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Individual differences in horizontal movements of yellowfin tuna (*Thunnus albacares*) in nearshore areas in French Polynesia, determined using ultrasonic telemetry

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Abstract − This article describes tracking experiments conducted on eleven yellowfin tuna using ultrasonic transmitters in French Polynesia between 1985 and 1997. Nine fish were caught near Fish Aggregating Devices (FADs) while the other two were tracked in coastal areas without FADs. The fish showed different patterns of horizontal movements: tight associations with FADs lasting several days, foraging movements confirmed by simultaneous acoustic observations of prey-sized fauna, movements parallel to the shore, and traveling between FADs. This intra- and inter-individual variety of behaviour might depend on the local environment (prey), and on individual biological differences. The influence of FADs, coastlines, and prey on tuna movements is discussed. The lack of information about the surrounding environment, the internal state of the fish and the recent history of the fish usually prevent scientists from adequately interpreting the observed movements. Ideas for future research to studying tuna behaviour near FADs are discussed. © 2000 Ifremer/CNRS/INRA/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

tuna / Fish Aggregating Devices / behaviour / horizontal movements / ultrasonic telemetry / French Polynesia

Résumé − Différences individuelles dans les déplacements horizontaux des thons albacores (*Thunnus albacares*) en zone côtière de Polynésie française, à partir de marquages ultrasoniques. Cette étude décrit onze expériences de télémétrie ultrasonique réalisées sur des thons albacores en Polynésie française entre 1985 et 1997. Neuf poissons ont été capturés autour de dispositifs de concentration de poissons (DCP) alors que les deux autres ont été suivis en environnement côtier sans DCP. Les poissons ont montré différents types de mouvements horizontaux : associations étroites avec des DCP durant plusieurs jours, mouvements de recherche ou d'exploitation de nourriture confirmés par des observations acoustiques simultanées d'organismes proies, mouvements parallèles à la côte, mouvements entre DCP. Ces différents comportements peuvent dépendre : (1) de l'environnement local (proies), (2) des différences biologiques individuelles. Les influences des DCP, de la côte, ou des proies sur les mouvements des thons sont discutées. Le manque d'information sur l'environnement local, l'état interne du poisson et son histoire récente empêche généralement les scientifiques d'interpréter de manière adéquate les mouvements observés. Des réflexions pour des futures actions de recherche pour étudier le comportement des thons autour des DCP sont proposées. © 2000 Ifremer/CNRS/INRA/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

thon / dispositif de concentration de poissons / comportement / mouvements horizontaux / télémétrie ultrasonique / Polynésie française

1. INTRODUCTION

Magurran (1993) started her chapter about individual differences and alternative behaviours with a citation from Darwin (1859): "No one supposes that all individuals of the same species are cast in the very same mould". Even though everyone knows that two individuals are biologically different (except identical twins), the scientific synthetic approach often needs to simplify the reality in order to draw common patterns for individuals. Individuals are usually classified into categories to reduce the complexity of observations in

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Table I. Characteristics of tracks of yellowfin tuna in French Polynesia.

Fish	Size (FL) (cm)	Dates of track (start)	Duration (h)	Archipelago
1	54	22 Nov. 1985	35	Society
2	62	11 June 1992	19	Society
3	48	2 Sept. 1992	28	Society
4	51	2 March 1993	64	Society
5	93	3 June 1993	34	Society
6	67	14 July 1993	20	Marquesas
7	130	24 July 1993	5	Marquesas
8	60	27-28 Oct. 1995	22	Society
9	100	14 Dec. 1995	11	Tuamotu
10	90	2 March 1996	81	Society
11	108	20 April 1996	91	Society

order to extract the main factors that affect individual behaviours. However, this approach might sometimes neglect important 'unique' events that occurred to an individual, or during a short period in an individual life span, especially when dealing with the behavioural ecology of pelagic fish for which in situ observations are often scarce.

Fish Aggregating Devices (FADs) have shown to be excellent sites for the observation of tuna movements using ultrasonic telemetry. These experiments are usually designed to collect information on behaviour of individual fish associated with FADs in order to improve our knowledge on this striking behaviour. Several yellowfin tuna were tracked in Tahiti (Cayré and Chabanne, 1986; Bach et al., 1998; Josse et al., 1998), Hawaii (Holland et al., 1990a; Brill et al., 1999), around the Comoros Islands (Cayré, 1991) or in La Réunion (Marsac and Cayré, 1998). Most of these experiments provided information about the movements of fish. However, drawing conclusions about their behaviour, i.e. the motivations for the observed movements, was less evident. The conclusions from these experiments, concerning the horizontal movements of fish, mostly concerned the attempt to deduce movement patterns in relation to FADs or coastlines. For the first time, Bach et al. (1998) and Josse et al. (1998) reported simultaneous observations on prey-sized fauna during sonic tagging experiments, providing new information about possible stimuli for movements.

The eleven yellowfin tuna that were tracked in French Polynesia from 1985 to 1997 (*table I*) are presented in this paper. The study is voluntarily restricted to one species in order to eliminate any species-dependent effect, and only horizontal movements are considered. The oceanographic parameters (sea temperature, dissolved oxygen, salinity), usually collected during sonic tagging experiments, play an important role on the vertical movements of the fish. However, their influence on fine-scale horizontal movements is usually low (see Block et al. (1997) for yellowfin tuna movements within the limits of their environmental range), especially in French Polynesia where the physical parameters of the surface layer are very stable. One way to study the role of FADs in tuna movements is to compare on-FAD movements to off-FAD ones (Holland et al., 1990a). A total of nine individuals were sonic-tagged around FADs, and two fish were tagged off any FAD. Tracks will be described by pointing out the individual differences, with a particular attention to the role of FADs, coastlines, but also prey, on the fish's horizontal movements.

2. MATERIALS AND METHODS

The movements of fish described in this paper were monitored with acoustic telemetry techniques. *Table II* shows the different apparatus used in French Polynesia to track tuna from 1985 to 1997. All the acoustic transmitters carried by the fish and the ultrasonic receiving equipment were built by VEMCO (Shad Bay, Nova Scotia, Canada). Acoustic tags were equipped with pressure sensors and thus telemetered information on the fish's depth. The hydrophone was deployed on a mounting pipe for the five first fish, while it was deployed on a V-Fin towed depressor for the others. For the first fish (fish No. 1), geographical positions were recorded manually from radar positions every five or ten minutes. For fish No. 2 to 5, coordinates were recorded manually every five minutes from a Global Positioning System (GPS) receiver. For fish No. 6 to 11, the GPS was connected to a PC and positions were automatically stored on disk. Swimming depths of fish were directly recorded by the VEMCO system, except for fish No. 1 where depths were recorded manually.

Fish were caught by different fishing techniques: drop-stone, vertical longline, trolling. Transmitters were attached onto the tuna's back with two nylon tie-wraps, except for fish No. 8 and 9. These fish were brought alongside the ship and the transmitter was attached while the fish remained in the water. A stainless steel arrowhead was attached to the transmitter and placed in the fish's anterior dorsal musculature using a tagging pole as described for marlin (Holland et al., 1990b; Brill et al., 1993).

Table II. Materials used during ultrasonic tagging experiments in French Polynesia between 1985 and 1997*.

Type	Tag	Hydrophone type	Receiver type	Fish
1	V3P-3 – 1000 PSI 65 kHz	V10	CR40 + CI40	No. 1
2	V3P-3HI – 500 PSI 50 kHz	V10	VR60	No. 2 to 7
3	V16P – 500 PSI 50 kHz	V10	VR60	No. 8, 9
4	V16P – 500 PSI 50 kHz	V41	VR28	No. 10, 11

* All materials were manufactured by VEMCO (Shad Bay, Nova Scotia, Canada)

For fish No. 8 to 11, simultaneous acoustic data were collected between 10 and 500 m of depth with a SIMRAD EK500 scientific sounder (SIMRAD, Horten, Norway) connected to a hull-mounted SIMRAD ES38B split-beam transducer (frequency 38 kHz, beam angle 6.9°). Acoustic data, along with vessel position, were simultaneously logged on a personal computer running SIMRAD EP 500 software.

More details about the materials and methods used for these sonic tagging experiments are provided in Cayré and Chabanne (1986), Bach et al. (1998), and Josse et al. (1998).

3. RESULTS

Currently available ultrasonic telemetry techniques provide only rough estimations of horizontal small-scale movements. The movements of the tracking vessel therefore reflect only in a very general way the

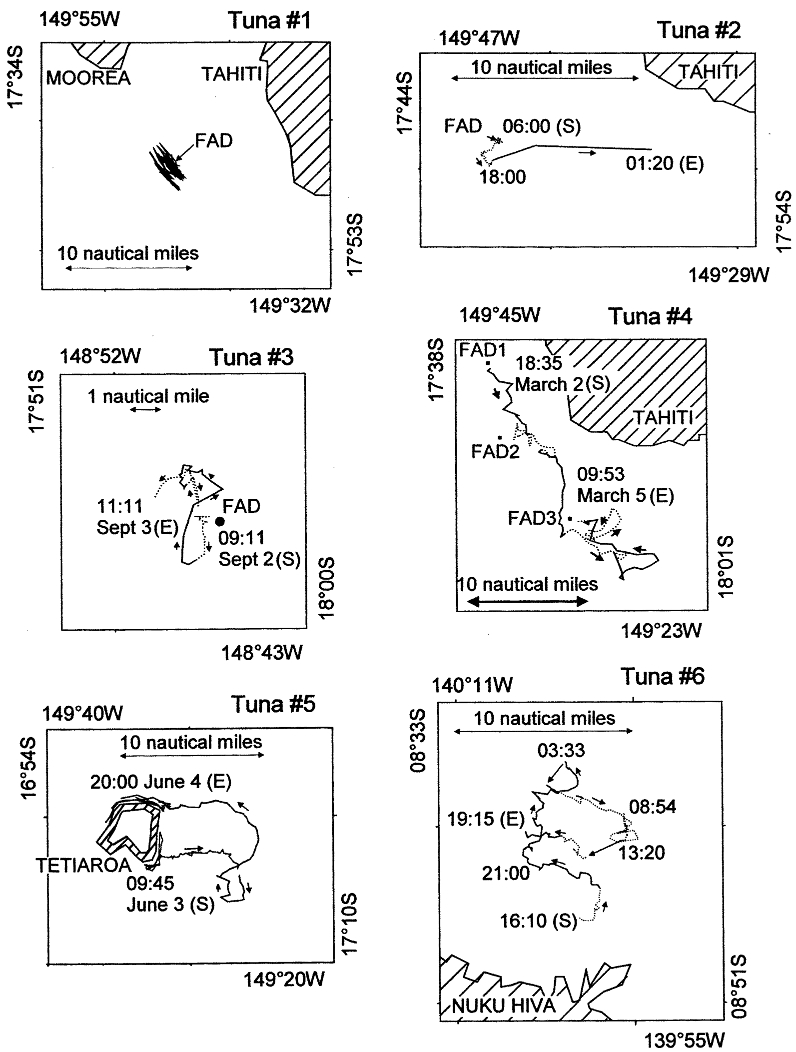

Figure 1. Horizontal movements of yellowfin tuna No. 1 to No. 6. Nocturnal and diurnal movements are represented in full and dotted lines, respectively. (S) and (E) correspond to start and end points, respectively. These indications are not given for yellowfin tuna No. 1, as this fish stayed close to the FAD during the whole tracking.

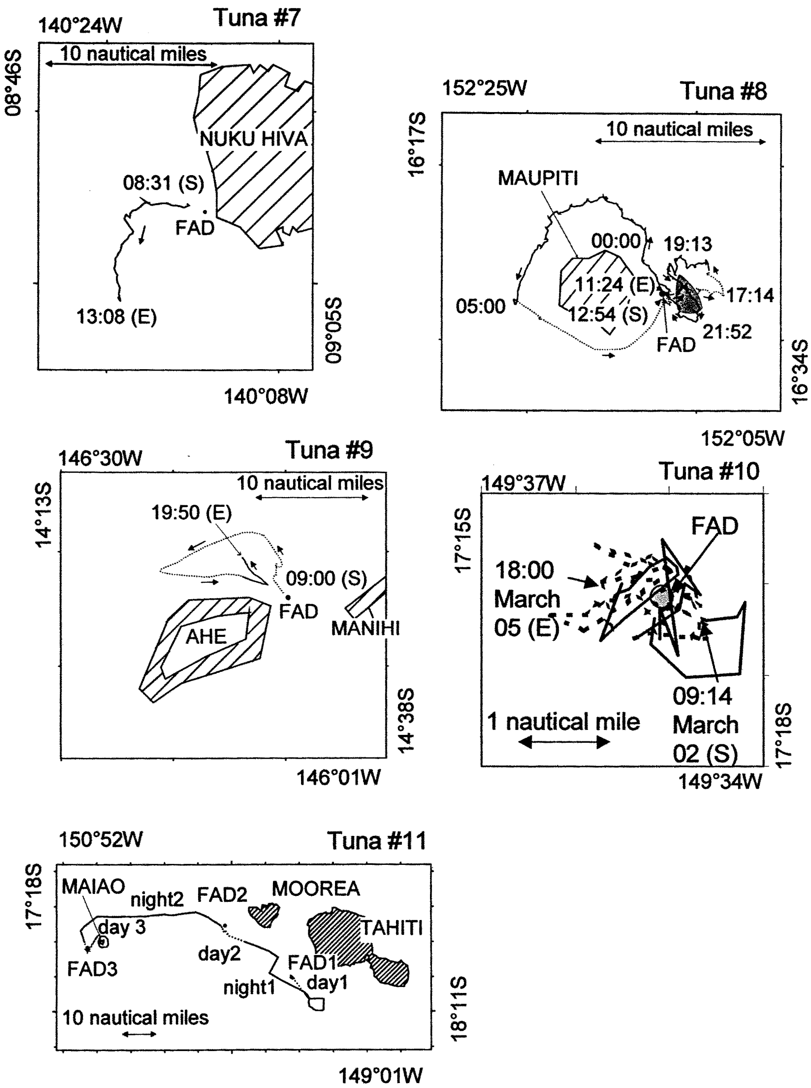

Figure 2. Horizontal movements of yellowfin tuna No. 7 to No. 11. Nocturnal and diurnal movements are represented in full and dotted lines, respectively. (S) and (E) correspond to start and end points, respectively.

minute to minute movements of the fish. Over periods of a few hours however, the movements of the tracking vessel may be used to estimate the fish's movements.

A brief description of the horizontal movements of each of the eleven yellowfin tuna tagged and tracked in French Polynesia is given below. *Figures 1* and *2* represent horizontal movements of yellowfin tuna No. 1 to 6, and of yellowfin tuna No. 7 to 11, respectively.

3.1. Yellowfin No. 1

This 54-cm yellowfin tuna was caught near a FAD located 11 nautical miles from the shore. This fish stayed in the close vicinity of the FAD, mostly in a half-mile area surrounding the FAD, during the four days of the experiment. The maximum distance to the FAD (~ 3 nautical miles) was recorded during the first night. This individual did not exhibit any diel pattern. Other FADs were located in the area but the fish never left the FAD where it was tagged to visit FADs anchored in the vicinity. This fish was abandoned after four days of tracking.

3.2. Yellowfin No. 2

This 62-cm yellowfin tuna was tagged at 06h00 under a FAD located at 8.6 nautical miles from the shore, southeast of Tahiti. During 2 h 30 min, the fish stayed within a radius of 200 m around the FAD. At 08h40, the fish started to move to the north of the FAD, then oriented its trajectory to the southwest, but was never located further than 1.2 nautical miles away from the FAD. At dusk, the fish headed west-northwest. From this moment, it was not possible to record the precise position of the vessel because of problems with the GPS on board. However, the fish was not lost and was swimming in a relatively straight direction. The straight movement reported in *figure 1* is not far from the real position of the vessel. During night-time, the fish swam to the west and was lost at 01h20 after 19 h of tracking, at 8 nautical miles away from the FAD and 3.5 nautical miles from the shore.

3.3. Yellowfin No. 3

The track of this 48-cm yellowfin tuna lasted approximately 28 h. It was tagged in the morning at 09:10 h near a FAD located 20 nautical miles east-southeast of Tahiti. The fish did not move more than 2 nautical miles away from the FAD. During the 4 h after tagging, the fish stayed close to the FAD, before swimming to the south (from 12h30 to 16h30) then southwest (from 16h30 to 18h00). The fish was then located at ~ 2 nautical miles from the FAD at sunset before heading north. It came close to the FAD (0.5 nautical miles) but did not stop by it. From 18h00 to 22h00, the fish swam at a constant speed (~ 1 knot). From 22h00 to the morning, the fish changed its horizontal behaviour, adopting an average swimming speed of 0.25 knot. Movements were restricted to a small area, contrasting with the previous relatively more extensive movements. At 06h30, the fish headed towards the FAD during 2 h (speed ~ 0.5 knot), but it did not stop by it and came back to the area where it was during the last part of the night, increasing its swimming speed to 2 knots. It then left this area, swimming to the west-southwest (speed 1.5 knot). The fish was then lost at 11h11 and relocated in the close vicinity of the FAD at 12h54, before it was voluntarily abandoned by the crew.

3.4. Yellowfin No. 4

This 51-cm yellowfin tuna was tracked during approximately 64 h. It was tagged at 18h35 near a FAD located 5.2 nautical miles from Tahiti's west coast. The fish left the FAD immediately after tagging. The fish then swam southeast parallel to the coast towards a second FAD located 6.1 nautical miles from the previous one. Between 09h15 and 12h45 the fish stayed approximately 3.5 h within a 2 nautical mile-radius around the FAD. Around midday, it headed again southeast, parallel to the coast, then south, leaving the shore. The fish arrived close to a third FAD (0.8 nautical miles from the structure) at dawn. This third FAD was located 5.9 nautical miles southeast from the second one. The fish did not stay close to this FAD for a long time; it swam round the FAD, staying within a distance between 1 and 4 nautical miles from the FAD. The fish then headed to the southeast and left the FAD in the afternoon. At 23h00, while at 8.5 nautical miles from the FAD, it changed its direction and swam back to the FAD. The fish then stayed in the vicinity of the FAD until it was abandoned at 10h00. While located near the FAD during the morning, observations from an echo sounder showed the presence of an aggregation of fish near the FAD, with the tagged fish inside this aggregation. A 43.5-cm yellow-

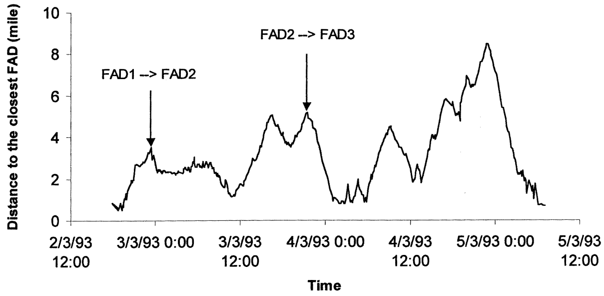

Figure 3. Distances between yellowfin tuna No. 4 and FADs during the tracking.

fin tuna was caught by trolling, which indicates that the fish was likely to be with other conspecifics.

Figure 3 shows the distance from the fish's position to the closest FAD, and there is no evident diel horizontal pattern from this figure. The fish stayed within a 2-nautical mile radius around the FAD in three cases: (1) around FAD2 between 09h15 and 12h45, (2) around FAD3 during the second part of the second night (00h30 to 06h20), and (3) at the end of the last night, until the end of the tracking (04h25 to 07h00). The time and duration of these events were not equal. The excursions away from FADs also did not show any pattern. The fish visited two FADs after leaving the first one although it did not actually associate with them. Between two FADs, it exhibited relatively straight movements. This pattern however, does not indicate that the fish used a spatial memory, or even detected FADs from a long distance. This fish perhaps simply swam parallel to the coast, or perpendicular to the coast. As FADs were also located on a line parallel to the coast, the fish logically encountered them during its move. In the middle of the last night, the fish headed back to the third FAD while it was at 8.5 nautical miles away from it. It is not possible to determine the fish's motivation: going back to the FAD, avoiding to go into an open ocean area, staying into a coastal area, or whether it concerns a completely random movement. These movements do show that the proximity of a FAD at ~ 2 nautical miles perturbed the movements of the fish. However, they do not prove anything about the sense used by the fish (memory or sensory detection), nor about the attraction area of a FAD, nor about a real motivation to visit the three FADs, which may result from a random encounter.

3.5. Yellowfin No. 5

A 93-cm yellowfin tuna was tagged at 09h45 in a 'tuna-hole' off the southeast coast of Tetiaroa Island. 'Tuna holes' are precise locations known for years by local fishermen to be good tuna fishing spots. The size of the fishing area around a 'tuna hole' is very similar to the fishing area around a FAD, i.e. a few hundreds of meters. The term 'tuna hole' does not mean that there is an actual hole or any particular topographic feature. Usually, these spots are located very close to the reef and correspond to particular shapes of the reef. No study however, has yet proven the attractiveness of these 'tuna holes', nor elucidated their exact characteristics. The yellowfin tuna stayed very close (a few tens of meters) to the reef until 15h00. From this moment until the middle of the night, it swam in an offshore direction, made a loop while swimming at a distance of 7 nautical miles from the shore before coming back to the island. It reached the reef located on the northwest part of the island at 02h00. In fact, the fish joined a second 'tuna hole'. The fish stayed at 0.5 nautical miles from the shore, then swam closer to it from dawn. The fish then stayed very closely associated with the reef during the whole day. At 20h00, the tracking was ended because of the risk generated by the proximity of the reef. The fish was observed very close to the reef the next morning at 06h00.

3.6. Yellowfin No. 6

This 67-cm yellowfin tuna was tagged at 16h10 on the north of Nuku Hiva, an island of the Marquesas Archipelago. No FAD was located in this area. After release, the fish headed north during 1 h, leaving the shore perpendicular to it. The fish then swam to the west/northwest during 4 h (17h20 to 21h20), before heading to the north again until 01h00. The fish made a loop. The greatest distance from the shore (13 nautical miles) was reached at 03h30 before contact was lost. The fish was located again 2 h later in the south. The fish swam to the east-southeast during 3.5 h (until 09h00). Until 13h20, it stayed within an area of 1.5 nautical miles in diameter. From 13h20 to 16h25, the fish was lost, then located again, 2.5 nautical miles west from the point where it was lost. From this moment, it swam to the west and was definitely lost at 19h10. The overall movements observed during the tracking were concentrated within a 6-nautical miles radius area.

3.7. Yellowfin No. 7

This 130-cm yellowfin tuna was tagged in the morning (08h31) close to a FAD anchored on the west-northwest part of Nuku Hiva. This fish was lost at 13h15, after being tracked during approximately 5 h. The track pattern exhibited after tagging is similar to the one showed by yellowfin No. 6, leaving the shore. Directly after tagging, the fish left the FAD and headed west. After two hours (10h30), it was at 3.5 nautical miles from the shore, then swam to the south. No other FAD was situated in the area.

3.8. Yellowfin No. 8

A 60-cm yellowfin tuna was tagged at 13h00 near a FAD located off the island of Maupiti, in the Society Archipelago. After tagging, the fish stayed associated with the FAD for 1 h. Then during the afternoon and until sunset it headed east, progressively leaving the FAD. The maximum distance from the FAD was 3.3 nautical miles. It then returned to the FAD during the first part of the night to reach it at 23h00. Simultaneous acoustic observations showed the presence of a scattering layer, which is likely to be formed by tuna prey. The fish crossed this layer a first time during the afternoon and a second time at night. The fish then swam parallel to the coast around the island. At 05h00, the fish associated with the tracking vessel and followed its movements. The vessel came back to the FAD together with the fish. The fish left the vessel and dove to join a group of fish detected by the echo sounder. These fish were likely to be conspecifics aggregated under the FAD.

3.9. Yellowfin No.9

This 100-cm yellowfin tuna was tagged at 09h00 while it was associated with a FAD off Ahe Island (Tuamotu Archipelago). Immediately after its release, the fish headed northwest and left the FAD. One hour later, the fish came up to the surface and drifted under the tracking vessel. The fish stayed strongly associated with the vessel until 16h25 when it tended to break the association. From 10h00 to 16h25, its movements were those of the tracking vessel. At 18h38, the fish was lost after an acceleration in a heavy rain. At 19h14, the fish was found again but it was not associated with the vessel anymore. Contact was lost at 19h50.

3.10. Yellowfin No. 10

A 90-cm yellowfin tuna was caught at 09h15 near a FAD located 14.2 nautical miles off the northern coast of Tahiti. During the 81-h track, the fish always remained at a distance smaller than 1 nautical mile from the FAD. Its track is very similar to the one of yellowfin No. 1 as both fish stayed in the close vicinity of FADs the entire duration of the experiment (4 days each time). Acoustic observations made during the tracking showed the continuous presence of a scattering layer. This scattering layer was located at 50 m depth during the day and 80 m depth at night, and was denser than layers that are usually observed in the area. The swimming depths of this fish corresponded to the depths of this scattering layer (see Bach et al., 1998) for swimming depths of the fish). This fish was caught 5 days after the end of the tracking by a local artisanal fishing boat under an other FAD located at the southwest of Moorea (the distance between the two FADs is ~ 30 nautical miles). In fact, the tracking vessel did pass this FAD, on its way to the port after the tracking experiment ended. The tracking system however, was not in use during the transit, so that it is not possible to know if the fish followed the vessel to this FAD and stopped under it.

3.11. Yellowfin No. 11

Yellowfin tuna No. 11 was caught at 07h38, close to a FAD that was located off Tahiti Island. Directly after tagging and releasing, the fish went under the tracking vessel. During the first day, the vessel stayed in the vicinity of the FAD. It is therefore difficult to determine if the fish was associated with the vessel or with the FAD. This behaviour looks like those exhibited by fish No. 1 and No. 4 that always stayed near the FAD. The vessel left the FAD (FAD1) to go to another one (FAD2, south of Moorea Island) and the fish followed the boat during this nocturnal-time move. A group of 20–50 kg yellowfin tuna, which was likely comprising the tagged yellowfin, was observed swimming close to the boat near the surface. The vessel stayed close to the second FAD during the second day and the fish was drifting under the boat again, like it did the first day. The vessel moved the second night from FAD2 to FAD3 southwest of Maiao Island and the fish continued following the ship. The vessel and the fish arrived at FAD3 the next morning. At 08h00, the yellowfin tuna followed the vessel when it was decided to move closer to the island in order to find better sea conditions. At 09h20, the vessel stopped northeast of the island. At 11h00, the vessel headed back to the FAD and the yellowfin tuna accompanied the vessel in its move. At 12h30, the ship stopped its engine and drifted close to the FAD. At 19h00, the vessel made several rapid accelerations away from the FAD. The fish did not follow the vessel and remained in the vicinity of the FAD. The fish stayed in the vicinity of the FAD during the fourth day (the track was sometimes interrupted to achieve experimental trolling and acoustic survey). The fish did not associate again with the vessel but its presence at the FAD was regularly observed. At 21h15, attempts to re-associate the fish were made. The fish seemed to follow the vessel again, but when the vessel was 0.5 nautical mile away from the FAD, the fish returned to the FAD. The fish remained associated with the FAD during the last night, when the operation was voluntarily stopped. Acoustic observations detected the presence of prey around the FAD during the experiment. Even if the layers were not very dense (they were less dense than during the tracking of yellowfin No. 10 for example), they may be sufficient to nourish the small group of yellowfin tuna observed during the experiment.

4. DISCUSSION

Individual behavioural differences might correspond to changes in an individual's motivation or needs or innate variation amongst individuals (Magurran, 1993). Individual differences can be viewed as the product of three mechanisms: (1) a variable environment, (2) phenotypic differences, (3) behaviour of other individuals. For the second mechanism, i.e. phenotypic differences, we prefer to refer to 'individual biological differences'. This in order to take into account both phenotypic differences and variations of the internal state of the fish, i.e. mainly the fullness of the stomach, which is likely to play a major role in the fish's feeding motivation. Under other circumstances, mating behaviour might influence behaviour.

It is now commonly accepted that behaviour is a compromise between costs and benefits. The associative behaviour of tuna with FADs can be viewed as a flexible behaviour. FADs represent a part of the environment of the tuna, but are not the only stimuli that influence their movements. As costs and benefits vary according to the internal state of the individual, its size, its species, and also the surrounding environment, it is likely that individuals exhibit a variety of behaviours around FADs. The exact influence of FADs on tuna horizontal movements is therefore not easy to study.

The different tracks of yellowfin tuna tagged around FADs in this paper illustrate the classification of behaviour determined by Holland (1996): (1) fish that leave the FAD, showing no tendency to return to it over the duration of the track; (2) fish that spend the entire duration of the track within a few hundred meters of the FAD; (3) fish that spend daytime at the FAD site, leave at night, and return to the same or an adjacent FAD the next day. We would like to add a fourth class: fish that visit FADs, spend some time in their vicinity (not necessarily the entire day), then resume their path. This in particular was recently observed for large yellowfin tuna in Hawaii (Brill et al., 1999). It is therefore necessary to investigate the reasons why the fish exhibited these different horizontal patterns, in particular by collecting pertinent external and internal factors that might be responsible for individual differences (internal state, presence of prey, conspecifics…).

4.1. Foraging movements, independent of FADs

The track of fish No. 8 shows that the fish exhibited different changes in direction while it was in the presence of prey-sized fauna observed by the echo sounder. Animals are known to increase the rate they change directions, or sinuosity, when they are located in an area with high prey densities (Benhamou, 1992). The presence of a FAD in the area of fish No. 8 does not seem to be responsible for its horizontal movements, which are likely to be foraging movements.

The pattern exhibited by this fish can be used to examine horizontal movements of other fish. If we consider that the pattern exhibited by fish No. 8 is likely to represent a foraging pattern, then some similar movements shown by fish in the current study may have the same origin. The tracks of fish No. 7 and 9 did not last sufficiently long to interpret their movements.

Foraging movements are thus characterized by direction changes that make the fish stay within an area of a few miles (1 to 3 nautical miles in the current observations). In particular, the movements of fish

No. 6 and the nocturnal movements of fish No. 5 are very similar to those of fish No. 8. Fish No. 2, 3, and 4 showed similar movements but in the close vicinity of FADs. In particular, movements exhibited by fish No. 4 (*figure 1*) in the vicinity of the second FAD, and especially the third FAD, may correspond to foraging movements. Are these fish located a few miles from the FADs because of the presence of the objects or because of the presence of prey? It may also be possible that the detection of a FAD (at 2 nautical miles for instance) triggered foraging movements if fish consider that floating objects are usually located in rich areas. This corresponds to the 'generic-log' hypothesis (Hall, 1992). Natural floating objects such as logs can be located in rich areas, drifting with them. The presence of logs could therefore indicate to the tuna that a prey is likely to be found in the area. This pattern can correspond to the movements exhibited by fish No. 4 in the vicinity of FAD2 and FAD3.

4.2. Fish showing a strong associative behaviour

Yellowfin No. 1 and No. 10 stayed the whole four tracking days around the same FAD, and fish No. 3 stayed 28 h around the FAD where it was tagged. These fish may have stayed more days around the FADs, but experiments were always voluntarily ended. Considering that the fish may have been present around the FADs for many days before tagging, or could have stayed more days around the FADs after ending of the tracking, the time of residency of these fish may be more than four days. This stationary behaviour of many hours or several days at a same place was rarely observed for non-FAD associated fish. An ultrasonic tagging experiment on a 50-cm yellowfin tuna in the Eastern Atlantic Ocean did show a similar pattern of horizontal movements during the second half of the night (Josse, personal communication), with no anchored or drifting floating objects, nor seamount in the area. This fish however, exhibited this stationary behaviour in the open ocean for only 6 h, which corresponds to a different duration as compared to those observed in the case of FAD-associated fish. Fish No. 5 in the present study did swim inside a restricted area, without any FADs, but this fish was very closely associated with the reef. Fish No. 6 also showed stationary movements during its track, but only during 4 h in the morning. It is therefore difficult to know if the stationary behaviour during several days is due only to the presence of FADs or if it can also be observed for open-ocean fish. More tracking studies on open-ocean yellowfin tuna should be developed. Similar to fish No. 1, 4, and 10, fish No. 11 stayed four days associated with FADs or the tracking vessel. Movements of these individuals can only be explained by a strong motivation to stay associated with floating objects (FADs and boat). The duration of an association may depend on the local biological environment and on the motivation of fish. An assumption may be that as long as the fish can feed from time to time in the vicinity of the floating object, the association is viable on a long term basis (in the order of more than four or five days for instance). For anchored FADs, it has been proposed that associated fish reduce swimming activity and have a lower energetic loss, compared to open-ocean fish. Yellowfin No. 11 however, swam at high speeds (several knots) while following the vessel, which does not correspond to an energy-saving behaviour. It is therefore possible that all these fish (including fish No. 11) might feed close to the floating objects, as acoustic observations tend to confirm. The southern part of the movements of fish No. 2 and the northern part of the track of fish No. 3 show a horizontal pattern that looks like a foraging pattern, similar to the ones shown by fish No. 6 and No. 8 (see next section), but in a narrower range. Their movements seem to indicate that the fish were foraging in the close vicinity of the FAD, still staying associated with it. This is in agreement with the hypothesis that tuna can stay several days around a FAD as long as they can feed from time to time in the vicinity of the object. Further studies are clearly needed to investigate the possible relationships between the duration of an association and the local prey environment.

4.3. Fish visiting several FADs and fish swimming parallel to the shore

Yellowfin No. 4 visited three FADs during its track. This behaviour was also observed in Hawaii (Holland et al., 1990a) and in La Réunion (Marsac and Cayré, 1998). However, it is noteworthy that yellowfin No. 4 also swam parallel to the coast during its path. Yellowfin No. 8 also exhibited a coastline-associated behaviour while swimming around the island. This fish did not exhibit any association to a FAD, as no FAD was present on its path. Considering the same behavioural pattern, i.e. swimming parallel to the coast, we conclude that fish No. 4 was attracted by the other FADs (by a sensory detection or a spatial memory), or did it find them because they were on its path along the coastline? Were its movements driven by the presence of FADs or by the presence of the shore? Holland et al. (1990a) clearly showed that yellowfin tuna may be tightly associated with the reef drop-off. As FADs are usually located alongside a line parallel to the shore, it is difficult to determine the exact motivation of fish exhibiting this kind of patterns. Marsac and Cayré (1998) also identified two types of behaviour for fish tagged in La Réunion, Indian Ocean: fish that remain in a coastal area, exhibiting a FAD-associated behaviour, and fish exhibiting an offshore-moving behaviour. However, in their experiments, the very high density of FADs in the coastal area of La Réunion Island necessarily implies an artificial spatial relationship between the tuna and FADs when the fish are located in the coastal area, which might not always reflect a real associative behaviour, but more likely reflects an exploratory behaviour in the nearshore area.

One important result shown by yellowfin tuna No. 8 is that it associates with the tracking vessel while it was swimming around the island. This behaviour can be compared to the one exhibited by fish No. 4 that stayed for a few hours close to FAD2 and FAD3, after passing close by them. It is like if these fish moved parallel to the coast, maybe to forage on reef-associated prey (see Holland et al., 1990a), and changed their horizontal patterns after encountering a floating object (FADs or boat). The association with the boat (fish No. 8) and the movements exhibited by fish No. 4 close to FADs might not correspond to the same motivation. Fish No. 8 associated with the tracking vessel at 5h00. The vessel finished its way round the island and came back to the FAD. When it came close to the FAD, the tagged yellowfin dove to join a group of large fish that was detected by the echo sounder. It is likely that these fish were conspecifics. This observation is in favor of the meeting point hypothesis (Dagorn and Fréon, 1999). As explained previously, fish No. 4 could have developed foraging movements in the vicinity of FADs. Similarly, fish No. 5 did swim around the island. This fish was so close to the reef that it is likely that it was foraging on organisms closely associated to the reef. This fish, however, also visited two ‘tuna holes’, which can be compared to FADs or boats, or more likely to any anomaly in the environment of tuna.

4.4. Effective range of influence of FADs

The effective range of influence of FADs is considered to be about 5 nautical miles. This result is based on the maximum distances that FAD-associated tuna travel away from a FAD before returning to it. This parameter is very important for modeling tuna behaviour around FADs (Dagorn and Fréon, 1999). However, tuna also exhibit such circular movements in the absence of any FAD. For instance, yellowfin No. 6 swam back after an offshore movement without any FAD in the vicinity. Fish No. 4 and 8 made returning movements towards the FADs while they were a few miles away from the objects (8.5 and 3.3 nautical miles respectively). They ended their paths at a FAD, but can we attribute their returning movements to a motivation to join the FADs? As postulated previously, some of these movements might result from a feeding motivation. The tuna may detect FADs only a very few miles away from them (2 nautical miles for example). Observed returning movements towards FADs, with high sinuosity, many miles away, may be attributed to foraging movements. Simultaneous observation of the biological environment of the fish, and studies on the ability of tuna to detect FADs, are clearly needed to better estimate the effective range of influence of FADs.

5. CONCLUSION

The approach used in this paper emphasizes the role of the adaptive behaviour of tuna. Despite a large amount of sonic tagging experiments on tuna around FADs, it is still very hazardous to interpret fish behaviour, in particular because of the lack of information about the most important stimuli: the environment of the fish, especially the biological environment (prey, conspecifics, competitors, predators), and the internal condition of fish (stomach fullness). It is possible that too much importance has been given to the role of FADs on tuna behaviour because it was not possible to observe the other parameters.

Rather than concentrating all sonic tagging experiments on fish captured around FADs, we propose to conduct experiments on both associated fish and non-associated fish, and to utilize a comparative approach. Observing the biological environment with an echo sounder while tracking fish revealed to be a significant advantage in the understanding of tuna behaviour (Josse et al., 1998; Dagorn et al., 2000). The horizontal movements exhibited by tuna No. 8 were useful to identify what parts of movements of other tracked fish can be attributed to foraging. Of course, all the conclusions for fish in the present study are speculative as the echo sounder was not always used to observe the biological environment, and sensors adapted to observe the fish’s activities are not yet available. These observations, however, argue in favor of a relationship between the time spent by a fish around a FAD and the prey located in the area. This topic should be clearly addressed in a near future. In this study, prey was observed when it was sufficiently aggregated. However, prey can sometimes be very scattered, but still exploitable by tuna. Recently developed software provides new possibilities to study very scattered small organisms observed with scientific echo sounders. Results of Target Strength (TS) values of yellowfin and bigeye tuna (Bertrand et al., 1999) allow to discriminate tuna or tuna-like echoes from echoes from other species. It is then possible to identify large fish and their prey, which provides information about the prey environment and on the presence of conspecifics. The role of other tuna can be of great importance, but has rarely been reported.

The first studies on the behaviour of tuna around floating objects were exploratory studies because it was first necessary to observe what movements tuna were achieving around FADs. After the great amount of knowledge that emerged from several studies in the world in the last two decades, we think that it is time to enter a second phase, directed to experimental tests designed to answer the following question: why does the fish make these movements? Electronic devices still appear to be the most appropriate tools to follow the fine-scale movements of tuna, with acoustic observations to examine both the prey environment and the aggregations (Josse et al., 2000). Ultrasonic tags should now be used in experiments with precise protocols to understand the exact role of FADs in fish movements, for instance to understand how tuna can detect a FAD, their navigation abilities, or the role of their surrounding biological environment (conspecifics, competitors, predators, prey). We should develop observations with appropriate sensors in order to collect more information about the activity of the fish. Multiple tagging experiments should also be developed to study the relationships between fish (Klimley and Holloway, 1999), as a complement to acoustic observations of aggregations, and movements of tuna at larger time and space intervals. Imaginative new equipment and experiments should also be developed in the future to achieve this goal. This objective requires collaboration between fish ethologists, ecologists, and private companies which develop the different equipment, especially the electronic tags, to obtain sensors for observing the fish's activity. Determining the motivations of the fish is of primary importance for investigating why the fish developed such associative behaviour with floating objects.

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