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RESEARCH ARTICLE

Behavior of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna in a network of fish aggregating devices (FADs)

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Abstract The influence of multiple anchored fish aggregating devices (FADs) on the spatial behavior of yellowfin (*Thunnus albacares*) and bigeye tuna (*T. obesus*) was investigated by equipping all thirteen FADs surrounding the island of Oahu (HI, USA) with automated sonic receivers (''listening stations'') and intra-peritoneally implanting individually coded acoustic transmitters in 45 yellowfin and 12 bigeye tuna. Thus, the FAD network became a multi-element passive observatory of the residence and movement characteristics of tuna within the array. Yellowfin tuna were detected within the FAD array for up to 150 days, while bigeye tuna were only observed up to a maximum of 10 days after tagging. Only eight yellowfin tuna (out of 45) and one bigeye tuna (out of 12) visited FADs other than their FAD of release. Those nine fish tended to visit nearest neighboring FADs and, in general, spent more time at their FAD of release than at the others. Fish visiting the same FAD several times or visiting other FADs tended to stay longer in the FAD network. A majority of tagged fish exhibited some synchronicity when departing the FADs but not all tagged fish departed a FAD at the same time: small groups of tagged fish left together while others remained. We hypothesize that tuna (at an individual or collective level) consider local conditions around any given FAD to be representative of the environment on a larger scale (e.g., the entire island) and when those conditions become unfavorable the tuna move to a completely different area. Thus, while the anchored FADs surrounding the island of Oahu might concentrate fish and make them more vulnerable to fishing, at a meso-scale they might not entrain fish longer than if there were no (or very few) FADs in the area. At the existing FAD density, the 'island effect' is more likely to be responsible for the general presence of fish around the island than the FADs. We recommend further investigation of this hypothesis.

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Introduction

Tropical tuna, such as yellowfin (*Thunnus albacares*), bigeye (*T. obesus*) and skipjack (*Katsuwonus pelamis*) tuna, are known to associate with floating objects, including man-made devices known as fish aggregating devices (FADs). Two general types of FAD are recognized—anchored and drifting. Of course, floating object aggregation behavior must have originally evolved in association with natural objects that were drifting, not anchored. Although a large number of scientific papers have been published on the topic of floating object-associated assemblages (see Dempster and Taquet 2004 for review), the underlying biological

significance of these associations remains undetermined. Several hypotheses have been advanced (as reviewed by Fréon and Dagorn 2000 and Castro et al. 2002), but none of them has been clearly confirmed. Aside from the debate over the evolutionary advantages to tuna of associating with floating objects, the exact effects of FADs—and networks of FADs—on the behavior of tunas are still not well documented.

Also, it has been hypothesized that FAD networks may represent an 'ecological trap' that could negatively impact tuna populations. Ecological traps can result from subtle but rapid anthropogenic alteration of habitat (Battin 2004). In the case of tuna, Marsac et al. (2000) suggest that in addition to making FAD-associated fish more vulnerable to fishing pressure, large numbers of FADs deployed in a particular location may be so effective in attracting and retaining tuna that the FAD array might significantly alter larger-scale migration patterns and therefore have a detrimental effect on the health of the population. The ideal approach to test this hypothesis (mainly advanced for drifting FADs) would be to compare tuna behavior before and after a FAD network was established. In practice, this is very difficult to achieve but significant insights into the impact of FAD arrays may nevertheless be obtained by documenting the behavior of tuna in a pre-existing array. For logistical reasons, we chose to focus on an existing network of anchored FADs rather than on drifting FADs that would be much more difficult to study.

Active sonic tracking studies have revealed that yellowfin tuna perform movements between FADs (Holland et al. 1990; Marsac and Cayré 1998; Brill et al. 1999; Dagorn et al. 2000), and a detailed path analysis of these data (Girard et al. 2004) demonstrated that yellowfin tuna can orient themselves towards a FAD from within a radius of about 10 km. However, these experiments were limited to a few continuous days of data per tagged fish and usually only applied to movements associated with a single FAD. Longer-term studies are therefore more appropriate for effectively examining between-FAD movements within an array of FADs located in any given area. Klimley and Holloway (1999) and Ohta and Kakuma (2005) both tagged tuna with long-lived coded acoustic transmitters and equipped moored FADs with automated sonic receivers (listening stations). The former demonstrated school fidelity and homing synchronicity within FAD aggregations while the latter determined FAD residence times for tuna and documented periodic excursions away from the FADs. The timing and duration of these excursions could not be linked to abiotic oceanographic phenomena such as current strength or direction. The spatial coverage and array size of these two studies were quite limited; Klimley and Holloway (1999) and Ohta and Kakuma (2005) monitoring only one and seven FADs respectively, and these represented only a fraction of the FADs that were deployed in the general area. By contrast, in the current study we placed acoustic monitors on all the FADs in a specific oceanic area—the waters surrounding the island of Oahu, Hawaii.

In order to provide further insights to the exact influence of an array of multiple FADs on the longer-term spatial behavior of tuna, experiments are required in which all the moored FADs in an area are monitored and three specific questions must be addressed:

- Do tuna visit neighboring FADs and, if so, is there a pattern to these movements?
- How long do tuna stay at individual FADs and in an array of FADs?
- Do multiple animals (tuna) leave a FAD at the same time?

Materials and methods

In order to address the objectives of the study, we implanted yellowfin and bigeye tuna with long-lived, individually coded sonic transmitters and equipped all FADs surrounding the island of Oahu (HI, USA) with automated sonic receivers. This protocol effectively turns the FAD array into a multi-element observatory of tuna behavior and the passive monitoring technique avoids the possible influence of tracking vessels on the movements of the tracked fish (Dagorn et al. 2001a).

Equipping a FAD network with sonic receivers

The state of Hawaii maintains a network of 56 anchored FADs at sites that surround all of the main Hawaiian Islands (Holland et al. 2000). Within the central portion of this FAD system, 13 anchored FADs surround the island of Oahu (Fig. 1). These FADs occupy a geographical area bounded by 21°E02′–21°E52′ N latitude by 157°E33′–158°E27′ W longitude and are anchored in depths of 565–2,480 m. The distance between adjacent FADs ranges from 7.3 to 31.1 km. The shortest distance from an instrumented FAD to a non-Oahu, non-instrumented FAD was approximately 40 km—(between HH FAD around Oahu and P FAD located in an offshore area). The 13 Oahu FADs were equipped with VEMCO VR2 sonic receivers designed to detect a wide range of uniquely coded sonic transmitter tags. The receivers were

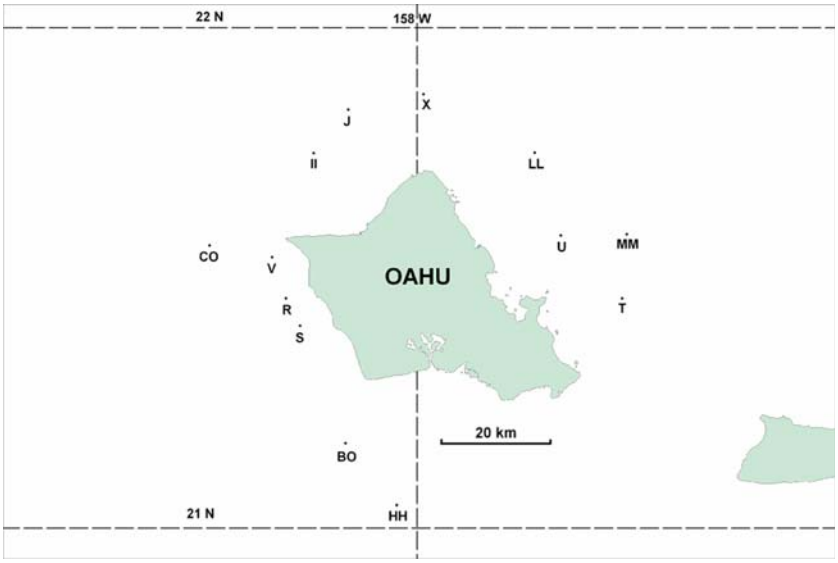

Fig. 1 Location of the 13 FADs around the island of Oahu (Hawaii)

mounted directly to the FAD mooring system 18 m below the surface with the hydrophone element in a downward orientation. The stored data were retrieved by regularly visiting the FADs and removing the receivers. At the same time, a replacement receiver with new batteries was attached to the FAD mooring gear.

Tag implantation

Tuna were captured within 500 m of FADs using surface trolling lures or baited lines with circle hooks fished to a depth of approximately 75 m. Single hooks with crimped barbs were used to minimize damage and expedite release of the fish. Immediately after capture, fish were placed in a wetted, padded cradle where the hook was gently removed and the eyes covered with a wet artificial chamois material while a saltwater hose was inserted in the mouth to provide oxygen to the gills. Tags were only placed in healthy fish with no significant bleeding from the mouth and no injury at all to the eyes or gills.

We inserted tags in the peritoneal cavity using standard fish tag implantation techniques (e.g., Meyer and Holland 2000; Schaefer and Fuller 2002). A scalpel was used to make a 1–2 cm long incision in the muscle of the abdominal wall 3–5 cm anterior to the anus and 2–3 cm to one side of the ventral midline. To avoid possible damage of organs by the scalpel, final entry into the abdominal cavity was made using a latex gloved finger to rupture the peritoneal lining. A coded Vemco V16 tag (69 kHz, V16-4H-R256, 5–30 s delay, rated battery life 344 days) was then inserted in the peritoneal cavity and the wound closed with two absorbable sutures. In order to make tagged fish noticeable by fishermen and maximize reporting of recaptures, all tagged fish were also marked with an external Hallprint 11 cm plastic dart tag inserted through the pterygiophores of the second dorsal fin. All fish were measured to the nearest cm prior to release. The total elapsed time that the fish were out of water was between 1 and 2 min, with all fish released within 300 meters of the FAD of capture.

VR2 receivers can record false detections that result from sonic collisions between two or more tags transmitting simultaneously or from ambient noise in the aquatic environment. In most situations, false detections are easily distinguished as they do not correspond to legitimate identification codes of deployed tags. On some occasions, a false detection by a VR2 may 1‘ correspond to a valid ID code making it difficult to determine if the fish was actually present or not. In order to rationalize this situation, we defined a detection as being valid when a minimum of two consecutive receptions were recorded within 60 min for the same ID code for a fish known to be at liberty. Range tests were performed by deploying a tag under a GPS-equipped vessel that was drifting away from the FAD. Four tests were performed and indicated that tags could be detected by VR2s from maximum distances between 600 and 1,100 m, depending on local conditions.

Tagging and data collection strategy

From August 2002 to March 2004, we released 45 yellowfin tuna (59–95 cm) and 12 bigeye tuna (55–108 cm) equipped with internal sonic tags (Fig. 2). Sonic tagging

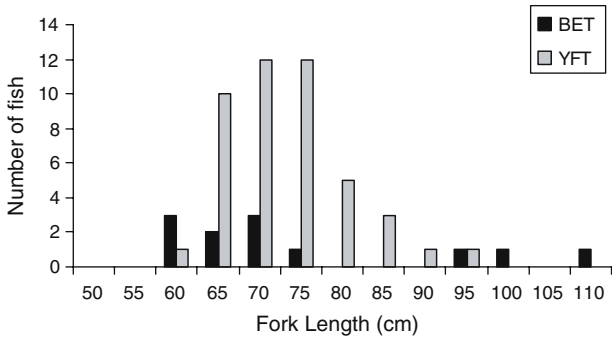

Fig. 2 Length frequency of tagged yellowfin and bigeye tuna

concentrated on three FADs during four time periods and, with the exception of three single releases, multiple fish were tagged and released during each tagging event (Table 1). The sonic receiver network on 13 FADs around the island of Oahu was operational during the entire 20-month release period and continued to be maintained and monitored through March 2005, one year beyond the last tag release (at which point all tag batteries were probably dead). A total of 15 yellowfin and one bigeye tuna were recaptured by local fishermen at their FAD of release, while 3 more yellowfin tuna were recaptured at other FADs.

Data analyses

- Do tuna visit neighboring FADs and is there a pattern to these movements?

To address this question, we first distinguished three categories of fish according to their movements:

- Category 1. Fish that were only detected for one continuous period at the FAD of release,
- Category 2. Fish that only visited the FAD of release, but made several repeat visits to this FAD after absences of >24 hours.
- Category 3. Fish that visited several FADs.

We quantified the number of fish that were only detected at the FAD of release (category 1 + 2) versus the number of fish that visited different FADs (category 3). In order to estimate the fraction of fish (of our population of tagged fish) that visited several FADs, we removed fish recaptured at the FAD of release from the total number of tagged fish, as it is not possible to know if those fish would have visited other FADs if they had not been recaptured.

We defined a valid movement between FAD 'A' and 'B' as when a tagged fish was detected first at FAD 'A' and then at FAD 'B' without being detected at any other FAD during the intervening period, regardless of the time between the last detection at FAD 'A' and the first detection at FAD 'B'. To determine if there was a directional component to inter-FAD movements (versus movement simply to the nearest adjacent FAD regardless of its compass bearing from the initial FAD) we defined two indices to characterize between-FAD movements. The first index is designated 'Adjacent FAD' and corresponds to an additive ranking based simply on the distance of the destination FAD from the initial (departure) FAD and relative to the distance of other nearby FADs from the initial (departure) FAD regardless of their compass direction. The second index (Linear FAD index) corresponds to an additive ranking that assumes a continuous unidirectional movement around the island of Oahu between the departure and arrival FADs. For example, a fish movement between FAD R and FAD CO (see Fig. 1) is ranked 3 by the Adjacent FAD index because FADs V, S are closer to R than CO but the same move receives a 2 with the Linear FAD index (because only V is geographically between R and CO). In some instances, some FADs were missing during a time period of inter-FAD movements and the indices were adjusted accordingly. Adjacent and linear FAD indices are calculated on first movements performed from the FAD of release and on between-FAD movements performed afterwards (secondary movements) to examine if there was any different pattern.

For each inter-FAD movement, we calculated transit speed as the straight line distance between the two FADs divided by the time interval between the last detection at FAD 'A' and the first at FAD 'B'. These

Table 1 Tagging strategy: cohort or individual release, FAD of release, tagging periods

FAD of release	Tagging strategy	Periods of tagging (range in days)	Number of yellowfin tuna tagged–number of bigeye tuna tagged
LL	Cohort release	7–8 Nov 02 (2)	1–5
CO	Cohort release	3–28 Feb 03 (26)	19–6
HH	Cohort release	10 Mar–5 May 03 (56)	9–1
LL	Cohort release	20 jan–11 Mar 04 (51)	13–0
MM (2), X	Individual release	27 May 03, 9 & 18 Feb 04	3–0

values do not necessarily correspond to instantaneous swimming speeds as the fish may have made several deviations from the straight line course between FADs. In previous active tracking experiments, sustained swimming speeds ranged from 2.6 to 5.8 km/h with one particularly high value of 10.4 km/h (Girard et al. 2004). Therefore, in the current experiment, we consider inter-FAD speeds greater than 2.5 km/h as being indicative of relatively straight or directed movements between FADs.

- How long do tuna stay at FADs and in a network of FADs?

Ohta and Kakuma (2005) operationally defined a continuous residence time (CRT) as the duration for which a tagged tuna was monitored around a FAD without a day-scale (>24 h) absence. We have adopted the same definition of CRT to measure the residence time of tuna at FADs. The residence time in the network of FADs is defined as the time period between the first and last detections within the network. It is calculated for the entire tagged population and for each of the three categories of fish (defined by the movements performed by the fish, see previous section).

When determining if tuna spent more time at their FAD of release compared to subsequently visited FADs, we only examined fish that visited more than one FAD. For each of these fish, a number of residence times $t_0,t_1,...,t_m$ were observed. The null hypothesis is that residence times at various FADs for each fish are equally distributed (but maybe different for different fish). The following normalized test statistic T_i is computed for the ith fish.

$t_{0,i}$ first residence time
$\bar{t}_i$ mean residence time of all but the first residence
$\hat{v}_i$ estimated variance of all observations on that fish

The test statistic is:

$$T_i = \frac{t_{0,i} - \bar{t}_i}{\sqrt{\hat{v}_i + \hat{v}_i/n_i}}$$

The term $\sqrt{\hat{v}_i + \hat{v}_i/n_i}$ is the estimated standard deviation of the difference between first residence time and mean of all subsequent residence times. The combined test statistic is $T=T_1 + \cdots + T_n$ from all fish.

Because the distributions of residence times were not normally distributed, we decided to use a bootstrap methodology. The bootstrap algorithm simulates N = 10,000 artificial datasets assuming the hypothesis. Each dataset is simulated by randomly calculating the observed residence times for each fish. Notice that the observations are not mixed from one fish to the next. The test statistic T is computed for each simulated dataset. If the observed value is extreme in the simulated distribution of T, we concluded that the null hypothesis was not supported by data and the hypothesis is rejected.

It is important to note that the CRT after release and any CRTs displayed by recaptured fish (either at the FAD of release or another FAD) are inherently underestimates. We cannot know how long a fish was in residence before it was captured and tagged and we cannot know how much longer a tagged fish would have remained at a FAD if it had not been recaptured. ''Unperturbed'' CRTs can therefore be estimated by removing these CRTs.

- Do tuna leave a FAD at the same time?

In order to be consistent with our operational definition of CRT, for this study we did not examine fine-scale synchronicity but only fish leaving a FAD within the same 24 h period. To distinguish fish leaving a FAD singly from fish leaving a FAD with others, we calculated the percentage of fish that left a FAD accompanied by at least one tagged companion within 24 h of each other. We also calculated the mean ratio of fish leaving a FAD versus those remaining at the FAD.

Results

All the tagged tuna were detected by the receiver mounted on the FAD of their capture/release, with 50 fish (88%) being heard within 38 min of release. The most delayed first detection was recorded 12 h after release.

- Do tuna visit neighboring FADs?

The majority of the tagged yellowfin and bigeye tuna belong to the first and second categories: they were only detected at the FAD where they were originally tagged and released (Fig. 3). For yellowfin tuna the results were: 29 Category 1 + 8 Category 2 = 37 out of 45 fish, i.e. 82%. For bigeye tuna: 11 Category 1 + 0 Category 2 = 11 out of 12 fish, i.e. 92%. Only eight yellowfin tuna and one bigeye tuna were detected at more than one FAD (Category 3).

Because 15 yellowfin tuna were recaptured at their FAD of release, they were removed from the total number of tagged fish used for estimating the probability of yellowfin tuna visiting other FADs. The total eligible yellowfin tuna then drops to 30 individuals, among which 8 visited other FADs. Therefore, the

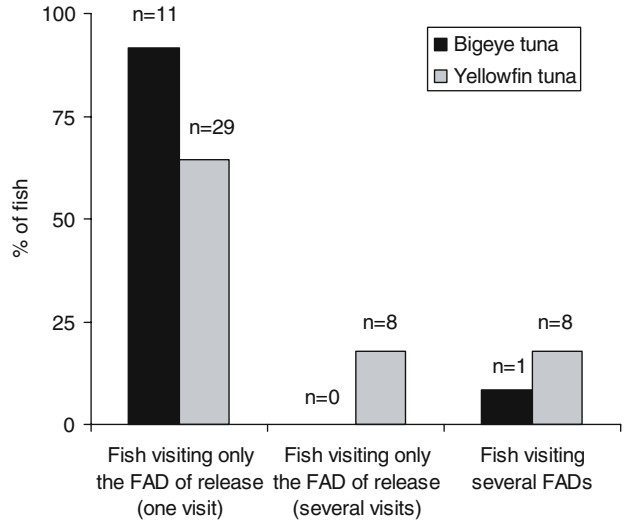

Fig. 3 Number of fish that only visited the FAD of release (several times or just once), or visited several FADs. *Grey bars* represent yellowfin tuna and black bars correspond to bigeye tuna

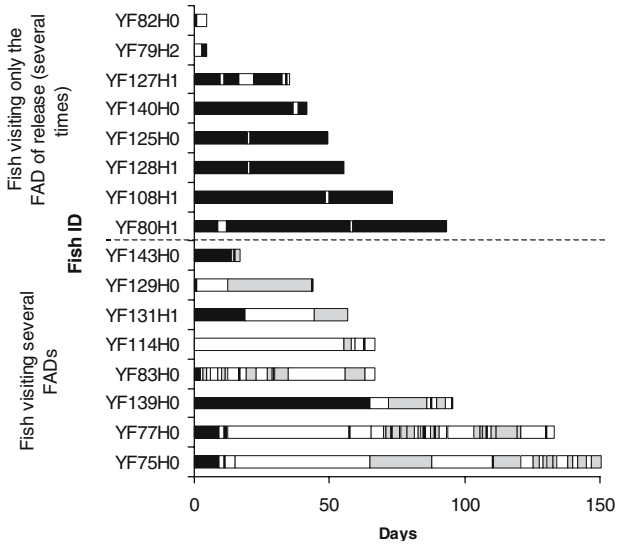

Fig. 4 Sequence of visits to FADs for yellowfin tuna. Fish above the dashed line were only detected at the FAD of release (only fish performing several visits), while fish below the dashed line were detected on several FADs. Black bars indicate visits at the FAD of release, grey bars show visits at other FADs and white bars represent absences. All start dates have been standardized to day 0 although release dates were different. Note that for the few fish for which the first CRT is not the longest, the longest residences occurred long after the initial CRT (e.g., YF75H0, YF77H0, YF83H0, YF114H0)

probability for a yellowfin tuna tagged in this study visiting other FADs was 8/30 = 27%. All tagged bigeye tuna except one (92% of the 12 bigeye tuna) were only detected at their FAD of release, with no departures and returns being recorded. One tagged bigeye was recaptured, resulting in 9% (1/11) of bigeye tuna monitored in this study visiting a FAD other than their FAD of release.

Eight yellowfin tuna made some off-FAD movements and returned to their release FAD following excursions of more than one day but without being detected at other FADs (Category 2). On average, those eight fish visited their FAD of release 2.5 times (SD 1.1) with mean absences between consecutive visits of 2.1 days (SD 1.4). These are the fish denoted above the dashed line in Fig. 4.

Eight yellowfin tuna visited several FADs (Category 3) with three making more than seven between-FAD movements (Table 2, Fig. 4). The mean number of between-FAD movements per fish was 5.1 (SD 5.1), with a mean travel time between FADs of 4.1 days (SD 8.8). About half of the observed inter-FAD movements lasted over 1.4 days (median value). Two yellowfin (YF83H0 and YF77H0) are notable as they performed the largest number of between-FAD movements reported by this or any previous study: 13 and 14 movements between FADs over the course of 67 and 133 days, respectively. Only one bigeye tuna (BE119H0) was detected at another FAD. This tuna left the release FAD LL to visit neighboring FAD U for only 7 min, returned to LL for 15 min and then left the FAD array never to be recorded again.

Tagged tuna exhibited a strong pattern of visiting the closest possible FAD regardless of whether the movement was from the FAD of release or other movements afterwards (Fig. 5). The Adjacent FAD index shows that between 40 and 50% of the between-FAD movements of both species were to the closest possible FADs

Table 2 Sequences of visits of FADs for the eight yellowfin tuna and the bigeye tuna (indicated by asterisk) that were detected at other FADs than their FAD of release

Fish ID	Duration of observation (days)	Number of between-FAD movements	Sequences of FAD visits, including returns to same FADs
143H0	17	2	LL-U-LL
129H0	44	2	CO-J-V
131H1	57	1	LL-MM
083H0	67	13	CO-V-R-CO-V-CO-V-R-V-X-V-CO-V-J
114H0	67	2	LL-X-CO
139H0	96	3	LL-J-X-V
077H0	133	14	CO-V-J-X-J-X-J-X-J-LL-MM-U-MM-U-MM
075H0	151	7	CO-V-II-LL-T-U-MM-U
119H0*	9	2	LL-U-LL

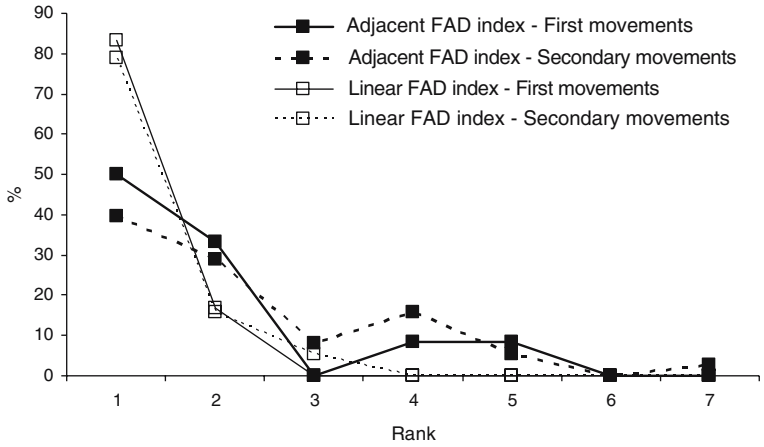

Fig. 5 Rank of the destination FAD for yellowfin and bigeye tuna performing movements between FADs, according to the adjacent and linear FAD indices

(Fig. 5, bold lines), while this percentage reaches around 80% when considering the linear FAD index, i.e. the closest FAD that was located in one continuous direction around the island (Fig. 5, normal lines). However, even though neighboring FADs were preferred, the quite long travel times between these FADs indicate that many of these movements were not straight line transits. The calculated direct-line speeds shows that 17% of the between-FAD movements (i.e., eight movements from four yellowfin and one bigeye tuna) were at calculated speeds greater than 2.5 km/h, which could represent directed movements between one FAD and another (Fig. 6). With one exception, these potentially straight line movements were between FADs less than 20 km apart (the exception being one longer transit of 37.2 km with a calculated direct-line speed 3.9 km/h). The fastest between-FAD movement was noted for a yellowfin tuna (YF77H0) moving 17.6 km from U to MM FAD in 2 h 51 m (6.2 km/h). However, the overall mean travel time between FADs was 4.1 days (SD 8.8). The longest time period between two FAD associations was 55.5 days (YF114H0).

- How long do tuna stay at FADs and in an array of FADs?

A total of 132 CRTs were measured (118 CRTs from the 45 yellowfin tuna and 14 CRTs from the 12 bigeye tuna). The CRTs of yellowfin and bigeye tuna are distributed differently. Yellowfin tuna CRT distribution is highly skewed due to a large number of individuals remaining at a FAD less than 2 days (although some stayed up to 64 days), while the bigeye tuna CRTs are more evenly distributed around a much smaller range. Although the two distributions may appear different, a non-parametric boot strap comparison of the mean difference, median, 75% and 95% quantiles, showed no significant difference between the residence times for yellowfin and bigeye tuna

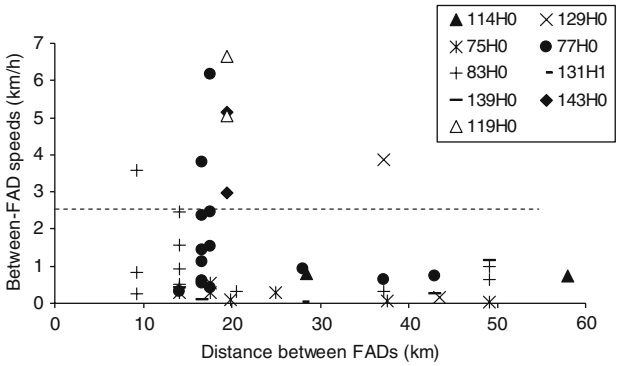

Fig. 6 Relationships between FAD distances and speeds for the eight yellowfin and one bigeye tuna that visited other FADs than the FAD of release. The *dashed line* indicates 2.5 km/h which can be considered, from active sonic tracking data, as a minimum threshold to determine directed movements between FADs

(yellowfin tuna: mean 8.0 SD 12.6; bigeye tuna: mean 4.8 SD 3.7, Table 3). It is worthwhile to note that for yellowfin tuna[1], 14% of the CRTs lasted less than 45 min (17 CRTs, and only 3 of them were first CRTs after release) while 19% of the CRTs lasted more than 14 continuous days (22 CRTs). The average duration of the first CRT after release for yellowfin tuna was 8.0 days (SD 12.6). The ''unperturbed'' residence time of yellowfin tuna at FADs (by excluding first CRTs after release or last CRTs of fish being recaptured) had a mean of 4.9 days (SD 9.8 days) with a maximum of 45.8 days ($N = 68$).

Considering all yellowfin tuna that visited more than one FAD, the normalized statistical test shows residence at the first FAD (FAD of release) is longer than the subsequent residence times at other FADs ($p = 0.018$). It is noteworthy that for the few fish for which the first CRT is shorter than subsequent ones

[1] Due to the low number of data on bigeye tuna, this species is not considered here.

Table 3 Continous residence times (CRT) at FADs, and residence times in the FAD network, for yellowfin and bigeye tuna

	Range of CRT in days	Mean CRT in days (SD)	Range of residence times in the FAD network in days	Mean residence times in the FAD network in days (SD)
Yellowfin tuna	0.0–64.7	8.0 (12.6)	0.0–150.7	28.7 (36.1)
Bigeye tuna	0.0–10.3	4.8 (3.7)	0.0–10.2	6.2 (3.3)

(e.g., YF83H0, 114H0, 75H0), the longest FAD associations (ranging from 35 to 65 days) occurred a long time after the end of the first CRT.

The mean residence time within the entire instrumented FAD array was 28.7 days (SD 36.1) for yellowfin tuna and 6.2 days (SD 3.3) for bigeye tuna (Table 3). In total, 75% of the tuna were observed for more than 4 days within the FAD network. Thirty five percent of tagged yellowfin tuna were observed within the FAD network for more than one month, with the longest record (150.7 days) being for a yellowfin tuna (YF75H0) that visited eight FADs. Observations of bigeye tuna were shorter; the longest recorded presence lasted 10.2 days. The shortest observation periods for yellowfin and bigeye tuna were 20 and 23 min, respectively, at their release FADs. The residence time in the FAD network depends on the ability of fish to make excursions and come back to the same FAD (Category 2) or to visit other FADs (Category 3). Fish in Category 3 have a mean stay in the network of 79 days (SD 45) and fish of Category 2 have a mean stay of 45 days (SD 31), while fish of Category 1 have a mean stay of only 10 days (SD 13).

- Do fish leave a FAD at the same time?

To illustrate how departure events were detected in our database, Fig. 7 shows the residency and departures of yellowfin and bigeye tuna at CO FAD (including those fish that were recaptured). Some fish left the FAD together (showing behavioral synchronicity) while others of the same tagging cohort stayed at the FAD. In total, when considering all departures from all FADs in situations where more than one tagged fish was present, we observed 34 departure events. When using 24 h as the measure of synchronicity, only 11 of these 34 events involved the departure of single individuals, which means that 68% (23/34) of departure events involved the synchronous departure of multiple tagged animals. On average, 65% (SD 26%) of the total local tagged population left the FAD on the same day (leaving 35% of the tagged fish remaining at the FAD). It is noteworthy that only 5 departures out of 34 (15%) corresponded to all the tagged fish present at the FAD leaving on the same day; most of the time, not all of the tagged fish present around a FAD left on the same day.

Discussion

This study describes the movement and residence time patterns of tuna observed in an array of anchored FADs surrounding a mid-oceanic high island situated in a very isolated chain of islands (the Hawaiian

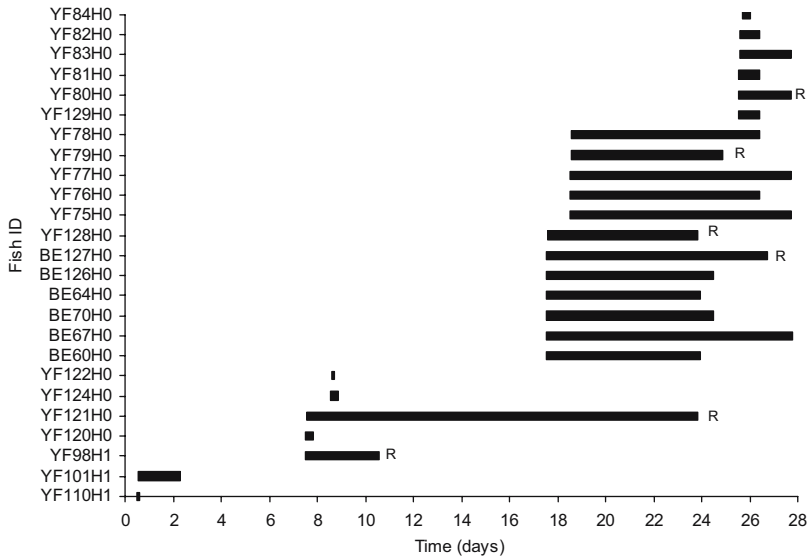

Fig. 7 Chronology of daily presence of tagged fish at release FADs, example with fish tagged at CO FAD on February 2003. Movements to other FADs (and recaptures at other FADs) are not shown. *R* means recapture by a fisherman

archipelago). The FADs in the study comprise the central part of a larger network surrounding the archipelago and the results of this study should be considered within the context of the larger environment in which these tuna reside. The use of passive acoustic data loggers placed on all the FADs surrounding one island resulted in extensive, long-term coverage of the local geographical area and the observed behaviors were not impacted by the presence of tracking or survey vessels.

It appears that tuna around FADs are highly vulnerable to fishing pressure: 40% of the yellowfin tuna (18 fish) and 8% of the bigeye tuna (one fish) were recaptured, mainly at their initial FAD of release. Previous conventional tagging conducted on the same array of FADs showed similarly high trends: 19.3% were recaptured (Itano and Holland 2000). These results show that FADs are efficient fishing traps. In the present study, many of the fish recaptured by fishermen (trolling or drop line) were short-term recaptures which suggests that tagged fish quickly adopted a normal feeding behavior. Moreover, the fact that 75% of the tagged fish were detected by the network of acoustic receivers for more than 4 days after release supports the assumption that these tagged fish were not significantly adversely affected by the capture and tagging procedures.

- Do tuna visit neighboring FADs?

Most of the time, the Oahu FADs seemed to act as single aggregation devices, with only modest levels of exchange of fish between FADs in the network. When a fish left its release FAD, it generally did not appear at other FADs (73% of yellowfin and 91% of bigeye tuna). When fish did move to other FADs, both the adjacent and linear FAD indices indicated a strong tendency for fish to visit the closest possible FAD (at least, the closest FAD located in one continuous direction). This pattern does not depend on the type of movement (first movement after release or other between-FAD movements). Further, the inter-FAD swimming speeds indicate that the great majority of quite high speed transits occurred between FADs less than 20 km apart which suggests that this distance might indicate the size of the array ''known'' to these fish—probably because of previous visits to these FADs. These various indicators of limited dispersal of fish from the point of release suggest that FADs work on a local (as opposed to regional) scale even when there are additional FADs in the area.

Although we can not know the precise details of the behaviors occurring during the between-FAD movements that were observed, several of the estimated speeds of between-FAD transits compare well to actual speeds recorded during active tracking studies when fish were observed making 'straight line' movements between FADs (Holland et al. 1990; Cayré 1991; Marsac and Cayré 1998; Brill et al. 1999; Dagorn et al. 2000). The longest of these possible directed movements observed in our study (37.2 km at 3.9 km/h) is very similar to a yellowfin tuna tracked by Brill et al. (1999) off the island of Hawaii, which made a relatively straight movement between adjacent FADs (38.2 km at 2.8 km/h, with an average instantaneous speed of 4.2 km/h). On the other hand, about half of the observed inter-FAD movements lasted over 1.5 days and indicate that although some tuna appear to leave one FAD with the clear goal of moving to another, other fish are leaving to spend time in non-FAD areas—possibly for the purpose of foraging.

Another interesting comparison between results from active and passive sonic tracking techniques is that both techniques yield the same percentage of yellowfin tuna visiting more than one FAD. Using active tracking around the same FADs around Oahu as used in the current study, Holland et al (1990) determined that 82% of yellowfin tuna visited only one FAD—the FAD at which they were originally captured and released. However, the longest active track was only 30 h (Holland et al. 1990) and none of the fish tagged in the present study moved between FADs that soon after tagging. Consequently, none of the subsequent between-FAD movements observed in our study would have been detected by active tracking and the current observations were only made possible by the use of passive receivers deployed over long time periods. Listening stations therefore appear to be a valuable and appropriate technique for monitoring movements of fish within a network of FADs on a long-term basis.

- How long do tuna stay at FADs and in an array of FADs?

We estimated the residence time of yellowfin and bigeye tuna at a single FAD to be about 5–8 days although some were much longer. Our results are similar to the findings of Ohta and Kakuma (2005). Conversely, Klimley and Holloway (1999) reported much shorter residence times but because they were interested in fine-scale synchronicity, they did not use the same definition for CRT. It is therefore not possible to compare their results with ours and those of Ohta and Kakuma (2005). In the present study, some fish remained continuously around a FAD for several weeks (maximum of 64.7 days), which also agrees with results of Ohta and Kakuma (2005), where the maximum stay at FAD was 55 days.

Our results indicate that for fish that visit several FADs, there is a tendency to spend more time at the original release FAD than at other FADs. This is congruent with results obtained by Girard et al. (2004) from active sonic tracking (short observations), who observed that tuna remained for longer times at the original release FAD and not at others. Girard et al (2004) explained this pattern with the following hypothesis: Fish that leave the FAD where they were tagged and released might not find suitable conditions at subsequent FADs that induce them to stay there. The few fish that did spend more time at subsequent FADs might represent animals that were captured and tagged at the original FAD while they were still involved in exploratory behavior and before they had settled on a particular FAD that suited their specific requirements. When searching for a suitable FAD, fish are likely to spend only short amounts of time at unsuitable FADs (i.e., become migrants) prior to locating a suitable FAD where they will remain for a while (becoming resident). Because there are more chances to catch fish that stay a long time at a FAD (they are therefore more accessible to fishing gears), we likely over-sampled fish that had already located a suitable FAD, as opposed to fish searching for such FAD. A larger dataset on fish visiting several FADs would be very helpful in elucidating the reasons underlying the variable residence times observed in the current study.

- Do tuna leave a FAD at the same time?

Our results indicate that, measured on 24 hour scale, a majority of tagged fish exhibit some synchronicity in their departure patterns. However, usually not all the tagged fish at a FAD left on the same day and typically small groups of fish left together while others remained. Using a finer time scale, Klimley and Holloway (1999) also demonstrated school fidelity and behavioural synchronicity in FAD associated yellowfin tuna. In combination, the results of these studies suggest that the aggregation of tunas associated with a FAD is comprised of multiple 'sub-schools'. Fish from different sub-schools might have different physiological states (e.g., starvation) or be comprised of different behavioral phenotypes, both of which could explain why some fish leave while others remain. There may be one behavioural phenotype that is more vagile than others and is responsible for the portion of tagged fish that move frequently between FADs but which remain longer in the overall FAD network.

- Why do fish leave a FAD and where do they go?

While several studies have proposed theories as to why tuna associate with floating objects (reviewed in Fréon and Dagorn 2000; Castro et al. 2002), very few address the question of why fish leave a FAD or how frequently they move to adjacent FADs. These are questions of major importance for fisheries management purposes. Ohta and Kakuma (2005) measured oceanographic parameters (current, sea water temperature, wave conditions) but could not identify any specific oceanographic conditions that could explain why fish leave a FAD. They suggested that the biotic environment (such as the local abundance of forage) could be responsible for changes in the associative behavior.

Our results tend to show that the majority of animals tend to leave the area completely without visiting other FADs or only briefly visiting nearby adjacent FADs. The fish may consider local conditions around a single FAD to be representative of the environment on a larger scale (the surroundings of the island, for instance). When those conditions become unfavorable relative to their specific requirements, they move to another area that, in this case, is apparently beyond the dimensions of the array of instrumented FADs. An unlikely possibility is that the fish remain in the vicinity but do not associate with the local FADs. Our results indicate that tuna might 'sample' the environment around an island by only visiting one or a few FADs. While the influence of FADs on tuna movements at fine spatial scale has been well established (Holland et al. 1990; Cayré 1991; Marsac and Cayré 1998; Dagorn et al. 2000; Girard et al. 2004), the information resulting from our study suggests that anchored FADs (at the spatial densities that we observed) may not modify the general movement or residence patterns of tuna at larger spatial scales. The Hawaii FAD network around the island of Oahu might not retain fish longer than if there were only a very few FADs in the area.

Under the conditions reported here (anchored FADs located around a remote island archipelago) there is no evidence of an 'ecological trap' as defined by Marsac et al. (2000). And, although some of the tagged fish (the 'phenotype' that visited multiple FADs) appear to be more susceptible to being entrained in the FAD network than others, in general terms, the 'island effect' is more likely than the FADs to be responsible for the presence of fish around the islands. The influence of islands, ledges, banks and seamounts is known to play a major role in the spatial behavior of tuna and clearly have a significant impact on their vulnerability to fisheries (Doty and Oguri 1956; Fonteneau 1991; Itano and Holland 2000). FADs may further concentrate the fish that are already in the area and in so doing, make them more vulnerable to fishing pressure. We suggest that islands

and seamounts affect residence times of fish at medium scales, while FADs act at smaller spatial scales. Such assumptions must be addressed in future research.

- Future research

The future research priorities should focus on the reasons that make fish leave a FAD and observe where fish go when they leave a network of FADs. As it is hypothesized that the biotic environment is responsible for departure events, it would be necessary to monitor the localized prey environment around FADs while monitoring the residence time of tagged tuna. Data on prey distribution and abundance could be obtained from regular acoustic surveys (e.g., echosounder and sonar) as well as regular sampling of gut contents from tuna caught in the area, but such protocols are logistically difficult and time consuming. Appropriate autonomous monitoring technologies and protocols must be developed to assist in observing both the abiotic and biotic environments around FADs. Such capabilities would have ecological research implications that go beyond the issue of FADs (Dagorn et al. 2001b). Prey might not be the only parameter explaining the presence of tuna around FADs because the size of the biomass of aggregated tuna themselves could also play an important role—especially if forage availability was a limiting factor. Measuring the biomass of tuna around each FAD, along with automated sonic monitoring of tagged fish, would allow researchers to examine possible relationships between residency time of individuals and the aggregated biomass, thus providing data to test the 'meeting point' hypothesis and other possible explanations of the phenomenon of FAD-associated aggregations (Dagorn and Fréon 1999; Fréon and Dagorn 2000).

In order to further investigate where tuna go when they leave a network of FADs, two research priorities can be identified for the future. First, it is important to extend the geographical range of coverage of the tagged animals by increasing the number of FADs equipped with sonic receivers, as well as monitoring natural nearshore aggregation sites. In addition, double tagging fish with geolocating archiving tags and acoustic transmitters would provide complementary information at different scales and precision for the same fish: acoustic transmitters would provide fine scale data in relation to instrumented FADs, while the archival tag would indicate if the fish was in the general area of the island, or if it has left it to visit another island or left the Hawaiian Islands completely. Such simultaneous utilization of two different types of tags would allow us to assess if a network of instrumented FADs can accurately describe the residency time of tunas around the islands. Secondly, to investigate possible FAD density dependent influences on tuna behavior, similar work should be conducted at FAD densities and numbers that are much higher than those found in Hawaii. Finally, determining the influence of drifting FADs on the spatial behavior of tuna should be a priority in the future as the majority of tropical tuna are currently caught in association with such floating objects in the three tropical oceans (Fonteneau et al. 2000).

Conclusions

We tagged 45 yellowfin tuna and 12 bigeye tuna, and equipped all thirteen FADs surrounding the island of Oahu (HI, USA) with automated sonic receivers, in order to investigate the behavior of tuna within a network of moored FADs. While the residence time of tuna at anchored FADs appears to be of the order of a few days, similar to the findings of Ohta and Kakuma (2005), the mean residence time in the network of FADs is of the order of a month. Fish that visit several times the same FAD or visit several FADs tend to stay longer in the network. However, most of the time, the Oahu FADs seemed to act as single aggregation devices, with only modest levels of exchange of fish between FADs in the network. The majority of the fish only visited the FAD where they were tagged and released. Some synchronicity of departures were observed at the day scale but usually some tagged fish remained after others had departed. This suggests the existence of several schools around the FAD instead of one homogenous aggregation. These component schools could represent fish with different physiological states or behavioral phenotypes.

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