. 21, 5:40.

ment to regain heat in the mixed layer), it is likely that the fish was injured (attack from a predator?) and slowly dying.

Horizontal distribution pattern around FADs

Most of the tuna were caught upstream from the FAD. This was also reported by Holland et al. op. cit., and

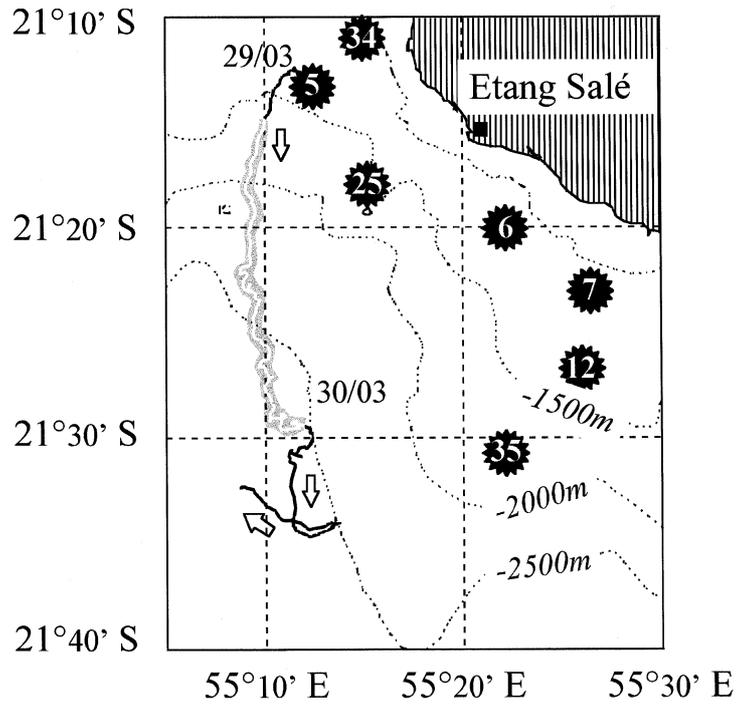


Figure 7. Course of the fish no. 4 (FL 95 cm), Mar. 29 1995, 13:00 to Mar. 30, 13:15.

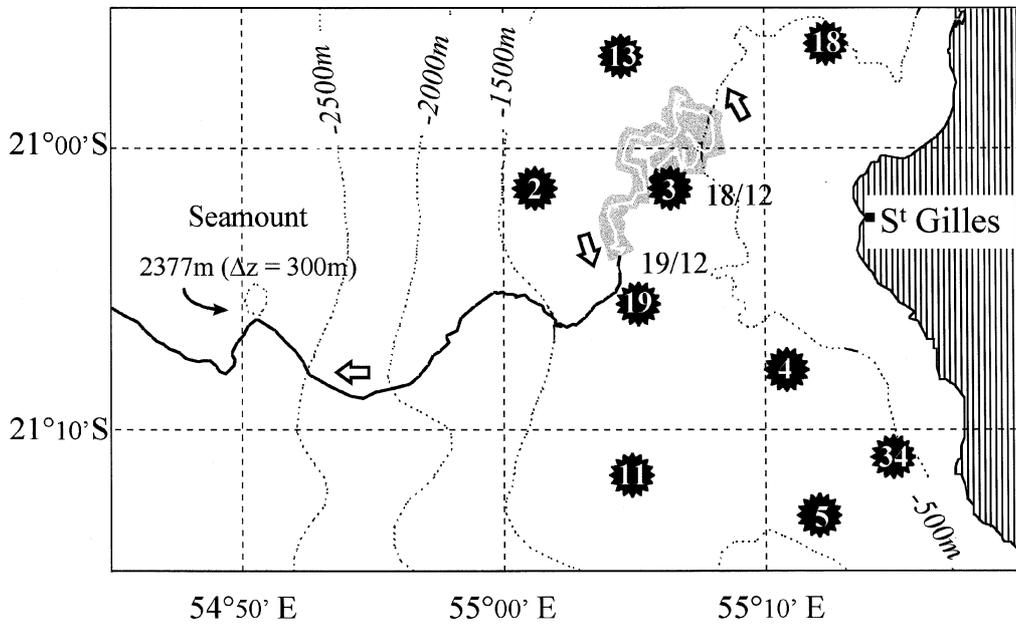


Figure 8. Courses of the fish no. 6 (FL 70 cm), Dec. 18 1995, 17:10 to Dec. 19, 14:30.

even in technical handbooks for fishermen in the South Pacific. The up-current orientation of the predators can be explained by a more efficient way to intercept

incoming preys joining the FAD for shelter. This position can also match with the distribution of prey staying at a slight distance from the structure, like baitfish

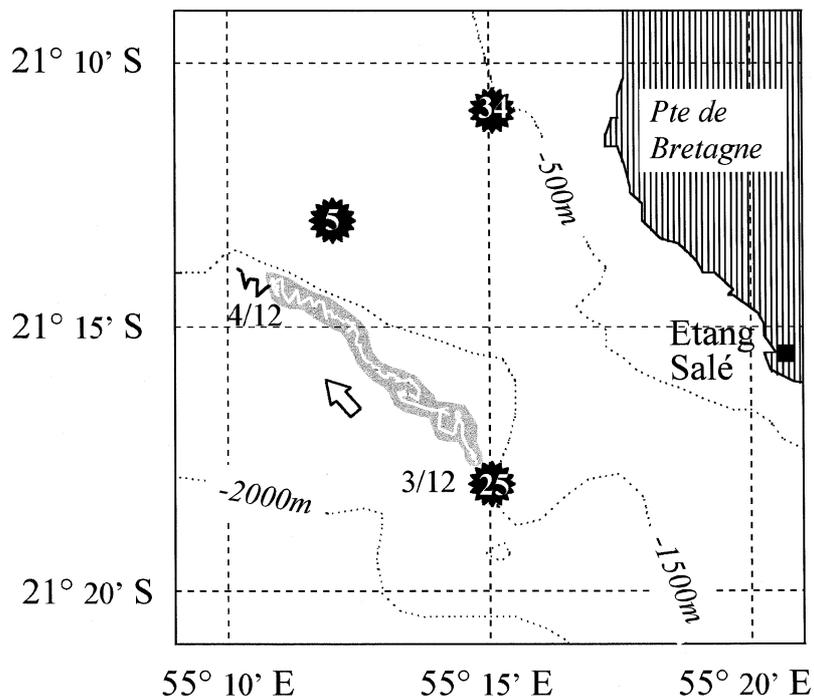


Figure 9. Course of the fish no. 8 (FL 76 cm), Dec. 3 1996, 17:30 to Dec. 4, 19:40.

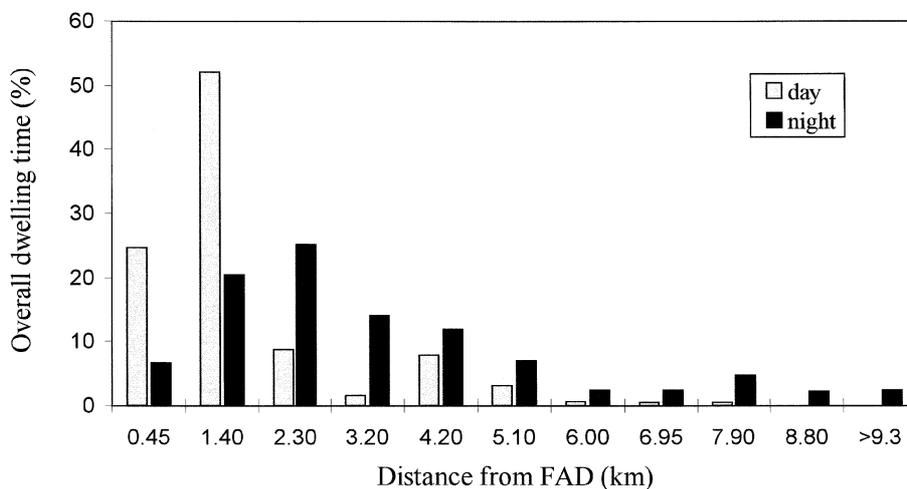


Figure 10. Overall dwelling time versus radial distance to FAD, by 0.90 km (0.5 nautical mile) interval.

groups maintaining an up-current position as observed in Florida (Klima & Wickam, 1971). However, this might not be an absolute rule, since downstream position has also been reported around FADs in Vanuatu (Cillauren, 1994).

All fish positions to a maximum distance of 18 km from the FAD were pooled to provide a general distri-

bution (Figure 10). The median of the daytime distribution is at 0.9 to 1.8 km whereas at night it is 1.8 to 2.7 km, with greater skewness. Most of the dwelling time of a yellowfin during its FAD-associated phase is spent within 9.3 km from the FAD (100% at day, 97.5% at night).

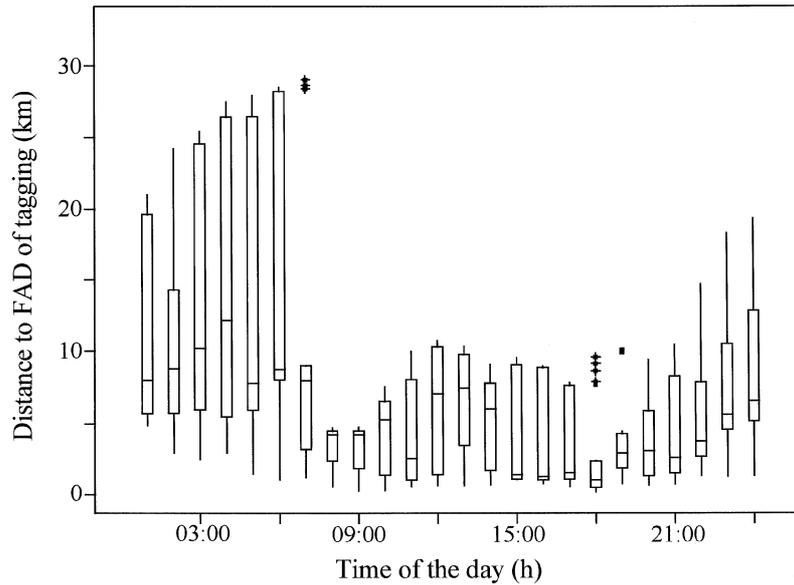


Figure 11. Box and whisker plot of the distance to FAD of tagging over the time of the day.

Considering the fish with a FAD-associated behaviour, the hour effect was tested with a non parametric ANOVA procedure, the Kruskal-Wallis one way analysis by ranks. The high value of the test statistic indicates a significant effect ($\alpha < 0.01$) of the hour. The FAD-dwelling phase is well defined from 7:00 to 19:00, and departure from the FAD appears progressively from 20:00 onwards (Figure 11).

Swimming speed

The swimming pattern appears to be affected when the fish is shifting from one behavioural phase to another, and between different periods. Some examples are given by the tracks of fish no. 3, 4 and 5. Swimming depths, VS and RS are presented in Figures 12 to 14. During the first hour of tracking, the vertical movements often showed a greater amplitude, a consequence of the stress following the tagging operation. This initial period being excluded, the FAD phase at daytime was characterised by a slow VS (0.08 to 0.12 m s^{-1}) and an RS within the range 0.22 to 0.32 m s^{-1} . According to the assumed underestimation of the horizontal speed by a factor of 2, the corrected RS would then be in the range 0.35 to 0.52 m s^{-1} . At dusk (18:00 to 19:00), while leaving the FAD and entering a transit phase, the fish drastically changed its swimming behaviour, moving actively upwards and downwards, increasing both VS (respectively 0.22 , 0.33 and 0.15 m s^{-1}) and

RS (1.40 , 1.20 and 0.90 m s^{-1}). At dawn, still in a transit phase, the vertical activity slowed down (0.08 to 0.11 m s^{-1}) whilst the average RS was maintained at the same level as during the night (1.10 m s^{-1}). Consequently, the day/night change affects the vertical activity, whilst the shift from a FAD phase to a transit phase controls the RS level. Overall, the tunas moving offshore have a median RS of 1.24 m s^{-1} . In the close surroundings of the FAD of tagging (0 to 5.5 km), the corrected RS is estimated at 0.87 m s^{-1} .

– Fish size effect?

Average RS and its variance were calculated for the transit phase only, for the three periods already defined, i.e. day, moonlight and night (Figure 15). The swimming speeds (RS) and their variances do not show any trend with the size of the fish (as already observed in Hawaii, Holland et al., op. cit.) and is comprised between 0.70 and 1.50 m s^{-1} whatever the periods considered.

– Hour of the day effect?

The median VS (0.05 m s^{-1}) corresponding to a FAD-associated behaviour within the interval 0 to 5.5 km, does not vary much over the hour. The largest skewness is observed from 15:00 to 22:00 (Figure 16a).

A very different pattern characterises the offshore-moving behaviour at distances greater than 9.3 km from the FAD, with a diurnal variability of the vertical activity (Figure 16b). The statistical tests (Kruskal-Wallis) discriminate three different phases: 19:00 to

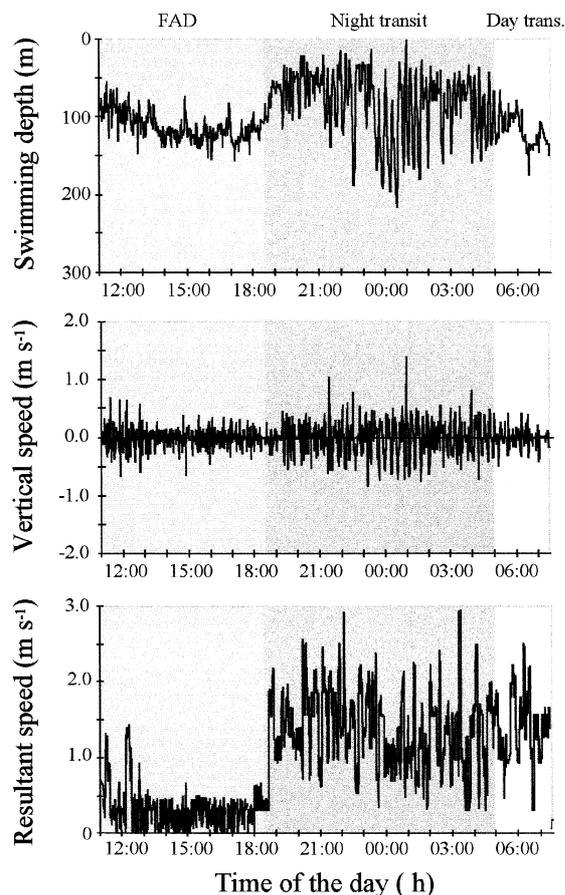


Figure 12. Swimming depth, vertical and resultant speed of the yellowfin no. 3.

3:00 (night) with high vertical speeds (0.35 m s^{-1}), 6:00 to 13:00 (day) with low activity (0.02 m s^{-1}) and 4:00 to 6:00 (morning twilight) as a transition situation between night and day patterns.

To a lesser extent, the RS in an offshore-moving behaviour exhibits a diurnal variability as well, with top speed in the middle of the day (1.8 to 1.9 m s^{-1}). There is no hour effect from 20:00 to 4:00, with a median speed of 1.20 m s^{-1} , but a significant hour effect for the rest of the day (Figure 17).

Discussion

Horizontal distribution of dwelling time

The tracked yellowfin tunas stayed closer to the FAD during the day than at night. This is likely to be the result of an attraction effect (vision and other factors)

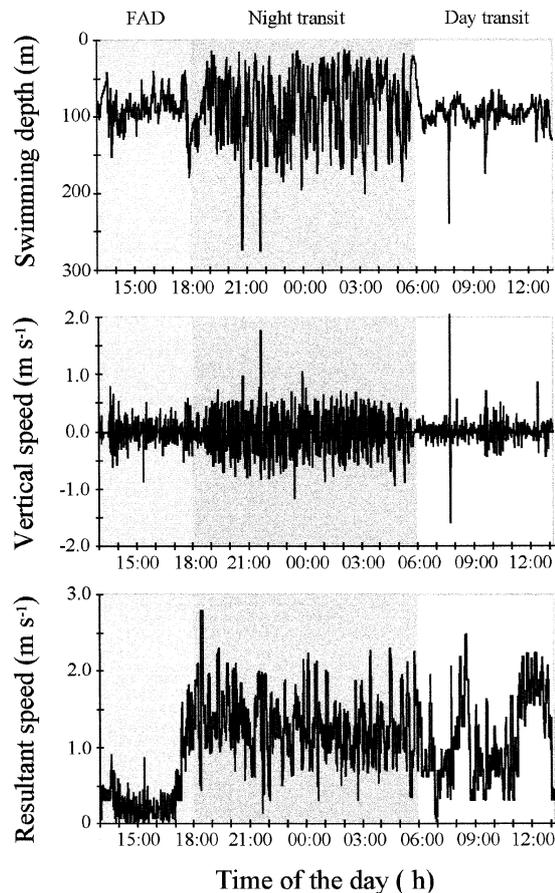


Figure 13. Swimming depth, vertical and resultant speed of the yellowfin no. 4.

exerted by the vertical anchor line which provides a spatial reference in a 3D environment. The device also aggregates other small species preyed on by tuna; this might be a significant stimulus to retain predators in the vicinity of the structure. Observations on stomach contents of yellowfin caught around FADs in La Reunion (Conand, pers. com.) indicate that foraging activity starts in the twilight period preceding the sunrise, and increases during the day. Though it is agreed that a FAD cannot supply a prey turnover supporting the feeding requirements of a whole school of tunas, opportunistic foraging activity does occur around FADs at daytime.

During daytime, the fishes remain close to the FAD (mostly in the interval 0.9–1.8 km). The bulk of the horizontal movements, during the FAD phase, are within a 1.8 km radius (77% of the total time). Conversely, the less pronounced mode at night (1.8 to 2.7 km) and the skewness of the distribution (as far as 9.3 km; Figure 10) denotes a disassociation, followed by overnight

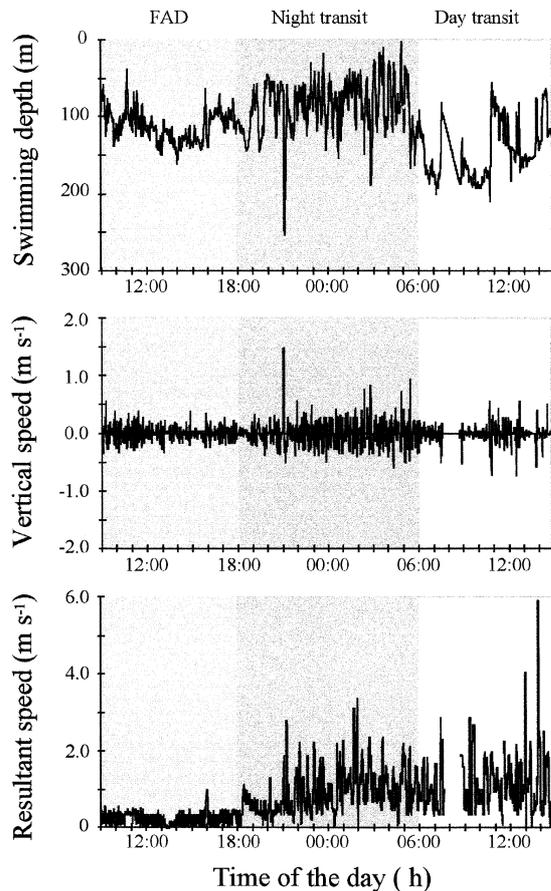


Figure 14. Swimming depths, vertical and resultant speed of the yellowfin no. 5.

excursions away from the FAD of tagging, a behavioural pattern reported by various authors in different regions. Buckley & Miller (1994) suggest that keeping in the immediate vicinity of stationary objects, such as FADs, could make yellowfin tuna (especially small individuals) more vulnerable to attacks by nocturnal predators, like swordfish. If so, it might bring a piece of explanation to the night departures of tunas off the FAD.

The overnight maximum excursion radius is 13 km whilst movements are confined within 9.3 km during the day. These values are in agreement with previous studies: 11 km in Polynesia (Cayré & Chabanne, 1986); 8 km calculated by model (Hilborn & Medley, 1989); 9.3 km in Hawaii (Holland et al., 1990), 13 km in Comoros (Cayré, 1991). Consequently, in La Reunion, the FADs should not be set at distances less than 18 km to avoid overlapping the respective radii of influence.

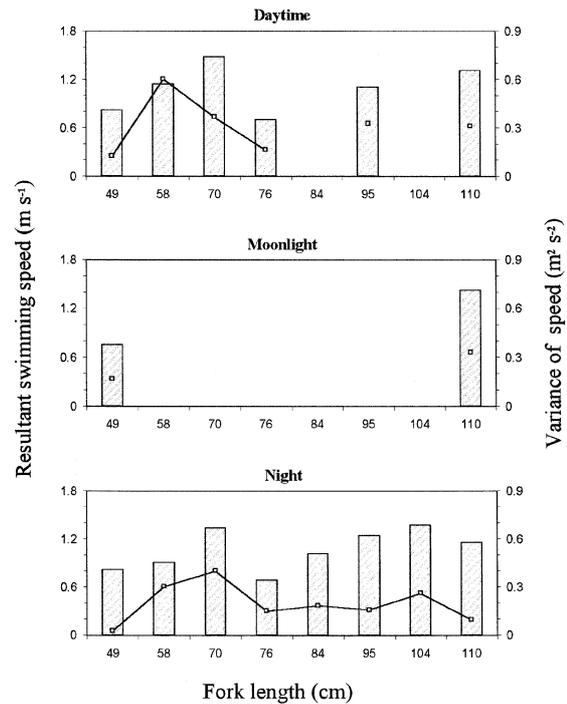


Figure 15. Resultant swimming speed (bars) and variance (line) by period of the day (daytime, moonlight and night) and size of the fish (fork length).

Composite distribution in a vertical plane

The vertical distribution of the fish is constrained by the surrounding oceanic environment features. The combination of temperature gradients and oxygen concentration can explain a great part of the swimming behaviour in depth (Cayré & Marsac, 1993). In La Reunion, the oxygen is not a limiting factor (3.5 ml l^{-1} at 200 m) and the thermocline is not strongly marked (0.5 to $1.4 \text{ }^\circ\text{C } 10 \text{ m}^{-1}$). Thus, the model is not properly applicable. However, relative swimming depths published by Marsac et al. (1996) for FAD can be used to depict the composite depth distribution of the FAD-associated yellowfin in La Reunion. The overall distribution has a prominent mode around 125 m and a secondary one at about 25 m depth (Figure 18).

The vertical plane is defined by the radial distance to FAD (X axis) and the depth (Y axis). Vertical distributions by 10 m steps, from 0 to 250 m, are available at each 900 m radial increment from the FAD, for both daytime and night time periods. The sum of the probabilities at depths for a given interval being equal to 1, it is then possible to merge the horizontal and vertical distributions and generate a matrix of probabilities by

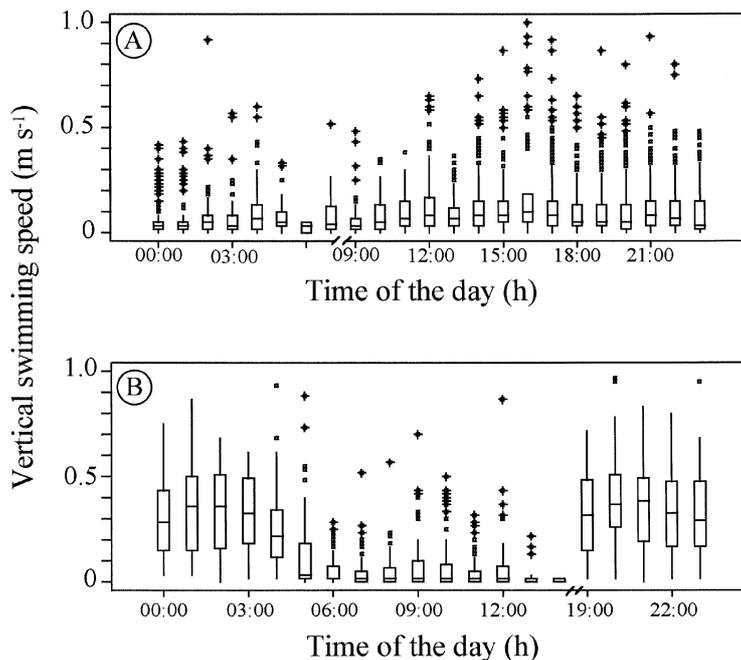


Figure 16. Box and whisker plot of the vertical speed of (A) yellowfin within a 5.5 km radius around the FAD of tagging and (B) yellowfin with an offshore-moving behaviour at distances greater than 9.3 km from the FAD of tagging.

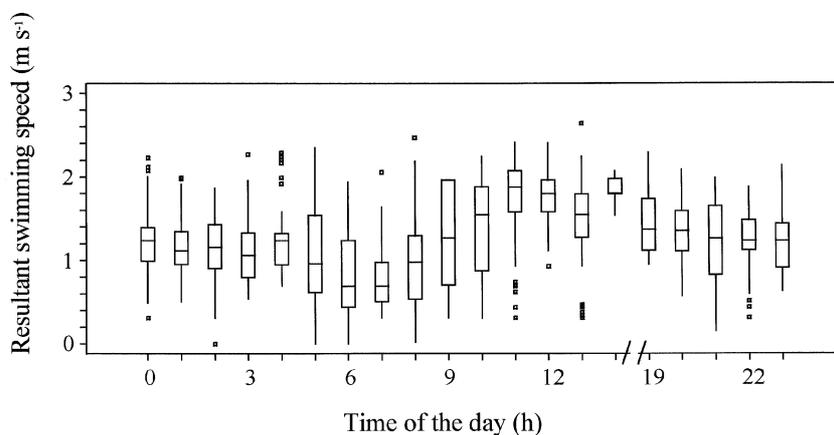


Figure 17. Resultant speed of offshore moving yellowfin at distances greater than 9.3 km from the FAD of tagging.

multiplying the values of the two distributions for each couple 'distance to FAD, depth'. When applied to a given biomass of tuna, the matrix of probability provides a set of values (in weight) which clearly indicates the places where the fish are likely to congregate. The distribution of the biomass in the vertical plane is then calculated is as follows:

$$B_{x,y,t} = B_{\text{FAD}} \cdot f(x,t) \cdot g(y,t),$$

where B_{FAD} = total biomass associated to a FAD; t = period factor (day or night); $f(x,t)$ = horizontal distribution at period t ; $g(y,t)$ = vertical distribution at period t .

As an example, we assumed that a $50 \cdot 10^3$ kg is associated to a FAD in La Reunion at daytime. The resultant matrix (Figure 18) shows a lesser biomass in the surface layer but a slow decreasing rate over the distance to FAD. Yellowfin congregate at 100 m depth

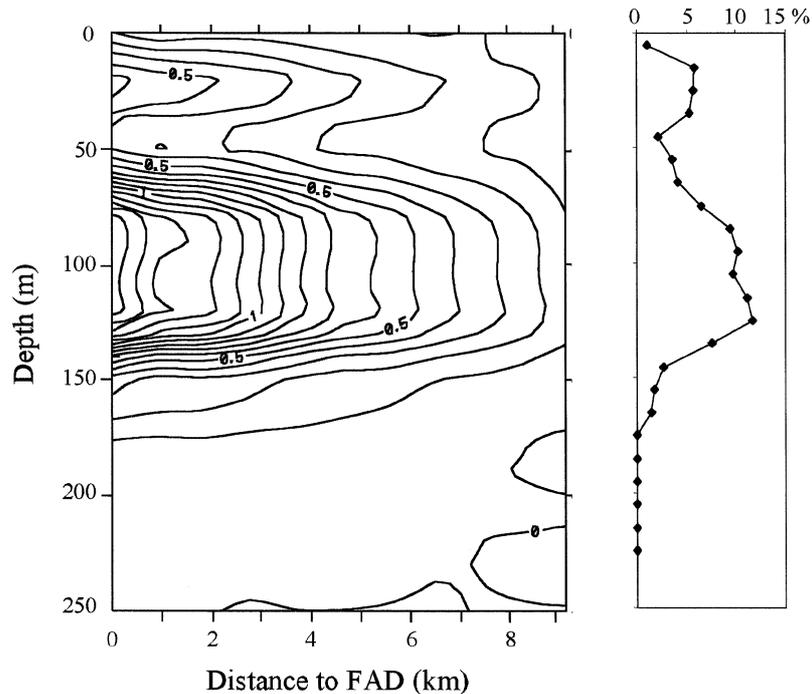


Figure 18. Spatial distribution (in 10^3 kg) in a vertical plane of a yellowfin biomass of $50 \cdot 10^3$ kg associated to a FAD at daytime (left) and relative dwelling time (in %) in depth used in the model (right).

with more than 1000 kg expected within a 3 km radius. If regular monitoring of the vertical distributions can be made around some FADs (using echosounding techniques for example, with relative scale of abundance in depth) this kind of figures can provide valuable information for the local fishermen, who can adjust the hooks depth of their fishing gears.

Swimming speed and behavioural inferences

From our observations, the median swimming speed (RS) of the yellowfin patrolling offshore is 1.20 m s^{-1} at night and ranges from 0.70 to 1.90 m s^{-1} during the day. These estimates match quite well with those calculated in Hawaii (0.89 to 1.81 m s^{-1} , Holland et al., op. cit.) and in the Eastern Pacific (0.67 to 2.17 m s^{-1} , Carey & Olson, 1982).

The swimming speed on FAD is estimated to be about 0.87 m s^{-1} . Those estimates are consistent with the Magnuson's model (1978) that predicts a sustained speed of 0.50 to 0.60 m s^{-1} as the threshold preventing a yellowfin from sinking. Cayré & Chabanne (1986) found much lower values (minimum speed of 0.20 m s^{-1} , and 0.60 to 0.80 m s^{-1} in periods of

strong activity). Recent experiments in French Polynesia gave estimates of the same magnitude (Josse, pers. com.). This points out the uncertainty in the calculation of the swimming speed when a fish exhibits very limited horizontal movements. In this paper, a correcting factor of 2 was proposed but it remains purely a working assumption. A more detailed analysis (by simulation) of different movements patterns of the fish within the audible sphere of the hydrophone, when the boats goes along straight transects at different time intervals appears necessary to provide a more objective estimate of the horizontal swimming speed. Another method would be a direct measurement of the speed using a mini-flowmeter set on the tag (like the model designed by VEMCOTM) or a rotor speedometer (Block et al., 1992). When comparing calculated speeds with the theoretical threshold proposed by Magnuson, we should also consider the flow of the current which provides naturally a gliding potential for the fish. In such a case, even a slow ground speed against the stream can prevent the fish from sinking.

The information provided by the analysis of VS and RS can be interpreted together with swimming behaviour, foraging activity and energy management.

a) Phase of tight association to FAD

The moderate swimming activity of yellowfin in the close vicinity of FADs could denote an optimal behaviour enabling hunting (opportunistic foraging) while saving energy by limited movements. The FAD would be perceived as an anomaly in the field of the natural topography of the nearby island and would enhance the probability of meeting conspecifics (meeting point hypothesis, Soria & Dagorn 1992, Dagorn 1994, Fréon & Misund, in press).

b) Transit phase

- general:
 - most of the night time transit sections are characterised by a high vertical activity, with repetitive and symmetrical movements upwards and downwards about the mean swimming depth. Periodograms of the vertical movements for one of the fish (fish no. 3) indicate a dominant period at 13 min. This behaviour can be interpreted in different ways: (a) resting or energy saving movement, with alternate sinking (passive gliding) and climbing (active swimming), or (b) systematic sampling of the water column in order to locate patches of food in the dark.
 - the moonlit night transit sections present an RS similar to the daytime transit sections and a relatively high vertical activity. These features might denote a feeding behaviour in shallow depth, among FADs:
 - yellowfin tuna exhibit a higher VS and sudden changes of RS (rushes) during daytime, which may indicate foraging activity in the lower part of the thermocline;
 - the tunas transit from one FAD to another: though they do not necessarily stop at the intermediate FADs, this behaviour points out the ability for tunas to memorise specific locations, possibly in relation to different clues. Auditive detection of the FAD's anchor line (low frequency sounds) might be possible; in the same way, olfactive detection from the object itself or from conspecifics (excretion matters) could be considered, but none of these assumptions have been experimentally tested. The underlying stimuli of the attraction to a floating object remain uncertain, but it is likely that tuna find in their surrounding environment a combination of clues and use them to navigate as optimally as possible.
- offshore, away from the FADs:

A striking feature is the low vertical speed and high resultant speed at daytime. This might indicate a clear oriented movement towards a target (for instance, a seamount as observed with fish no. 6) at a stable depth.

Tunas are essentially day-feeders and the feeding activity is presumed to be limited at night (Kobayashi & Yamaguchi, 1971; Legand et al., 1972; Roger & Grandperrin, 1976). However, active hunting behaviour during the night was observed around the artificial source of light supplied by a vessel. Tunas have special adaptations to benefit from their habitat and maximise opportunistic foraging. In particular, the head of the pineal body (a light-sensitive organ) is large and lies below a cartilaginous window in the frontal bone (Rivers, 1953). This organ is activated during twilight and can play as a detector of shadows (Hanyu, 1978). Moreover, advanced predatory species benefit from a more efficient visual system in low ambient light (a larger proportion of retinal cones) than their prey (Munz & McFarland, 1973). Therefore, the success rate of attacks is increased during the short twilight periods. Bright moonlit nights would also allow tunas to chase and prey upon the migrating mesopelagic fauna coming up from deep daytime depths, as it is known that species of this fauna (crustaceans, bathypelagic fishes, cephalopods) constitute a prominent component of yellowfin diet (Brock, 1985; Roger, 1994a, 1994b). The diel variability in the dynamics of baitfish schools can also be taken into account to explain a continuing feeding activity during crepuscular and moonlight hours. At dusk, the schools start dispersing, but to a lesser extent than expected, especially for big schools which remain easily detected by echo-sounder (Fréon et al., 1996), thus providing easy targets for predators.

Conclusions

This analysis points out particularities in the swimming behaviour of yellowfin patrolling in an area where FADs are anchored. Behavioural changes can be noticed when fish shift from a tight association phase with a FAD to a transit phase, either to swim among other FADs or to escape from a network of coastal FADs. The diel variability need to be considered as well. Overall, it appears that the day/night change affects the vertical activity, whilst the shift from a FAD phase to a transit phase controls the resultant swimming speed.

The fish remain tightly associated to the FAD during the day, at a short distance from the mooring line

(less than 2 km), and the distribution ends at a maximum distance of about 9 km. The attraction potential of a FAD will be optimised if there is no overlap with the neighbouring ones. Therefore, we can consider that in La Reunion, the distance between FADs should never be less than 18 km. However, it must be kept in mind that the attraction potential also depends on the available biomass in the area. FAD will not generate tuna but alter the distribution and vulnerability of the resource that is present. The seasonal variation in abundance is even more marked when the area where FADs are anchored is at the boundary of the geographical distribution of the species.

Swimming speed appears to be an indicator of foraging activity and nature of movements. However, the technique used to estimate swimming speed is only reliable in relatively long and straight tracks and remains questionable in situations of small horizontal movements (the FAD situation, in particular). Direct measurement of the flow by a specific sensor set on/inside the tag would enable a better estimate of this parameter. The average speed calculated while yellowfin are moving offshore (1.24 m s^{-1}) is reliable and appear very consistent within those calculated in other regions for this species (Hawaii, Eastern Pacific).

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