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School fidelity and homing synchronicity of yellowfin tuna, *Thunnus albacares*

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Abstract Thirty-eight yellowfin tuna (*Thunnus albacares*) were tagged with coded ultrasonic beacons between 6 March and 4 December 1996 near two buoys off the western coast of Oahu, Hawaii. Two to four tuna were captured, tagged, and released on the same day in as rapid succession as possible in an effort to tag members of the same school. Automated "listening" monitors attached to the buoys recorded when these marked individuals entered within a radius of $\leq$ 1.1 km of the buoys during a 13 mo period. Twenty-seven of the tuna returned to the site of tagging. The mean number of returns was 4.2 per tuna (max. = 17), and visits ranged from 1 to 910 min (median = 2.7 min, mean = 40.1 min). The intervals between successive returns varied from 1 to 257 d (median = 3.0 d, mean = 17.4 d). Seventy-three percent of the tuna returned together with tunas tagged on the same day, exceeding the frequency of returns of tuna tagged on another day or arriving alone. This social cohesion is supported by the pattern of return visits by five tuna tagged on 6 March at Monitoring Station R. Two or more of these tuna arrived together on 24 of 35 d when tagged tuna were detected. All five individuals visited R on 11 April, a month after tagging, three arrived together 5 mo later on 4 August, and three returned 6 mo later on 1 December 1996. Tuna often arrived at the same time of day, e.g. Individuals 1 and 3 visited R at 09:15 hrs on 12 April and at 09:00 hrs 8 mo later. The returns were also site-specific. The 22 tuna tagged at R made 182 return visits to R (92.4%) and only 15 visits to Monitoring Station K (7.6%), 10 km away. An allegiance of tuna to one school, a predilection for returning to the site of tagging, and precise timing when visiting sites, are consistent with tuna having migratory pathways consisting of "waypoints" that are visited with temporal regularity.

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Introduction

The schooling habit is common among fishes. Even species that are solitary as adults usually school as juveniles (Shaw 1978). Although the behavior of individuals within schools and the functional significance of schooling have been well described (see reviews: Shaw 1978; Partridge 1982; Pitcher 1986), we know little about the constancy of school composition in the ocean over time. The evidence is contradictory; although similar genotypes of school members (Sharp 1978), common parasites (Lester et al. 1985), and behavioral preferences for kin (Van Havre and Fitzgerald 1988) indicate school cohesion, marking of tunas suggests mixing of schools (Bayliff 1988; Hilborn 1991). It is not known if school integrity is maintained during migration nor whether schools visit locations with precise seasonal timing to forage or reproduce.

The main objectives of this study were to describe the degree of fidelity of acoustically-tagged yellowfin tuna (*Thunnus albacares*) to a particular school and to ascertain whether that school repeatedly visited the same site and not a closely situated site. Acoustic tagging was carried out at two fish-aggregating devices (FADs), buoys moored near islands to improve commercial and sport fishing (see review of FADs: Holland 1996). Fishes may concentrate at these anchored buoys due to an innate propensity to aggregate at natural landmarks in the oceanic environment such as seamounts and small islands. We monitored the presence of the tagged tuna over a 12 mo period at both sites with automated tag-detecting devices.

Materials and methods

We tagged 38 yellowfin tuna (*Thunnus albacares*) with coded ultrasonic beacons during a 9 mo period between 6 March and 4 December 1996. These tuna were tagged < 1 km from two monitoring stations, Romeo (R) and Kaena (K), southwest of Kaena Point on the island of Oahu, Hawaii (Fig. 1). Each station consisted of a tag-detecting monitor attached to a permanent mooring made of a 1.5 m-diam metal buoy, 30 m of heavy-duty galvanized chain, a variable length of polypropylene line, 30 m of chain, and a 1 m^3 concrete block on the sea floor. Station R was 7 km offshore in water 700 m deep; Station K was 4 km offshore in water 40 m deep. The buoy at Station R floated on the sea surface; the buoy at K was 5 m under the surface. A fisherman could watch the R buoy and ensure that the tuna were tagged within the range of the monitor. The K buoy could not be seen from the surface, and the helmsman on the tagging boat had to rely on GPS coordinates or landmarks to stay close. Some tuna may have been tagged outside the range of the monitor on the K buoy, and may not have been detected upon return to the site of tagging. The two monitoring stations were separated by 10 km. Twenty-two tuna were tagged at R and 16 at K. A tag-detecting monitor was attached to the R mooring on 12 March 1996, and was maintained for 13 mo until 4 May 1997. A similar device was placed at K at 25 April, and remained for 11 mo until 5 May 1997.

To determine the maximum signal-detection range of each monitor, we lowered a transmitter to a depth of 10 m and recorded the distance by either radar or differential GPS as the boat and transmitter drifted away and was slowly motored back to the buoy. The maximum distance over which Monitor R detected tags was 1.10 km, in seas with 0.5 m-high waves (hatched circle, Fig. 1). The detection range of Monitor K was 0.80 km in 1.5 m seas (hatched circle, Fig. 1). During 2.0 to 3.0 m seas, the range of Monitor K dropped to 0.65 km. The difference between the ranges of the two monitors was probably due to different ambient noise conditions and not to varying receiver sensitivity.

The tuna were caught by rod and reel. They were rapidly reeled in and lifted aboard ≤ 2 min after being hooked. Each tuna was weighed in a net with a scale built into its handle, and the hook was removed from the mouth by hand. The tuna's length was measured with a rule while the fish was supported on a wet towel. This was folded over the tuna's head to block its vision and minimize stress. Salt water was pumped through a vinyl hose into the tuna's mouth, across its gills, and out through its branchial aperture to enable the fish to breathe while out of water. We made a ventral incision, 2 cm long and 1 cm deep (just short of the peritoneum), that was 4 cm anterior and 2 cm dorsal of the vent on the left side of the fish. The peritoneal membrane was punctured with the "pinky" finger in a sterile rubber glove, and the ultrasonic beacon was inserted through the opening; this was then closed with surgical staples (Precise Vista Skin Stapler 35 W). Neither the staples nor the scar from the incision were apparent on two tuna with beacons examined 2 mo after release. Tagging and release took < 1 min. Recovery from this surgical procedure was evidenced by the high frequency of return visits by tuna to the site of tagging and the absence of any perceptible damage to the tissues near the tags on two tuna caught after spending 2 mo in the ocean. We tried to catch the tuna in rapid succession in an effort to tag members of the same school. We then hoped to record when school-mates entered and left the detection range of the monitoring stations. The interval between tagging of individuals ranged from 10 to 310 min (mode = 40 min).

The transmitters (VEMCO Ltd., V16–6L) were cylindrical, 16 mm in diameter, 106 mm long, and with a net weight in water of 16 g. They emitted 10 ms tone-bursts of 70 kHz separated by 1000 to 1500 ms intervals. The amplitude of the pulses was 147 dB (ref. 1 μP) at a distance of 1 m. The theoretical operating life of the transmitters was 476 d. Each tag was distinguished on the basis of a unique pulse-interval by automated tag-detecting monitors (VEMCO Ltd., VR-20) attached to the R and K buoys. The monitors were briefly removed from the buoys once a month, and brought to the surface where the files of tuna attendance were downloaded and the batteries replaced.

We used log-survivorship analysis (Fagen and Young 1978) to ascertain whether the tagged tuna returned to the monitoring stations after favored time periods. A frequency histogram of the time intervals between randomly occurring point-events in a Poisson process is described by a negative exponential distribution (Cox and Lewis 1966). A log-survivor plot of these intervals generates a straight line with a slope proportional to the probability of an event occurring at a given time after the preceding event. This analysis is used to identify intervals between events that occur more frequently than expected by chance, because the resulting curve is more easily contrasted with a straight line than the corresponding frequency-histogram with a negative exponential curve. An inflection in the log-survivor curve also indicates a change in the probability of an event occurring at a given time after the last event; in our case, the time between successive arrivals of tuna within the ranges of the R and K monitors.

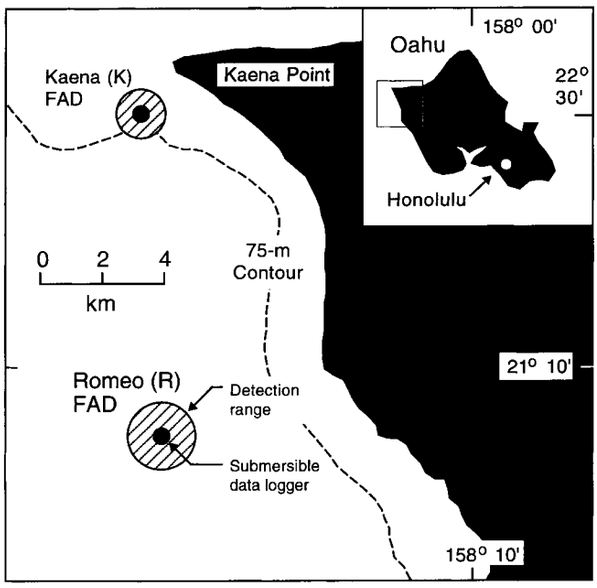


Fig. 1 Locations of Monitoring Stations R (Romeo) and K (Kaena) at Kaena Point, Hawaii (●), with 1.1 and 0.8 km signal-detection ranges (*hatched*) (*FAD* fish-aggregating device)

Results

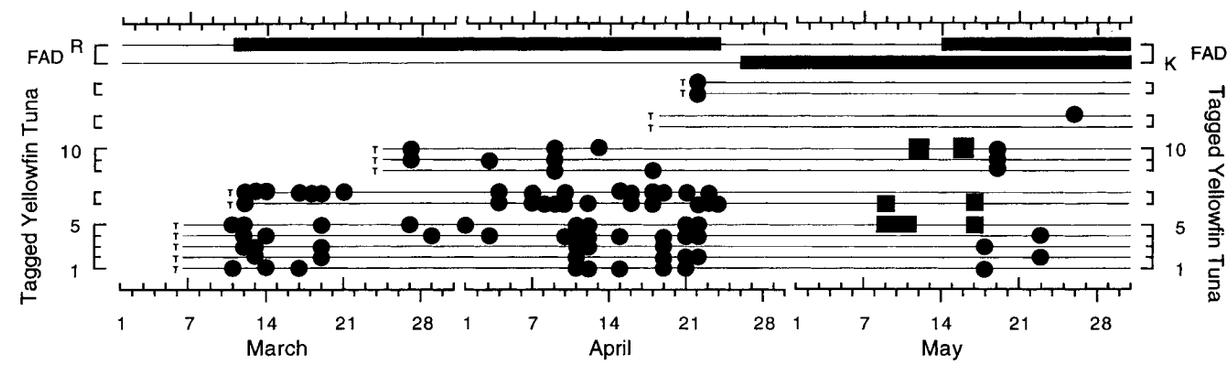
General pattern to homing in *Thunnus albacares*

The tagged yellowfin ranged in total length from 73.7 to 97.8 cm (mean = 84.8) and weighed 6.8 to 18.2 kg (mean = 10.7 kg; Table 1). A mean of three tuna was tagged per day, with a maximum of five individuals on 6 March and minimum of one on 30 September 1996. We recorded 219 return-visits by 22 tuna (mean = 9.95) at Station R (Fig. 2). Sixty-eight return-visits by 16 tuna (mean = 4.25) were recorded at Station K during the same period.

Tuna visited the monitoring stations more often during daytime (67.6% of arrivals) than nighttime (32.4%). Arrivals at Station R peaked 08:00 to 13:59 hrs, with a second peak in arrivals occurring from 18:00 to

Table 1 *Thunnus albacares*. Length and weight of each of 38 yellowfin tuna tagged in present study, and date, time, and location of tagging (i.e. R or K monitoring station). Also given are percentages of return visits when tuna were accompanied by individuals tagged on same day or on other days, as well as when they returned "alone", i.e. without a tag-mate (*FAD* fish-aggregating device)

Tagging information						Romeo (R) FAD				Kaena (K) FAD			
						Tuna tagged on:				Tuna tagged on:			
Tuna No.	Date	Time (hrs)	Site	Length (cm)	Weight (kg)	same day (%)	other day (%)	alone (%)	visits (*N*)	same day (%)	other day (%)	alone (%)	visits (*N*)
1	6 Mar. 1996	09:30	R	87.6	11.8	57.1	28.6	33.3	(21)				(0)
2		10:15	R	73.7	9.6	66.6	16.7	25.0	(12)				(0)
3		11:00	R	83.8	10.0	60.0	45.0	20.0	(20)				(0)
4		11:35	R	82.6	8.2	55.0	55.5	20.0	(20)				(0)
5		14:00	R	90.2	14.3	73.7	47.4	20.1	(19)	0	40.0	40.0	(5)
6	12 Mar. 1996	10:30	R	88.9	10.0	42.1	42.1	42.1	(19)	0	100.0	0	(5)
7		11:00	R	96.5	18.2	21.2	27.3	63.6	(33)				(0)
8	24 Mar. 1996	10:10	R	87.6	11.4	57.1	42.9	28.6	(7)				(0)
9		13:15	R	78.7	8.0	57.1	42.9	14.3	(7)				(0)
10		15:05	R	91.4	15.0	30.0	40.0	40.0	(10)	0	0	100.0	(2)
11	18 Apr. 1996	14:10	R	81.3	9.1	66.7	33.3	0	(3)	0	0	100.0	(1)
12		17:30	R	97.8	15.5	66.7	33.3	0	(3)				(0)
13	23 Apr. 1996	16:45	R	88.9	13.7	50.0	0	50.0	(2)				(0)
14		16:55	R	81.3	9.6	14.3	85.7	14.3	(7)				(0)
15	12 June 1996	08:23	K	85.1	10.2				(0)	25.0	16.7	75.0	(12)
16		08:56	K	81.3	9.3				(0)				(0)
17		09:14	K	82.6	11.8				(0)	20.0	6.7	80.0	(15)
18	5 July 1996	07:22	K	78.7	6.8				(0)	25.0	50.0	50.0	(4)
19		08:50	K	81.3	8.4				(0)	50.0	50.0	50.0	(2)
20		14:01	K	83.8	10.0	50.0	100.0	0	(2)	50.0	50.0	50.0	(2)
21		14:35	K	83.8	9.1	50.0	100.0	0	(2)				(0)
22		16:10	K	85.1	10.0	42.9	100.0	0	(7)	100.0	100.0	0	(1)
23	28 July 1996	13:48	K	88.9	12.5	66.7	0	33.3	(3)	100.0	0	0	(1)
24		14:04	K	83.8	12.3	100.0	0	0	(2)	12.5	12.5	75.0	(8)
25		14:31	K	85.1	14.3	33.3	0	66.7	(6)	0	0	100.0	(5)
26		16:35	K	81.3	10.0				(0)				(0)
27	22 Sep. 1996	12:10	K	83.8	10.2	0	100.0	0	(3)				(0)
28		14:00	K	85.1	10.5				(0)	100.0	0	0	(1)
29		14:30	K	87.6	10.5	0	20.0	80.0	(5)	100.0	0	0	(1)
30	30 Sep. 1996	10:20	K	87.6	10.9				(0)	0	0	100.0	(1)
31	24 Nov. 1996	09:00	R	88.9	10.0	0	100.0	0	(1)	0	0	100.0	(1)
32		09:30	R	82.6	9.6	0	0	100.0	(2)	0	100.0	0	(1)
33		12:00	R	81.3	8.2	0	100.0	100.0	(1)				(0)
34		12:10	R	85.1	10.5	100.0	0	0	(1)				(0)
35		14:00	R	81.3	9.8	0	0	100.0	(1)				(0)
36	4 Dec. 1996	14:20	R	80.0	8.0				(0)				(0)
37		09:00	R	88.9	10.7				(0)				(0)
38		11:00	R	81.3	9.1				(0)				(0)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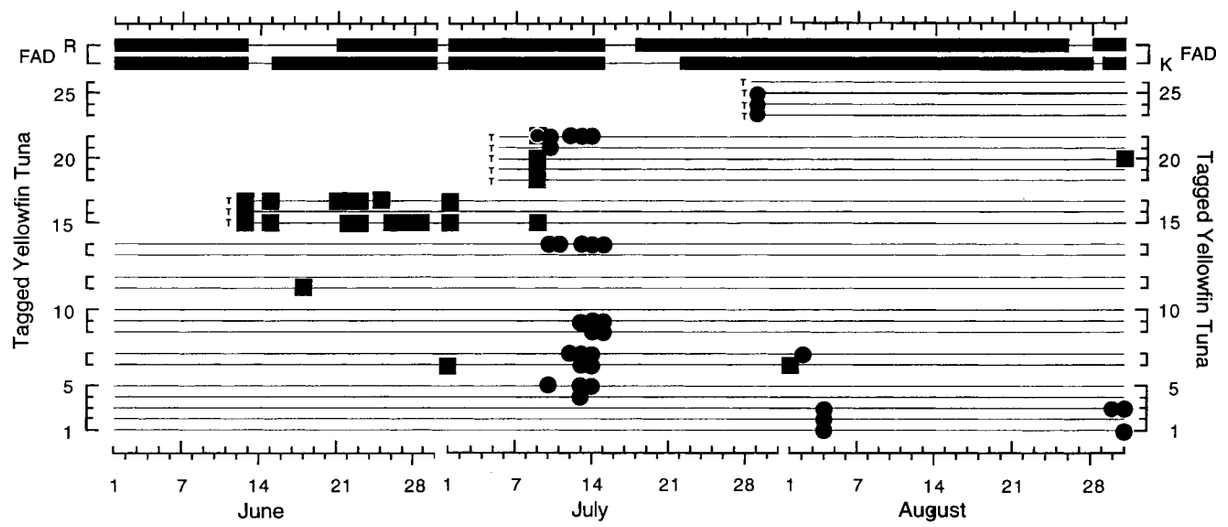
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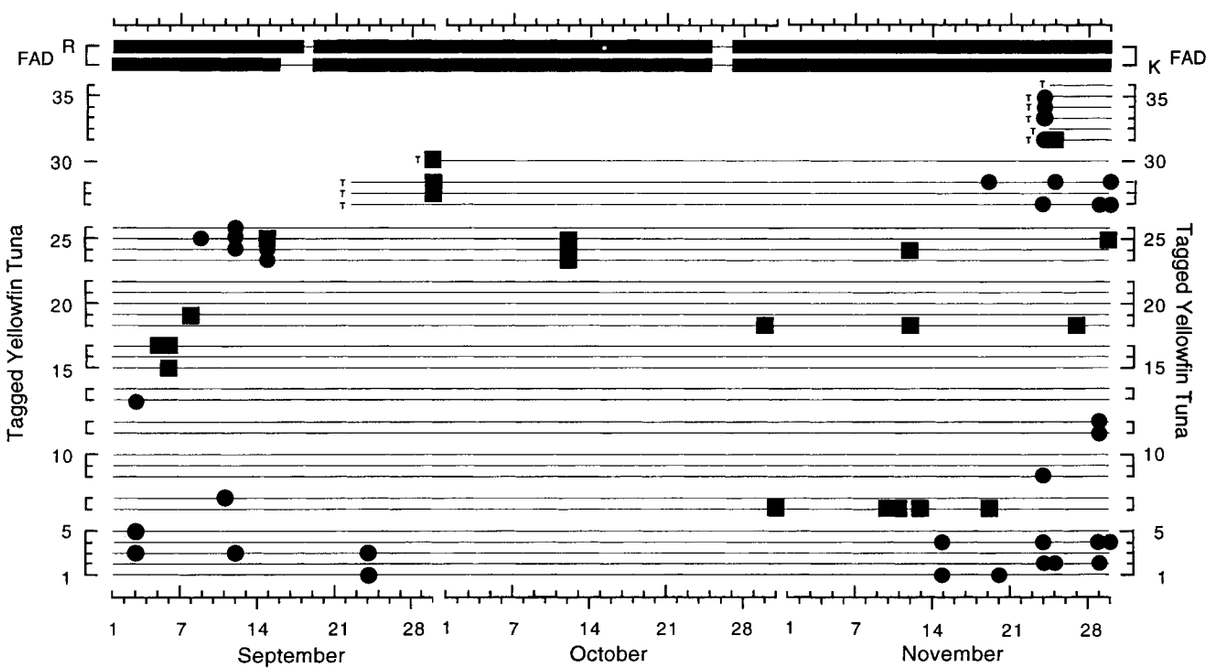
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Fig. 2 *Thunnus albacares.* Chronology of daily visits by tagged yellowfin tuna to Monitoring Stations R and K during first 9 mo of study (● visits of tuna to R; ■ visits to K; *concentrically larger symbols* indicate tuna returning on same day; *small T* denotes date of tagging; *horizontal lines* indicate when tagged fish were at large; *black bars at top* show when data loggers were "listening" for coded ultrasonic beacons)

19:59 hrs (Fig. 3a). Tagged tuna arrived most frequently at Station K from 10:00 to 11:59 hrs, and were also frequent 12 h later (Fig. 3b). The temporal distribution of arrivals at R roughly complements the distribution for Station K; the peaks are located at different times of the day. This distribution is consistent with separate schools of tuna passing through each area at different times of the day.

Tuna tagged at the Station K often returned 12 h after a prior visit. The change in slope of the log-survivor curve at 12 h (Fig. 4a) indicates a decrease in the probability of arrivals after longer intervals. No large inflections are apparent in the curve for the tuna tagged at R. On an expanded time scale, tuna returned to both sites more frequently after absences of 10 d and to Station K more commonly after intervals of 50 and 110 d (Fig. 4b). The two "staircase" inflections in the curve for R at intervals of >140 d depend upon few returns and are probably not significant. The longest interval between two arrivals was 257 d for Tuna 10.

Tagged tuna usually stayed at the monitoring stations briefly upon their return. Eighty five percent of the visits lasted $\leq$ 1 h (Fig. 5a). Sixty four percent of those visits of $\leq$ 1 h were $\leq$ 5 min (Fig. 5b). Only 2% of the visits lasted for >5 h (Fig. 5a). Although most visits were short and the median duration was 3.0 min, a few visits were long (max. = 910 min) and the mean duration was accordingly higher, i.e. 40.1 min (N = 283). We believe that the tuna usually passed only through the edge of the listening sphere and were not within range of the monitors very long. Yellowfin tracked during day-

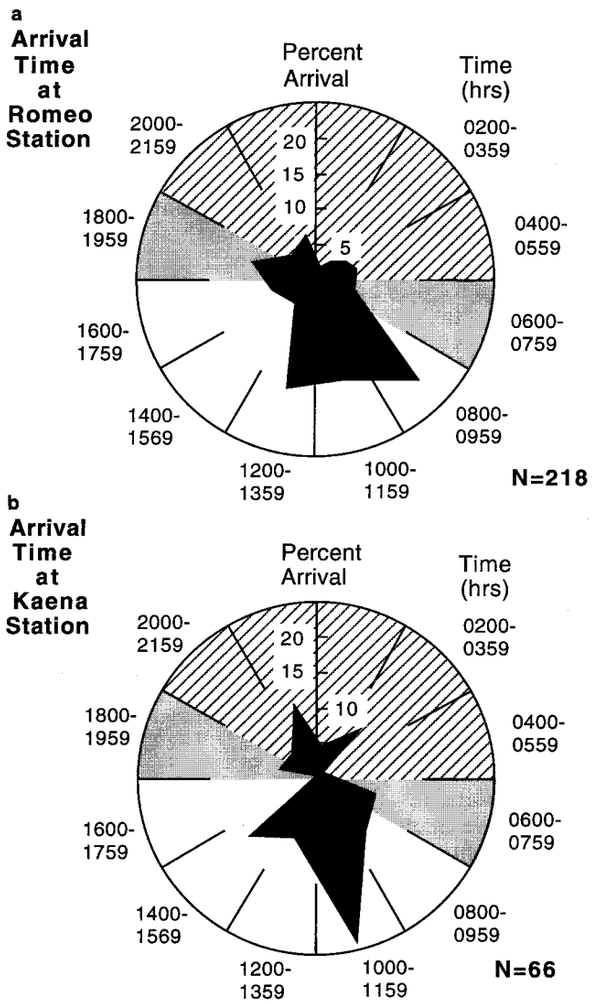

Fig. 3 *Thunnus albacares.* Percentage of visits by yellowfin tuna at different times of day at Monitoring Stations R (**a**) and K (**b**) (*White area* daytime; *hatched area* nighttime; *shaded area* period over which sunrise and sunset varied during study)

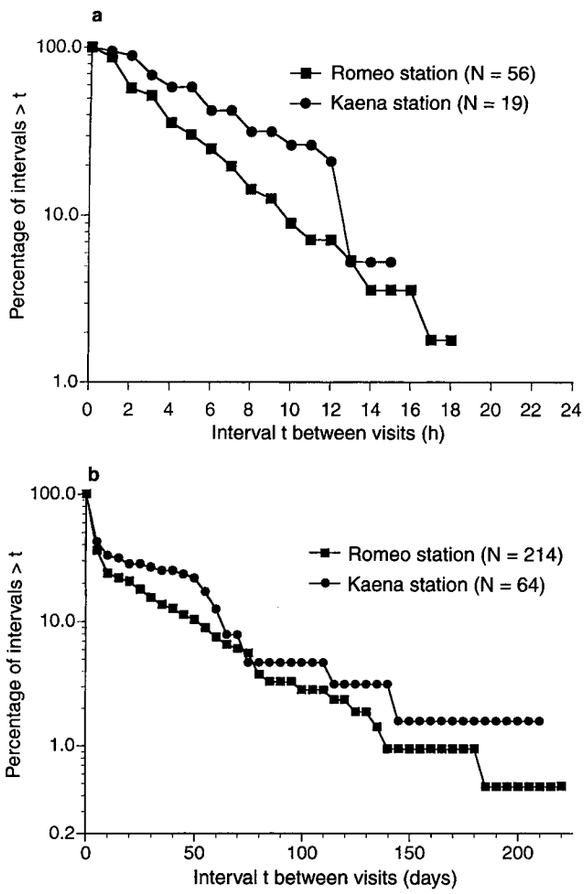

Fig. 4 *Thunnus albacares.* Log-survivor plots of percentages of intervals between successive tuna arrivals > Time t at Monitoring Stations R (■) and K (●) over 24 h (**a**) and 220 d (**b**) periods (*Abscissa* time interval, t, between visits; *ordinate* percentage of intervals with durations > Time t)

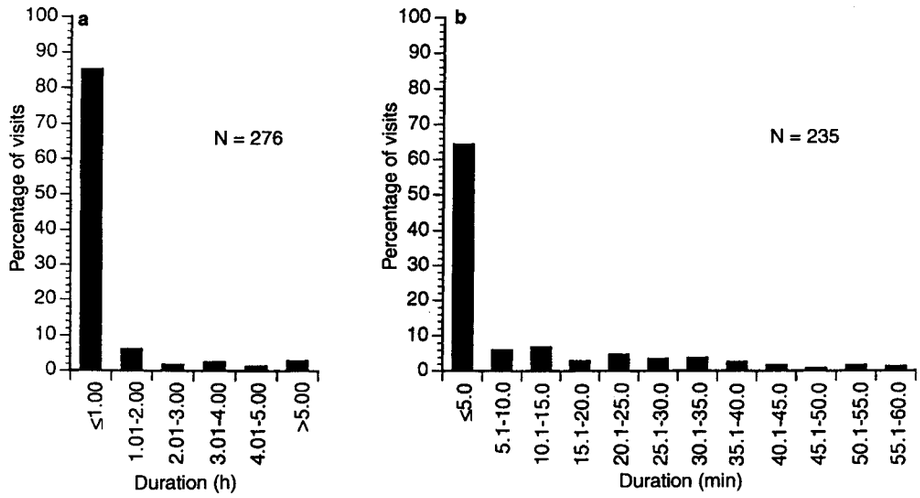

Fig. 5 *Thunnus albacares.* Percentages of visits made by tuna to the two monitoring stations on temporal scales of 5 h (**a**) and 1 h (**b**)

time near the three fish aggregation buoys at Kaena Point swam at a mean rate of 1.24 m s^{-1} (Holland et al. 1990). A tuna swimming at this speed would traverse the 2200 m-diam of the detection sphere of Monitor R (2 × 1100 m range) in 29.6 min, a stay six times longer than the most frequent return interval. A tuna swimming at the same speed would cross the 1600 m-diam "listening" sphere of Monitor K (2 × 800 m detection range) in 21.5 min, a duration four times longer than those of 65% of the visits.

School fidelity

If tuna remain in a school, those tagged in rapid succession at a monitoring station should return at the same time. We found that tuna tagged at the stations returned with individuals tagged on the same day more often than with those tagged on another day. Furthermore, tuna returned more often with tuna tagged on other days than alone. Of the 15 tuna returning more than once to Station R, 11 (73.3%) arrived more often with (or as frequently as) others tagged on the same day than with those tagged on another day (Table 1). Twelve of these tuna (80.0%) arrived more often with others tagged on the same day than alone. This social cohesion is apparent in the pattern of the returns of Tuna 1 to 5, tagged on 6 March to Station R (Fig. 6). Two or more arrived together on 24 of 35 d on which the tagged tunas were detected by the monitor. All five individuals visited R on 11 April, roughly 1 mo after tagging, three arrived together 5 mo later on 4 August, and three returned 6 mo later on 1 December. Another individual might have returned within the group (making 4 of 5), had it not been captured on 29 November 1996.

A similar pattern of arrivals was observed for Tuna 15 and 17 tagged at Station K on 12 June 1996 (see Fig. 2). Unlike many other individuals tagged at K, the monitor detected these tuna at the time of tagging. The tuna visited K on 13 d spanning a 3 mo period. Two or more of the tagged tuna arrived together on six of these days.

If tuna stay together in the same school, they should swim in and out of the listening range of the monitors simultaneously. The synchronous nature to the tuna movements is apparent upon examination of 24 h records for Tuna 1 to 5 at Monitoring Station R (Fig. 7). Tuna 2, 3, and 5 arrived on 19 March at 09:45 hrs and two of three departed at 10:15 hrs. Tuna 2 and 3 visited on 10 April for 0.25 h at 08:45 hrs and again for a similar period at 23:00 hrs. All five yellowfin arrived on 11 April between 08:45 and 09:00 hrs, left within 0.5 h of each other, stayed out of detection range for 3.0 h, and returned for 0.5 h at 13:15 hrs. Two or more tuna arrived and left concomitantly during March, April, August, September, and December. Tuna 15 and 17 displayed a similar synchronicity to their movements during the night of 23 June 1996, twice moving in and out of the range of Monitor K together (Fig. 8).

Homing specificity

Tuna returned to the monitoring station at which they were tagged and rarely to the adjacent station, despite the stations being only 10 km apart. The 22 tunas tagged at R made 182 return visits to that station and only 15 visits to Station K (Table 1). The five tuna tagged on 6 March 1996 made 92 visits on 34 d to R and only five visits on 4 d to K (Figs. 2 and 6). The composition of the group varied from day to day, indicating that the location of the site was known by each of the tuna. The three tuna tagged at K on 12 June 1996 returned 27 times during 13 d, spanning a 3 mo period, while never visiting R (Fig. 2). The degree of site-specificity exhibited by other tuna tagged at K was less pronounced than at R. In all likelihood, the lower rate of return to K was due to our not tagging tuna within the monitor's tag-detection range. These tuna would return to a point outside the

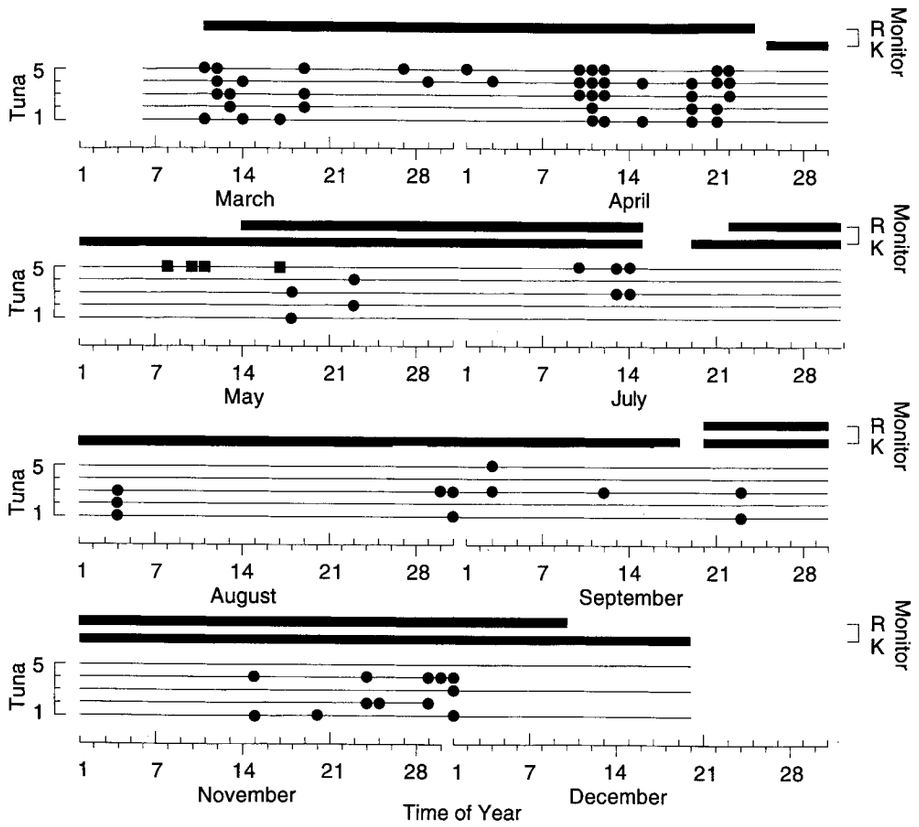

Fig. 6 *Thunnus albacares.* Chronology of return visits of Tuna 1 to 5 tagged at Monitoring Station R to Stations R (●) and K (■) (*Five horizontal lines above ordinate* indicate when tagged fish were known to be at large; *black bars* denote when data loggers were deployed on R and K buoys and "listening" for the five coded beacons)

range of the monitor. The monitor on the K buoy failed to detect 12 of 16 tunas tagged at K at the time of tagging.

Homing timing

The tuna visited the monitoring stations with high temporal precision. Two or more of the five individuals tagged on 6 March arrived and departed between 09:00 and 11:00 hrs on 10, 12, 19 March; 11, 12, and 22 April; 4 and 31 August; and on 3 September 1996. Within that 2 h period, there were even briefer "target" periods when the tunas were detected more often at the monitoring stations. These periods were centered at 09:05, 09:25, and 09:55 hrs. As an example, let us consider the 09:05 hrs target period. Tuna 1 arrived at 09:04 hrs on 12 April, Tuna 3 at 09:05 and 09:02 hrs on 12 April and 12 September, and Tuna 4 at 09:09 and 09:06 hrs on 3 and 12 April 1996.

If members of a school of tuna were tagged while visiting a favored location, one would predict that they would return together and at the same point in time. If this were so, the difference between the times of successive arrivals and the time of tagging would be less than the difference between these times and randomly generated times. We generated random "arrival" times by dividing the integers taken from a table of random digits by the number of minutes in a day and converting this number to decimal hours of the day (see Table D.45 of Zar 1984). The true and random arrival times of each tuna were then subtracted from the time when each tuna was tagged. The maximum time separation possible was ± 12 h. Tuna returned most frequently <1.9 h before or after the time of tagging, and arrived less often the further away from the temporal "target" (Fig. 9). One reason for the tuna arriving at times other than when they were tagged, is that they visited twice or more times during the same day after a long period of absence. For instance, Tuna 15 and 17 often returned to K after periods <12 h (see Fig. 8). In contrast, randomly generated arrival times had no relationship to the time of tagging.

Foraging sites

An allegiance of tuna to one school, a predilection for returning to the site of tagging, and precise timing when visiting sites are all consistent with tuna having traditional migratory routes. The record of arrivals of Tuna 15 and 17 tagged at Monitoring Station K (clock diagrams, in Fig. 8) suggests that the "way points" along these routes are known by each member of the school. On 23 June, Tuna 15 and 17 visited together at 20:30 and 23:45 hrs. Tuna 15 returned to the buoy "alone" at 20:30 hrs on 29 June and at 23:45 to 24:00 hrs

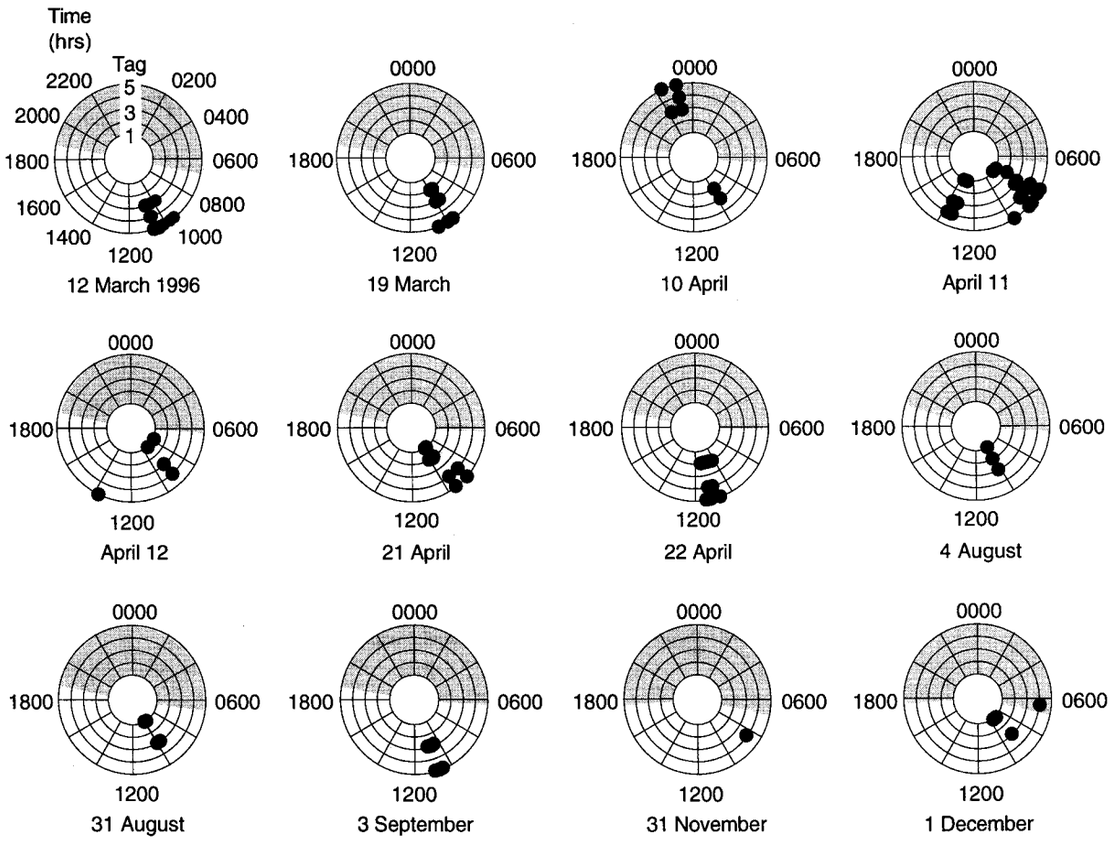

Fig. 7 *Thunnus albacares*. Presence of Tuna 1 to 5 at Monitoring Station R during 12 d over 9 mo period. Clock diagram consists of five concentric rings, each ring corresponding to a different tuna tagged on 6 March 1996 (*Shading* nighttime; ● detection of beacon-tagged tuna by automated monitor during 15 min interval)

on 29 June. Tuna 17 returned "alone" at 23:30 to 24:00 hr on 21 and 22 June 1996. Both individuals arrived separately at the buoy at 11:00 to 12:00 hrs on different days. At times, schools break up and members of subgroups visit the same sites by themselves, as evidenced by Tuna 17 returning to the Buoy K on 3 d days at 03:30 to 03:45 hrs without Tuna 15.

Discussion

Do individual *Thunnus albacares* stay together in a school? Our results indicate a degree of constancy to the composition of tuna schools. Other studies to assess school cohesion have provided conflicting conclusions. Genetic evidence from yellowfin and skipjack tunas (*Katsuwonus pelamis*) indicates that a greater number of related fishes occur in schools than expected by chance association (Sharp 1978). School-mates often have the same rare alleles and are similar in length, implying a common birth date and site. Species of parasites found on skipjack tuna within schools at a location are the same on the scale of weeks, indicating short-term school cohesiveness that permits parasite exchange between school members (Lester et al. 1985). Less mobile freshwater species such as the three-spined stickleback *Gasterosteus aculeatus*, the guppy *Poecilia reticulata*, and the European minnow *Phoxinus phoxinus* chose schools with familiar individuals in laboratory tests (Van Havre and Fitzgerald 1988; Magurran et al. 1994; Chivers et al. 1995).

Our data are inconsistent with other field observations and marking studies, which suggest a dynamic nature to schools of migratory fishes. Large nighttime schools of bluefin tuna (*Thunnus thynnus*) separate into smaller foraging groups during daytime (Scott and Flittner 1972). Numbers of marked versus unmarked skipjack tuna caught in schools indicated random mixing after intervals as short as 1 mo of liberty, and after 3 to 5 mo in all cases (Bayliff 1988). Mark- and-recapture studies have indicated that skipjack tuna move quite rapidly between schools: 16 to 63% of the marked individuals left a school each day to join other schools (Hilborn 1991). Ultrasonic tracking of tunas from boats has provided little insight into school coherence because only a single tuna is monitored at a time.

The tuna tagged during our study returned repeatedly to the site of tagging. In contrast, Hunter et al. (1986) found that mark- and- recapture studies provide "little

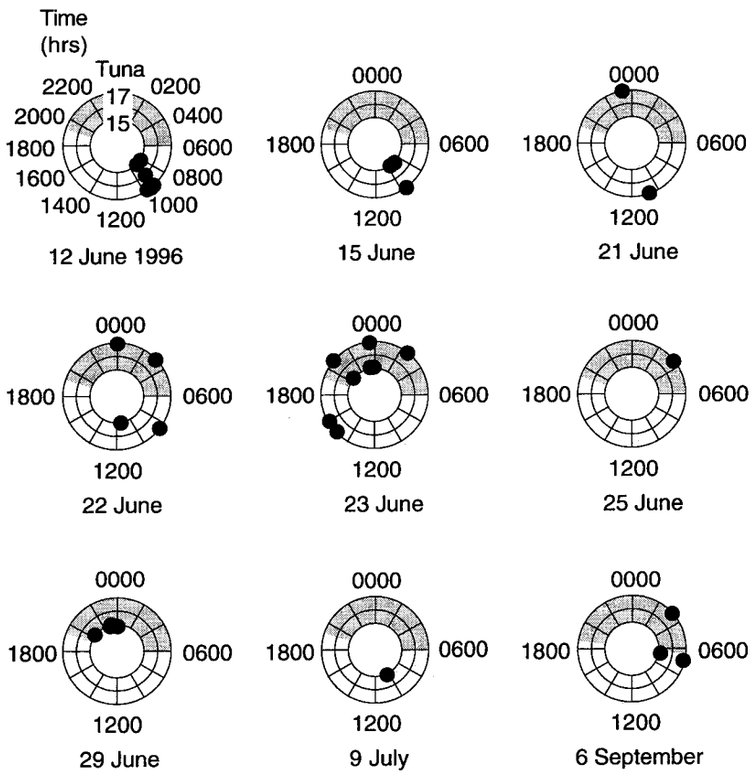

Fig. 8 *Thunnus albacares.* Presence of Tuna 15 and 17 at Monitoring Station K during 9 d over 9 mo period. Clock diagram consists of three concentric rings, each corresponding to a different tuna tagged on 12 June 1996 (*Shading* nighttime; ● detection of beacon-tagged tuna by automated monitor during 15 min interval)

or no evidence of (long term) homing ... for the yellowfin." It is difficult to discriminate whether tuna later caught at the site of tagging are long-term residents or have returned after extensive migrations, because only the points of tag and recapture are known. This ambiguity can be resolved by using position-determining archival tags as well as listening stations. For example, a plaice (*Pleuronectes platessa*) carrying a depth-sensing data-storage tag was tracked in the North Sea by comparing water-depth estimates based on the fish's surface-to-bottom excursions to local tidal heights at different times of the year. Although the point of release and recovery were only 88 km apart, the plaice swam 150 km north of the release site, reversed direction, and swam 420 km in the opposite direction, again reversed its direction, and moved back toward the release point (Metcalfe and Arnold 1997). Listening stations can repeatedly detect a fish tagged with an ultrasonic beacon at a site, unlike traditional mark- and- recapture methods, by which a marked fish is harvested and thus unable to return to the site. The number of marked individuals captured at the site decreases with time, giving the false impression that the fish migrate from the site. Short-term ultrasonic tracking of fish by boat has shown that tunas do return to buoys, reefs, and banks after extensive nocturnal movements into the surrounding waters. Tunas tagged with these transmitters have been tracked for periods of up to 1 wk (for track durations, see Table 5 of Hunter et al. 1986). For example, yellowfin and bigeye tuna tagged at the three fish-aggregating buoys at Kaena Point remained close during daytime, moved as far away as 9 km at night, and returned to the same buoy on the following morning (Holland et al. 1990). Skipjack tuna tagged at Penguin Bank off Hawaii made 25 to 106 km excursions away at night, and returned on the following day (Yuen 1970).

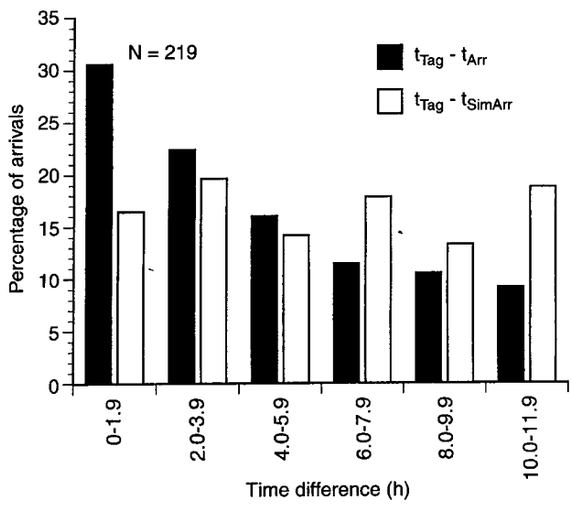

Fig. 9 *Thunnus albacares.* Comparison of temporal separation between when each tuna was tagged and its successive arrivals (*black bars*) and random "arrival" times (*white bars*) generated from table of random numbers

Our estimate of homing rate is low, because tuna would not be detected when: (1) caught by sport and commercial fishermen, (2) carrying beacons that ceased to transmit, or (3) tagged outside the monitor range. We suspect that the four tuna that a fishermen reported tagging at Monitoring Station K on the morning of 28 July were, in actuality, tagged during the afternoon on 29 July at R, where the tags were first detected and later returned (Fig. 2).

The brevity of the tuna visits to the R and K monitoring stations appears inconsistent with evidence for the attraction of tunas to FADs (for review see Holland 1996). Ultrasonic tracking studies have shown that yellowfin tuna do orient to FADs. For example, two yellowfin tuna tagged at FADs near Kaena Point on Oahu Island, Hawaii, moved away at night and returned on the following morning (see Fig. 2 in Holland 1990). A yellowfin tagged at a FAD off Anjouan Island, Comoros Islands, made a similar nocturnal excursion before returning to the FAD during the next morning (Cayré 1991). The yellowfin off Kaena Point spent much of the day swimming in a 1.5 km-diam circle around the buoy (see Fig. 2a in Holland et al. 1990). This particular tuna may have been outside the detection range of the monitor much of this time, particular if the seas were rough. The range of the VEMCO VR-20 receiver decreases as sea state increases, and elevates the surrounding level of ambient noise (see Fig. 2 in Klimley et al. 1998). Monitor R had a listening range of 1.20 km in 0.5 m seas; K had a smaller range of 0.80 km in 1.5 m seas that decreased to 0.65 km in seas of 2.0 to 3.0 m. Sea conditions are most commonly 2 to 3 m off Oahu, Hawaii. It is thus possible that our monitors did not detect the tuna when orienting to the buoys at greater distances. Although most visits were short, some tuna remained within range of our monitoring stations for up to 15 h.

Tuna visited our monitoring stations twice as often during the day, yet the frequency of nocturnal visits of tuna to the buoys in our study contrasts with the absence of nighttime visits by tuna tagged and tracked by boat off Kaena Point and Anjouan Island (see tracks in Holland et al. 1990; and Cayré 1991). Some individuals were detected at the R listening station for >6 h during nighttime. An increase in attendance recorded by the automated monitors might be expected because they provide a more comprehensive record of the occurrence of the tuna at FADs than boat tracking, which is limited by effort, weather and cost to <1 wk. In contrast, our monitoring stations were able to detect 38 tunas during a 13 mo period when seas were often too rough for tracking by boat.

We found that tuna appeared together at our monitoring stations with precise timing, as also has been observed for individual fish at FADs (Holland et al. 1990) and banks (Yuen 1970). The high temporal precision of these visits to a site could result if two or more yellowfin at widely separated locations timed their departures and transits to coincide with those of the others, or could occur if they simply returned together within the same school. We favor the latter explanation because they arrived <1 min apart after absences of many days and then moved in and out of the range of the monitors together. This high degree of synchronicity is most parsimoniously explained by a school of tuna moving from location to location.

One must consider the implications of precisely timed homing despite the variable tidal and wind-driven currents around the Hawaiian Islands. To arrive with such temporal precision, tuna would need to know the location of the monitoring station, their present position while away from the site and their rate of movement, so that they might arrive "on time." In fact, Yuen (1970) noticed this awareness of time in skipjack tuna. He wrote "when it was unusually far from the bank, the tuna at Kaula Bank averaged 8 km/hr, seven times its average speed for that time of the day, as if it were compelled to arrive at the bank by a certain time."

The precise and different timing of arrivals at the two monitoring stations is consistent with the hypothesis that tuna schools have foraging sites that they visit with regularity. Of interest is whether schools follow specific routes while migrating in the open ocean, or move in widely separated trajectories only to converge later at a particular site. A yellowfin tuna tracked intermittently for 6 d moved back and forth along a similar offshore path between the S and V buoys at Kaena Point during three nights and returned to the same section of shoreline (see Fig. 7 in Holland et al. 1990). However, little similarity was apparent between the Day 1 and Day 2 tracks of another yellowfin tuna at Buoy V (see Fig. 2 in Holland et al. 1990).

The extent to which yellowfin migrate is evident from the 926 km modal distance between the site of tagging and recapture after <180 d (see frequency distribution in Fig. 10 of Hunter et al. 1986). Modeling studies based upon tag- and- recapture use rates of diffusion to describe the large-scale movements of tuna in the Pacific (Sibert and Fournier 1993; Kleiber and Hampton 1994). Such models might be improved by adding a mathematical treatment of homing behavior.

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