FAD: Fish Aggregating Device or Fish Attracting Device? A new analysis of yellowfin tuna movements around floating objects

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(Received 17 September 2002; initial acceptance 18 October 2002; final acceptance 6 July 2003; MS. number: 7469R)

Tropical tuna are known to associate with floating objects. Because fish are easier to detect and to catch when around these objects, fishermen have extensively deployed a large number of artificial floating objects in the tropical oceans. Although such objects are referred to as Fish Aggregating Devices (FADs), there is yet no strong evidence that fish do show an aggregative behaviour around them. The high probability of finding tuna around FADs may be the result of an aggregation process (high density of fish because fish stay for a long time around FADs) as well as an attraction process (high flow of fish through FADs). We analysed the movements of 14 yellowfin tuna, Thunnus albacares, in relation to FADs moored in the Indian and Pacific Oceans (corresponding to all the published tracking data) to determine whether the observed movement patterns resulted from an aggregation or an attraction process. Tuna appeared to be attracted by FADs. In general, they did not stay for long close to the FADs reached, and so did not aggregate there. Some FADs may nevertheless act as Fish Aggregating Devices. The possible reasons why tuna associate with floating objects are discussed in the light of these results.

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A direct way to distinguish between these two possibilities would be to measure the phenomenon at the population level, that is, in terms of density and flow. To date, however, reliable measures at this level are not available. A detailed movement analysis at the individual level can indicate whether the resulting collective output is likely to correspond to an aggregation of fish around a FAD or to a flow of fish through the FAD area. Indeed, whereas an aggregation should result from an area-concentrated behaviour enabling tuna to increase the time they spend around a FAD, a high flow should result from an orientation behaviour enabling tuna to move towards it. These behaviours may obviously be used successively, as tuna may aggregate around FADs after orienting towards them.

Our aim in this study was to determine whether FADs should be considered as (1) Fish Attracting Devices, according to whether fish actively orient towards them or reach them through random movements, or as (2) Fish Aggregating Devices, according to whether fish modify their movement patterns so as to reduce their net displacement (i.e. the beeline distance between a location reached at a given time and another location reached some time later) or continue to swim without modifying their movement characteristics when they are close to them. We analysed all the published tracking data of yellowfin tuna in relation to FADs moored in the Indian and Pacific Oceans (Holland et al. 1990; Marsac & Cayré 1998; Brill et al. 1999; Dagorn et al. 2000) where fish visited at least two FADs or the same FAD twice after an off-FAD excursion (except unusable data on one fish from Cayré 1991).

METHODS

Movement Recording and Preliminary Data Treatment

The database we used consisted of 14 records of individual movements totalling 39 path sections ending at a FAD. We focused only on the horizontal component of these movements. Figure 1 illustrates one of these 14 tracks, and Table 1 presents their characteristics. Movements were recorded with acoustic telemetry techniques: fish were equipped with ultrasonic transmitters and the signal was received by hydrophones towed by a tracking vessel whose successive locations were recorded using radar, bathymetric and visual landmarks, or a GPS receiver. See the original papers listed in Table 1 for further details. All fish were tagged close to a FAD, except PO4, PO5 and PO6. Given the effective range of acoustic perception, a tagged tuna was assumed to be within 0.5 km of the tracking vessel. The tracking data were standardized using the smoothing procedure proposed by Bovet & Benhamou (1988) with a constant rediscretization step length of 0.5 km. Thus, each track was reduced to a discrete sequence of 0.5-km steps alternating with changes of direction. The times assigned to the rediscretized points were computed by a linear interpolation (assuming a constant tuna horizontal speed between two successive fixes).

For each tuna, the movements were distributed into two classes: on-FAD movements, performed when the tuna was associated with a given FAD, and off-FAD movements otherwise. Setting a reliable criterion specifying that a tuna was or was not associated with a given FAD was far from trivial, however, because the actual maximum distance beyond which a tuna is no longer associated with a FAD is unknown. The influence radius of a FAD may be about 7–13 km (Holland et al. 1990; Cayré 1991; Marsac & Cayré 1998), but this distance would correspond to a possible detection range rather than to the actual association radius, which should be much lower. According to Marsac & Cayré (1998), the on-FAD movements of yellowfin tuna would correspond to horizontal movements within a 1.8-km radius around a given FAD. Furthermore, the reference (published) locations of the FADs corresponded to the initial locations of the FADs, but as FADs are always anchored with mooring lines longer than the sea depth, they move around the anchor location with a radius of several hundred metres (e.g. Marsac & Cayré 1998). To take the uncertainty about the actual locations of the FADs into account but also to avoid overestimating the distance from which a tuna is really associated with a FAD, we considered that a tuna was associated with a FAD if it was less than 2 km from the reference location.

When possible, we analysed on-FAD and off-FAD movements at both the individual and the ocean level (Indian versus Pacific) to check whether (1) possible absence of effects at the ocean level could be caused by a large heterogeneity at the individual level, some tuna behaving...
Means are given ± SD. M: Marsac & Cayré (1998); H: Holland et al. (1999); B: Brill et al. (1999); D: Dagorn et al. (2000).

*Parts of the paths where individuals obviously associated with the tracking boat or followed a coast were excluded from analysis.

**Mean speeds were computed as the averages of the speed values measured at each step (rather than the ratio total length on total time).

The angular mean was computed as the orientation of the mean vector and the angular standard deviation as $180(\bar{r})/\sqrt{n}$, where $\bar{r}$ is the mean vector length (see Batschelet 1981).

**On-FAD values were computed without taking the tagging FAD into account.

in one way and some in another, and (2) possible effects at the ocean level could be caused by the atypical behaviour of a few individuals. If no difference between the tuna from the two oceans appeared, the data were pooled and statistical analyses were conducted at this global level.

Analysis of Off-FAD Movements

We analysed off-FAD movements to determine whether a tuna reached a given on-FAD area after a random search movement or whether it actively oriented itself towards the FAD. A powerful means for conducting such analyses consists in looking at the evolution of the diffusion and the drift as a function of the path length travelled (Fig. 2). The diffusion is the beeline distance between the starting point and the animal's current location. In random search paths, it is on average proportional to the square root of the path length travelled (Bovet & Benhamou 1988). Note that this type of relation is based on an approximation which is valid for a large step number, but it can still be used with a relatively small step number provided the mean cosine of changes in direction is less than 0.9 (Benhamou 2004), and this was systematically the case in the present study. In contrast, the drift is the beeline distance between the starting point and the projection of the animal's current location on the starting point–goal axis. In oriented paths, it increases proportionally on average with the path length, whatever the type of orientation mechanism involved, and the proportionality factor measures the orientation efficiency (Benhamou & Bovet 1992). This is formally true when the goal is located at infinity, but still applies with a good approximation when the goal is a finite distance from the starting point.

When an animal moves and eventually reaches a given goal, the diffusion and the drift take rather similar values (they become equal when the animal reaches the goal). Their evolution in relation to the path length travelled can therefore be very informative: a linear relation indicates an oriented movement whereas a square-root distance between the starting point and the projection of the starting point on the path, BBD corresponds to both a backward drift and a backward diffusion distance.

**Table 1.** Key characteristics of yellowfin tuna horizontal movements

<table>
<thead>
<tr>
<th>Fish</th>
<th>Fork length (cm)</th>
<th>Tracking duration (h)</th>
<th>No. of path sections leading to a FAD</th>
<th>Off-FAD path length (km)</th>
<th>Orientation efficiency within 7 km of a FAD</th>
<th>Off-FAD changes in direction (°)</th>
<th>On-FAD path length** (km)</th>
<th>On-FAD speed** (km/h)</th>
<th>On-FAD changes in direction** (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>IO1 (YF9401 in M)</td>
<td>110</td>
<td>44</td>
<td>3 (1 loop)</td>
<td>76</td>
<td>0.93</td>
<td>4.9 ± 1.6</td>
<td>−2 ± 31</td>
<td>13</td>
<td>4.8 ± 1.9</td>
</tr>
<tr>
<td>IO2 (YF9402 in M)</td>
<td>49</td>
<td>17</td>
<td>1 (1 loop)</td>
<td>17</td>
<td>−1</td>
<td>2.6 ± 1.0</td>
<td>13 ± 33</td>
<td>4</td>
<td>3.3 ± 1.1</td>
</tr>
<tr>
<td>IO3 (YF9501 in M)</td>
<td>104</td>
<td>20</td>
<td>2 (0 loop)</td>
<td>43</td>
<td>0.86</td>
<td>4.8 ± 1.7</td>
<td>−2 ± 33</td>
<td>8</td>
<td>5.0 ± 2.0</td>
</tr>
<tr>
<td>IO4 (YF9503 in M)</td>
<td>58</td>
<td>30</td>
<td>3 (2 loops)</td>
<td>42</td>
<td>0.91</td>
<td>3.1 ± 1.5</td>
<td>1 ± 48</td>
<td>6</td>
<td>4.1 ± 2.3</td>
</tr>
<tr>
<td>IO5 (YF9506 in M)</td>
<td>70</td>
<td>21</td>
<td>2 (1 loop)</td>
<td>72</td>
<td>0.66</td>
<td>5.0 ± 2.1</td>
<td>−2 ± 36</td>
<td>6</td>
<td>5.0 ± 2.0</td>
</tr>
<tr>
<td>IO6 (YF9507 in M)</td>
<td>84</td>
<td>12</td>
<td>1 (0 loop)</td>
<td>19</td>
<td>0.76</td>
<td>3.2 ± 1.2</td>
<td>3 ± 38</td>
<td>4</td>
<td>11.4 ± 8.7</td>
</tr>
<tr>
<td>PO1 (YF8404 in H)</td>
<td>51</td>
<td>48</td>
<td>3 (3 loops)</td>
<td>38</td>
<td>0.80</td>
<td>3.4 ± 3.1</td>
<td>−4 ± 45</td>
<td>16</td>
<td>2.7 ± 1.8</td>
</tr>
<tr>
<td>PO2 (YF8305 in H)</td>
<td>55</td>
<td>24</td>
<td>3 (2 loops)</td>
<td>44</td>
<td>0.80</td>
<td>3.9 ± 2.0</td>
<td>4 ± 33</td>
<td>30</td>
<td>6.5 ± 4.3</td>
</tr>
<tr>
<td>PO3 (YF8504 in H)</td>
<td>47</td>
<td>30</td>
<td>1 (0 loop)</td>
<td>19</td>
<td>0.79</td>
<td>3.6 ± 2.4</td>
<td>7 ± 30</td>
<td>5</td>
<td>3.6 ± 2.5</td>
</tr>
<tr>
<td>PO4 (YF2 in B)</td>
<td>148</td>
<td>86</td>
<td>12 (6 loops)</td>
<td>296</td>
<td>0.92</td>
<td>5.0 ± 2.0</td>
<td>2 ± 29</td>
<td>49</td>
<td>4.7 ± 2.3</td>
</tr>
<tr>
<td>PO5 (YF3 in B)</td>
<td>157</td>
<td>10</td>
<td>2 (0 loop)</td>
<td>45</td>
<td>0.93</td>
<td>5.8 ± 2.2</td>
<td>−2 ± 39</td>
<td>9</td>
<td>7.0 ± 3.4</td>
</tr>
<tr>
<td>PO6 (YF4 in B)</td>
<td>167</td>
<td>20</td>
<td>2 (0 loop)</td>
<td>68</td>
<td>0.97</td>
<td>4.9 ± 2.0</td>
<td>−1 ± 40</td>
<td>6</td>
<td>5.5 ± 2.1</td>
</tr>
<tr>
<td>PO7 (YF8 in D)</td>
<td>60</td>
<td>16</td>
<td>1 (1 loop)</td>
<td>62</td>
<td>−1</td>
<td>10.4 ± 9.4</td>
<td>2 ± 35</td>
<td>4</td>
<td>13.3 ± 12.1</td>
</tr>
<tr>
<td>PO8 (YF8 in D)</td>
<td>51</td>
<td>59</td>
<td>3 (2 loops)</td>
<td>131</td>
<td>0.99</td>
<td>4.9 ± 5.9</td>
<td>4 ± 51</td>
<td>7</td>
<td>4.0 ± 2.2</td>
</tr>
</tbody>
</table>
relation indicates a random search movement. The validity of this procedure is confirmed by the formal demonstration by Marsh & Jones (1988) that the expectation of the square of the diffusion increases quadratically or linearly with the number of steps depending on whether the movement is oriented or not oriented.

This procedure can obviously provide reliable results only if the fish display homogeneous behaviours, that is, if they orient themselves directly from one FAD to another or if they systematically reach the FADs by moving at random. A visual examination of the paths suggested that a tuna that leaves a FAD may first move at random for a while, and later orient itself to another FAD (or even return to the same one). This may occur because a tuna needs to be relatively close to a FAD to be able to detect it or because a tuna leaving a FAD is not motivated to reach another FAD immediately.

To deal with such a possibility, we designed a new procedure. It consists in starting from the end point of a path and moving backward along the path. Then, the backward beeline distance is plotted against the backward path length for every preceding animal’s location, from the end point back to the starting point of the path. At any given animal’s location, the backward beeline distance is the beeline distance between the end point of the path and this location and the backward path length is the length of the path joining this location to the end point (Fig. 2). The backward beeline distance measured at any given animal’s location obviously corresponds to the diffusion of the path between that location and the end point. However, being systematically connected to the end point of the path, which is a potential goal towards which the animal orients, the backward beeline distance can be considered as a measure of the drift as well. Consequently, if the animal reached the goal only by chance, the evolution of the backward beeline distance in relation to the backward path length should on average fit a square-root relation. Otherwise, this backward evolution should show a linear relation, corresponding to the late oriented stage, possibly followed by a nonlinear relation, corresponding to the early random search stage. The point at which the curve shifts from a linear to a nonlinear relation then indicates the distance at which a tuna actively orients itself to the goal, and the slope of the linear relation (falling between 0 and 1) measures the orientation efficiency without taking into account the initial random search movements. We applied this backward procedure to all off-FAD path sections reaching an on-FAD area, taking the entrance point to the on-FAD area as the end point of the path section, to ascertain whether tuna reached on-FAD areas only by chance or actively oriented towards them, and if so, to estimate the orientation distance and the orientation efficiency. We determined the most suitable type of relation (linear versus square root) by computing the sums of residual squares in regression analyses (least square method) with the intercept fixed at 0, because the backward beeline distance is necessarily null when the backward path length is null in both random search and oriented movements. For statistical reliance and consistency, we conducted these analyses on the last 5 km of the beeline distance before a tuna reached a 2-km radius on-FAD area (i.e. when the tuna was within 7–2 km of the FAD itself), including loop sections where tuna moved at least 5 km away from the on-FAD area before returning to it (shorter loop sections were discarded from the analysis).

Analysis of On-FAD Movements

We compared on-FAD and off-FAD movements to determine whether yellowfin tuna altered their movements spatially or temporally when swimming close to a FAD. Indeed, if fish, at a population level, actually aggregate around FADs, we predict individuals would swim more slowly or follow more convoluted paths when associated with a FAD. Both solutions enable the animal to reduce the dynamic (spatiotemporal) diffusion of its movement, that is, the beeline distance between two locations after a given time interval (review in Benhamou 1992). We first compared the horizontal swimming speeds of yellowfin tuna making on-FAD and off-FAD movements. Second, we conducted purely spatial analyses focusing on the distributions of changes in direction. There are two main ways an animal can concentrate its movements in a given area. (1) The animal may choose to turn systematically on the same side; this results in a distribution of the changes in direction with a mean significantly different from zero. (2) The animal makes larger changes in direction; this results in a distribution of the changes in direction centred on zero but with a higher variance (i.e. a lower mean vector length; see Batschelet 1981) in on-FAD movements than in off-FAD movements. In addition, an animal that tends to alternate right and left turns should avoid doing that to increase the time spent in a given area, involving a change in the autocorrelation between successive changes in direction. Statistical tests comparing on-FAD and off-FAD movements were systematically one tailed because the alternative hypothesis (H1) is that the speed should be lower and the variance of changes in direction should be higher in the former than in the latter.

RESULTS

Off-FAD Movements

Visual inspection of the paths showed that tuna seemed to orient themselves towards the next FAD as soon as they left the previous one in only 14 of 39 sections. In this context, the direct evolution of the drift or the diffusion in relation to the path length travelled could not provide clear results: for about a third of the sections, the relation seemed to be roughly linear, but in the other cases, no particular pattern appeared to emerge. Consequently, we looked at the evolution of the backward beeline distance with respect to the backward path length (starting from the on-FAD area reached). For most off-FAD sections ending at an on-FAD area, this backward evolution indeed showed clear linear patterns (Fig. 3) and provided evidence that tuna actively oriented themselves towards
FADs when they were at some distance to them. We analysed the backward evolution on the last 5 km of the beeline distance of the 31 off-FAD sections where a tuna reached an on-FAD area from a place at least 5 km away (i.e. about 7 km from the FAD itself; we had to discard from analysis eight short loop sections by which a tuna re-entered an on-FAD area a few steps after leaving it). The sum of residual squares (with an intercept fixed at 0) was greater for linear regressions than for square-root regressions in six off-FAD sections. Consequently, in these sections tuna mainly performed random search movements and eventually oriented towards the FAD only when they were very close to it. In the other 25 off-FAD sections, tuna reached an on-FAD area by actively orienting to the FAD at least when within 7 km of it. Additional linear regression analyses with a free intercept (to compute the coefficient of determination) showed that the backward evolution of the last 5 km of the beeline distance of these 25 sections was characterized by both a very low intercept (restricted to the range $\pm 250$ m) and a very high coefficient of determination ($r^2 \geq 0.98$). The linear regression slope therefore constituted a reliable estimate of the orientation efficiency. The mean orientation efficiencies obtained were high: 0.82 and 0.89 for the Indian (IO) and Pacific (PO) tuna, respectively (Table 1), and the difference was not significant (two-tailed Mann–Whitney test: $U = 10.5$, $N_{IO} = 5$, $N_{PO} = 7$, NS). The distance at which tuna were actively attracted by a FAD was deduced by visual examination from the point at which the curve shifts from a linear to a nonlinear relation (Fig. 3). For both oceans, the range of this distance was 2–15 km from the on-FAD area (i.e. 4–17 km from the FAD itself), but mainly 7–9 km (i.e. 9–11 km from the FAD; Fig. 4).

**On-FAD Movements**

Nine of the 11 individuals caught and tagged near a FAD spent much longer near the ‘tagging FAD’ than near any other visited FAD (Fig. 5): 82% of the associations with the tagging FADs lasted at least 90 min, while 71% of the associations with the other FADs were shorter than 90 min. A statistical analysis confirmed that the mean residence time around tagging FADs was significantly longer than that around other FADs (two-tailed Wilcoxon test: $T = 3$, $N = 11$, $P < 0.01$). Thus, most tuna clearly restricted their movements for a while around the FAD where they were tagged. What occurred in the vicinity of other FADs was not so clear. We therefore conducted a detailed analysis to compare on-FAD movements (excluding the tagging FAD) and off-FAD movements in terms of speed and path structure. Figure 6 illustrates the speed adopted by a tuna at each 0.5-km step. For each tuna, we computed the mean speed separately for on-FAD (excluding the tagging FAD) and off-FAD movements (Table 1). At the individual level, the speed was never significantly lower in

![Figure 3](image-url)

**Figure 3.** Six examples of the evolution of the backward beeline distance in relation to the backward path length of off-FAD path sections. Origin point (0,0) of the graph corresponds to the end point of the paths, i.e. the entrance point to the on-FAD area reached. The backward evolution was computed by regression analysis from the data points lying under the dashed horizontal line ($Y \leq 5$ km). For the five solid curves, the linearity of the backward evolution proved to be excellent ($R^2 \geq 0.99$) and the orientation efficiency was then computed as the slope of the regression line. For one of them (black solid curve), the shift from the linear to the nonlinear relation is indicated by a dashed arrow and corresponds to a distance of 9 km from the on-FAD area. The dashed curve illustrates a path section of a tuna that reached the on-FAD area mainly by chance.

![Figure 4](image-url)

**Figure 4.** Frequency distribution of the orientation distances to on-FAD areas. Note that, with 2-km radius on-FAD areas, the distances to the FADs themselves should be longer by about 2 km.
The mean, variance and autocorrelation of the distributions of changes in direction were also computed separately for on-FAD (excluding the tagging FAD) and off-FAD movements of each of the 14 yellowfin tuna. Of the 28 mean changes in direction obtained (Table 1), only one was significantly different from zero (IO6 on-FAD: angular mean confidence interval chart at $P = 0.05$; Batschelet 1981, page 86). The variance of the changes in direction was significantly higher for on-FAD than for off-FAD movements (Fisher test at $P = 0.05$ based on the ratio on-FAD angular variance over off-FAD angular variance; Batschelet 1981, pp. 122–124) for four individuals only: PO1, PO2, PO3 and PO4 (Table 1). At the ocean as well as at the global level, the variances of the on-FAD and off-FAD movements were not significantly different (one-tailed Wilcoxon tests: Indian Ocean: $T = 38, N = 6$; Pacific Ocean: $T = 16, N = 8$; global: $T = 38, N = 14$). Examining the autocorrelations of the changes in direction did not provide further information: for only one fish (IO4), the autocorrelation was significantly negative in off-FAD and not significantly different from 0 in on-FAD movements (Spearman test at $P = 0.05$).

**DISCUSSION**

**FAD: Fish Attracting Device?**

Using a detailed path analysis (in contrast to previous studies with simple visual inspection of tracks), our first aim in this study was to determine whether tuna actively orient towards FADs or reach them through random search movements. It appeared that most of the yellowfin tuna oriented themselves towards a FAD with a high efficiency when they were within a radius of about 10 km from it. This orientation distance is similar to the maximum excursion radius found by Holland et al. (1990), Cayré (1991) and Marsac & Cayré (1998) for fish returning to the same FAD (7–13 km). However, tuna seemed to be able to swim in a straight line for a while just by following coastal or bathymetric features. For example, the last off-FAD section of PO3 was 18 km long parallel to the coast, and was characterized by a high orientation efficiency (0.8), although it was not directed towards a FAD (there was no FAD at the end of this last section). As FADs are often moored on lines parallel to coasts or reefs, it is difficult to distinguish the fish’s goal: whether patrolling along a topographic feature or heading to a FAD (Holland et al. 1990; Dagorn et al. 2000). Thus, the highest orientation distance obtained (15 km) may correspond to a tuna that reached an on-FAD area by chance just by swimming along a bathymetric line. Nevertheless, in most cases with shorter orientation distances, the on-FAD areas were reached by tuna moving across bathymetric lines. Consequently, our study provided good evidence for the attractiveness of FADs for tuna swimming within about 10 km of them. Future research should determine what cues fish use to orient towards FADs from such distances. Because of the high orientation distances involved, fish may orient by using the sounds produced by the FAD itself (Fréon et al. 2000) or by the biological community present at the FAD. Further studies (on behaviour and
FAD: Fish Aggregating Device?

Excluding the FADs where tuna were tagged, our analyses strongly suggest that, globally, the tuna did not show area-restricted movements close to FADs. Neither the swimming speeds nor the spatial characteristics of the paths showed clear differences between off- and on-FAD movements. Thus, the individual behaviours of tuna were not likely to lead, at the collective level, to any aggregation around the FADs. Yellowfin tuna are attracted to FADs, but when arriving close to them, it seems that most of the time, they continue to swim without noticeably altering the temporal or spatial characteristics of their movement. This result is in agreement with the low residence times measured by Klimley & Holloway (1999) based on automated FAD-attached listening stations (see Introduction).

It is worth noting, however, that most of the individuals we studied were caught and tagged close to a FAD and that they stayed significantly longer close to this first FAD than to any of the other visited ones. Sometimes yellowfin tuna stayed with the FADs where they were tagged for the whole tracking period (up to almost 4 days; for details see Cayré & Chabanne 1986; Holland et al. 1990; Cayré 1991; Dagorn et al. 2000). Using automated listening stations in a 2-month experiment close to Okinawa (Japan), Ohta et al. (2001) obtained similar results: six of eight tagged yellowfin tuna were observed only at the FAD where they were tagged, with residence times up to 24 days. Such long residence times around a particular FAD might be the result of short-term effects of tagging. Another, maybe more plausible explanation, would be that tuna usually remain for a long while with a particular FAD. Indeed, if we assume that the probability of capture of a tuna is the same for ‘resident’ and ‘migrant’ individuals, and that there is no noticeable tagging effect on the residence time, the fact that most tuna caught and tagged near a FAD remain in the area for a while suggests that, for most FADs, the proportion of residents is greater than the proportion of migrants. If so, FADs would also act as aggregating devices.

Conclusion

Our results suggest that, for yellowfin tuna, FADs act as Fish Attracting Devices, and sometimes as Fish Aggregating Devices. The space use pattern that appears to emerge is as follows. Tuna wander in the ocean until they detect a FAD (usually when they are swimming within about 10 km of it). Then, they orient towards this FAD but would decide to remain in the surrounding area only if it presents some interesting characteristics (possibly the new area should appear more profitable to the tuna than the previous residence area). As this may rarely occur, the tuna would continue to wander and visit a number of FADs before finding a new suitable on-FAD area. After staying for a while in this on-FAD area, they give up. Eventually this pattern would reflect a kind of ideal free distribution of tuna among the on-FAD areas constrained by rather high emigration rates (see Bernstein et al. 1999 for a theoretical approach).

Six hypotheses (not mutually exclusive) have been advanced in the literature to explain why pelagic fish may associate with floating objects (see review in Fréon & Dagorn 2000).

1) The shelter from predator hypothesis may be valid for small fish, but is unlikely for large predators such as tuna.

2) According to the spatial reference hypothesis, fish may use floating objects as ‘seamarks’ which may act as waypoints along a migratory path in the otherwise unstructured pelagic environment. This hypothesis would imply that yellowfin tuna orient themselves towards a new FAD as soon as they leave the previous one, but our analyses showed that this was not usually the case.

3) The comfortability stipulation hypothesis, according to which fish stay near floating objects to rest and regenerate energy after foraging in the area, could be supported by our results if we assume that only a FAD (or more likely an on-FAD area) presenting some well-defined characteristics will be rated by tuna as suitable for that purpose. Conditions found around a FAD are likely to be the reason for tuna staying or not at a FAD.

4) The concentration of food supply hypothesis appears not to be supported by our results, as efficient foraging usually involves movement alterations (in terms of speed or path structure) that lead to an increase in residence times (see Benhamou 1992). The high residence times spent by yellowfin tuna around some FADs suggest only that tuna may forage preferentially close to a limited number of floating objects.

5) According to the indicator-log hypothesis, tuna would visit floating objects to gain some information about the local richness of the environment, as such objects are often drifting in streams where the primary productivity is relatively high. This hypothesis appeared to be more plausible than the previous one (4) because it does not involve an automatic increase in residence time.

6) According to the meeting point hypothesis, floating objects would enable tuna to form larger schools by attracting them in a radius of several kilometres (see numeric simulations in Dagorn & Fréon 1999). Like hypothesis 5, it does not involve an automatic increase in residence time, and thus appears to be equally plausible.

The last three hypotheses (concentration of food supply, indicator-log and meeting point hypotheses) focus on what tuna may expect to find around floating objects: prey or conspecifics. Unfortunately, these parameters are seldom measured. Particular scientific efforts should be conducted on the simultaneous observations of prey and conspecifics while observing the behaviour of tuna around floating objects (e.g. see Josse et al. 1998). Many aspects of the striking FAD-related behaviour of tuna remain unknown and there is therefore a clear need to measure more residence times of tuna around FADs and to determine their possible causes. It is also worth noting that all published studies have been conducted on tuna around anchored FADs and nothing is known about their
behaviour around drifting FADs, although more than 50% of the world catch of tuna is made under such objects.

Acknowledgments

We thank all the scientists, in alphabetical order, Pascal Bach, Richard Brill, Patrice Cayré, Kim Holland, Erwan Josse and Francis Marsac, who kindly provided the raw tracking data of their published works. We are also very grateful to an anonymous referee whose comments helped improve this paper. C.G. acknowledges La Réunion Région for the grant that allows her to conduct her Ph.D. research.

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