Abstract.- The horizontal and vertical movements of yellowfin tuna *Thunnus albacares* and bigeye tuna *T. obesus* captured near fish-aggregating devices (FADs) were determined using pressure-sensitive ultrasonic transmitters. The movements of these FAD-associated fish were compared with the tracks of yellowfin tuna not associated with FADs. Tracks from 11 yellowfin and 4 bigeye tuna were obtained; these included 23 complete 24-hour periods of observation. Whether associated with FADs or a 40-fathom (75-m) reef dropoff, most yellowfin and bigeye tunas exhibited similar diurnal patterns. The fish tended to remain tightly associated with FADs or the reef dropoff during the day, move away at night, and return the next morning. The maximum range of these nighttime excursions averaged approximately 5 nmi. These tunas apparently treated the FADs as outliers of the coastal topography. This may not be the same behavior that results in the association of these species with drifting objects such as logs. Tuna can learn FAD positions and navigate precisely between FADs that are at least 10 nmi apart. When not associated with FADs or the 40-fathom dropoff, yellowfin tuna oriented to the bottom of the mixed layer (50–90 m) in daytime, whereas the bigeye occupied depths between 190 and 250 m. The daytime distribution of bigeye tuna seemed to be influenced by the depth of the 15°C isotherm. Both species swam closer to the surface at night. Swimming strategies possibly associated with energy and thermoconservation were observed.

Horizontal and Vertical Movements of Yellowfin and Bigeye Tuna Associated with Fish Aggregating Devices*

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Tropical and subtropical pelagic fishes aggregate around natural, drifting debris such as logs and mats of algae. Man-made, anchored floating objects, known as fish aggregating devices (FADs), have also proven effective in attracting and holding commercially important pelagic species (Shomura and Matsumoto 1982, Matsumoto et al. 1981, Brock 1985). Species commonly found around FADs in Hawaii are yellowfin tuna *Thunnus albacares*, bigeye tuna *T. obesus*, skipjack tuna *Katsuwonus pelamis*, dolphin or mahi-mahi *Coryphaena hippurus*, and wahoo or ono *Acanthocybium solandri*. The first commercial FADs were deployed in the calm waters of the Philippines in the early 1970s to attract yellowfin tuna (Kihara 1981), and in 1977 experimental FADs designed for use in high-energy, deep-water environments were anchored around the Hawaiian islands (Matsumoto et al. 1981). Due to the success of these bouys in aggregating fish, FADs have come to play an important role in the commercial, subsistence, and recreational fisheries of all the tropical and sub-tropical oceans of the world.

Despite the widespread use of FADs, left unanswered are important questions concerning their range of influence, optimal placement, and impact on surrounding fish populations. The behavioral patterns that result in fish being associated with floating objects of any type are poorly understood and not widely agreed upon (Gooding and Magnuson 1967, Hunter and Mitchell 1967, Fedoryako 1982). However, the underlying mechanisms of aggregation have generally been assumed to be the same for both free-floating phenomena such as logs, and anchored man-made objects such as FADs (Shomura and Matsumoto 1982). To better understand the behavior of tunas associated with FADs, the movements of yellowfin and bigeye tuna caught within 500 m of these devices were tracked using pressure-sensitive ultrasonic transmitters. The movements of these fish were compared with those of tunas that were not associated with FADs, but with the reef perimeter surrounding the islands. In Hawaii and elsewhere in the Pacific, yellowfin tuna can be found in the vicinity of the 40-fathom (75-m) isobath where the island topography abruptly descends into very deep water. In fact, the dropoff of the outer reef edge is often so steep that

the horizontal distance between the 40-fathom and 100-fathom (187-m) isobaths is measured in tens of meters. To observe the behavior of non FAD-associated tuna, three yellowfin tuna were tracked that were caught on or near the 40-fathom isobath around Oahu, Hawaii.

The influence of FADs on the vertical movements of these species was investigated by comparing the depth distributions of the two species in on-FAD (within 500 m of a FAD) and off-FAD (beyond 500 m of a FAD) situations. The depth distributions were analyzed with respect to ambient ocean temperatures, as measured by expendable bathythermographs.

Methods

The horizontal and vertical movements of individual fish were monitored by pressure-sensitive, 50 KHz ultrasonic transmitters (Vemco, Halifax, Nova Scotia, Canada). Fish caught on the tracking vessel by trolling and pole-and-line techniques were fitted with transmitters by passing two nylon "tie-wraps" through the dorsal pterygiophores and trunk musculature adjacent to the second dorsal fin (Fig. 1). The fish were out of the water for approximately 1 minute during this procedure. The fish were then released and followed using a directional hydrophone mounted on the tracking boat. Whenever possible, a distance of approximately 200 m was maintained between the fish and the boat. Geographic position was determined every 15 minutes by a combination of Loran-C, radar, bathymetric, and visual fixes. These techniques evolved from pioneering work in tuna tracking by Yuen (1970), Laurs et al. (1977), Carey and Olson (1982), and Carey (1983). A summary of previous ultrasonic tracks of tuna has been compiled by Hunter et al. (1986). A detailed account of the methods used in the current study has been published previously (Holland et al. 1985, Bayliff and Holland 1986).

The transmitters were equipped with pressure sensors, which modulated the rate of pulse transmission in response to changes in water pressure (depth). Thus, vertical movements of the fish were determined by measuring the time between signal pulses. These pulses were recorded on audiocassettes for analysis ashore. Expendable bathythermographs deployed approximately every 3 hours provided ocean temperature profiles, which were superimposed on the vertical movement plots. Pooled time-at-depth and time-at-temperature histograms were constructed from all
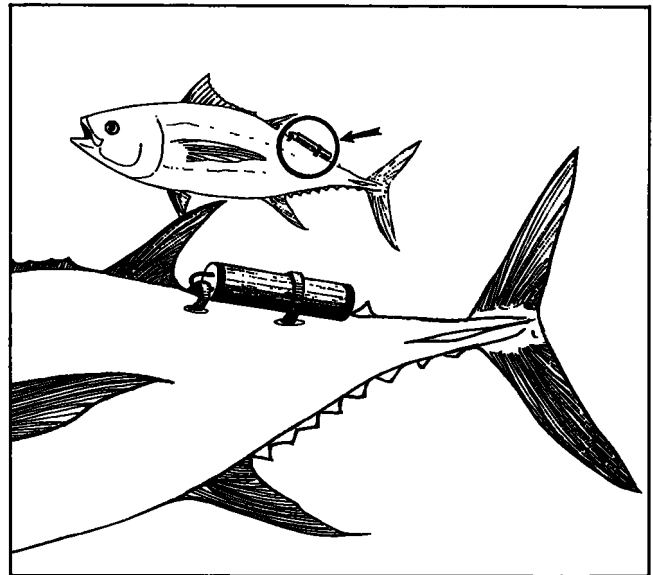
Figure 1
Transmitters were attached to yellowfin and bigeye tuna with two nylon straps inserted through the dorsal musculature and pterygiophores associated with the second dorsal fin (from Holland et al. 1985).

tracks combined, using 10-m and 1°C bins averaged every 10 minutes. The data were analyzed for daytime and nighttime depth distributions. Differences in the temperature and depth distributions for day-versus-night and on-FAD versus off-FAD were analysed by factorial analysis of variance (SAS General Linear Models Procedure, SAS 1985). Portions of tracks occurring on-FAD or near the reef dropoff were not included in these calculations. Thus, the depth histograms and overall averages are compiled from movements that were not constrained by bottom topography or influenced by the presence of floating objects.

The tracking techniques used in this study are not capable of detecting small-scale changes in the horizontal swimming direction of the fish. Consequently, sustained swimming speeds have been calculated only from sections of tracks in which fish demonstrated prolonged straight-line movements. Swimming speeds were calculated as distance traveled per unit time and in terms of body lengths (fork length, FL) per second. Swimming speeds were calculated for each complete hour of "staight" running; these hourly rates were averaged to yield a sustained swimming speed for the relevant section of each track. Vertical movements were not included in these calculations.

Daytime and nighttime time-at-temperature histograms were generated for both yellowfin and bigeye tuna. Because of differences in absolute ocean-surface temperatures between different tracks, and because of

previous indications that ocean thermoclines may be important orientation cues for tuna (Carey and Olson 1982), the time-at-temperature data were analyzed relative to the surface mixed layer. Thus, the mixed layer is referred to as ML, and the progressively colder 1°C isotherms as ML-1, ML-2, and so on.

Results

The results reported here are from tracks of 11 yellowfin and 4 bigeye tuna. Duration of tracks from release to track termination ranged from 5 hours to 6 days, with an average duration of 31.6 hours. Overall, these tracks encompass 23 complete 24 hour periods of observation. All 4 bigeye and 8 of the 11 yellowfin tuna were caught within 500 m of FADs. The remaining three yellowfin tuna tracks were from fish caught on or near the 40-fathom contour around the island of Oahu.

Horizontal movements

For yellowfin tuna, a clear pattern of horizontal movement was apparent. That is, during daylight the fish usually moved within a home range, staying in proximity to certain well-defined physical features, such as FADs or the outer reef dropoff. Eight of the 11 yellowfin tuna and 2 of the bigeye tuna showed aspects of this behavior, and this pattern was exhibited by both the FAD-associated and coastline-associated fish. Most of these fish made diurnal movements away from these daytime haunts, with the initial change in location often occurring around sunset.

FAD-associated yellowfin tuna These tuna spent daylight hours very close to the FADs, and then left those locations sometime between late afternoon and early nighttime to embark on extensive nighttime excursions, returning to the same or another FAD the following day. Five of the eight FAD-associated yellowfin tuna displayed aspects of this diurnal on-FAD and off-FAD behavior. A sixth FAD-associated fish showed signs of displaying this behavior, but was lost before this could be confirmed. The following is a brief synopsis of their horizontal movements.

Yellowfin tuna YF8404 (51 cm FL) was caught and tagged at V FAD at 0927, and stayed within 100 m of the FAD for 11.3 hours before leaving it a few minutes after sunset (1925, Fig. 2A). The fish then made a nighttime excursion totaling 12 nmi before returning to within 100 m of the FAD by 1312 the next day. During the last few hours of this approach the fish moved very slowly, as if it was drifting in the prevailing current. Once at the FAD, the fish again stayed close to the buoy until departing at sunset on a second
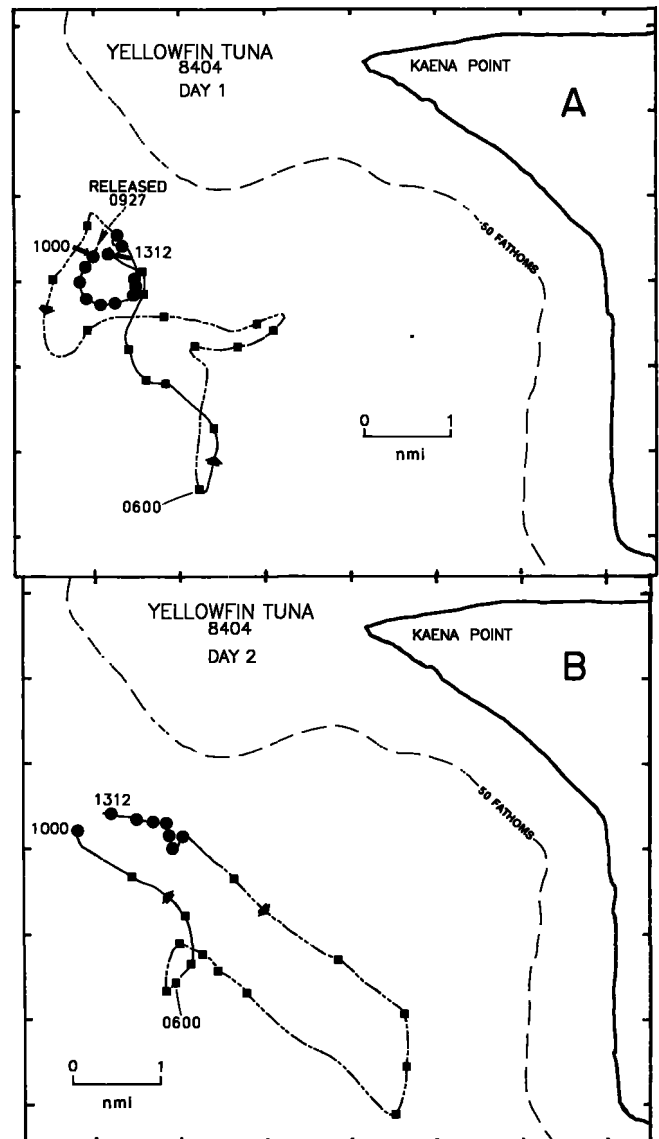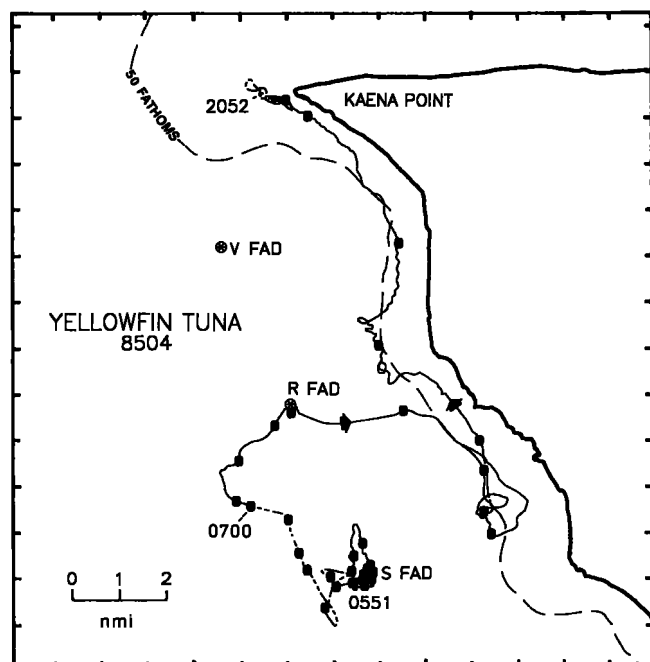

Figure 2

(A) 48-hour track of yellowfin tuna YF8404 tagged and released at 0927 at V FAD, Oahu. Circles = hourly marks when fish is on-FAD; squares = hourly marks when fish is off-FAD. In this and subsequent figures, solid line = daytime movements, dashed line = nighttime movements, and marks on figure axes = 1° divisions. On the first day (A) the fish remained very close to the FAD as it moved in a circular path in the current, departed the FAD after nightfall, and returned at 1312 the following day. The second day's behavior (B) was similar, despite a different pattern of movement by the FAD.

nighttime excursion of 11.25 nmi. The maximum distance away from the FAD was 3.0 nmi on the first night and 5.0 nmi on the second. On both excursions, the fish commenced moving back toward the FAD immediately after sunrise (Fig. 2A,B).

Two hours after fish YF8504 (47 cm FL) was tagged and released at S FAD at 0551, it made a 4-hour, 1-nmi excursion away from the buoy before taking up a posi-
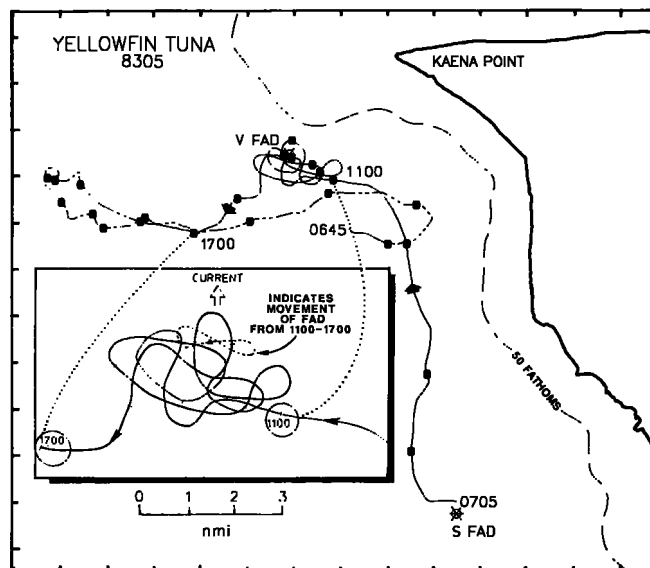
Figure 3

Yellowfin tuna YF8504 spent 8 daylight hours on the upcurrent side of S FAD before moving away at night. The next morning it moved to R FAD until disturbed by a school of porpoises, when it immediately took a direct course to the island dropoff, which it patroled for the rest of the day. In this and subsequent figures, squares = hourly position marks.

Figure 4

Yellowfin tuna YF8305 departed S FAD immediately after release at 0705 and took a direct course to the next nearest FAD, V (R was off station at the time), where it patroled almost exclusively in the upcurrent area (insert) before making an overnight excursion totaling 15 nmi.

tion within 50 m of the FAD for the remaining 8.0 hours of daylight (Fig. 3). During this time the fish was almost exclusively on the upcurrent side of the bouy. At 2345 the fish left the FAD and moved offshore; by sunrise the next day, it was 3.25 nmi from S FAD. The fish then moved 3.0 nmi in a direct course to the nearest adjacent FAD (R) arriving there at 0910. Once there, it stayed extremely close to the FAD and in the company of a school of other yellowfin tuna that could be seen from the surface. At 1020 a group of porpoises arrived and dove through the school of tuna, which appeared to scatter in all directions. The tagged fish dove and swam to the 40-fathom contour of the island, where it stayed for the rest of the day. Contact was lost just after sunset on the second night.

Fish YF8305 (55 cm FL), after being tagged and released at S FAD at 0705, swam for 4.0 hours on a direct course to V FAD, approximately 10 nmi away from the release point (Fig. 4). The fish spent 95% of the next 5.0 hours moving around on the upcurrent side of this FAD. In the late afternoon, the fish departed the FAD and spent most of the night farther offshore, moving in a 15-nmi loop before heading back toward V FAD the following morning. Just after first light, when the fish had returned to within 2 nmi of the FAD

and appeared to be headed back even closer, the transmitter was shed.

The tracks of fish YF8406 (62.5 cm FL) and YF8501 (44.0 cm FL) were similar. During the daytime, both fish stayed very close to their respective FADs (for 9 and 12 hours, respectively), and both were lost at sunset in deteriorating sea conditions. Because there was no evidence of transmitter failure, and exhaustive searches at the FAD locations after dark failed to relocate the signal, it is reasonable to assume that both these fish were lost when they made sudden evening departures from the vicinity of their respective FADs.

Fish YF8302 (64 cm FL) was caught and tagged at S FAD, but lost 5.0 hours later. When contact was lost, the fish had departed the release site, but appeared to be curving back toward the bouy.

Fish YF8502 (74.5 cm FL) was similar to other FAD-associated yellowfin tuna in that, for the first 5.0 hours of the track (0600–1100), it stayed in close proximity (within 100 m) to S FAD. However, it then moved steadily away but was lost 12 nmi southwest of the buoy due to equipment failure after 13.5 hours of track and before any possible long-term trend had become apparent.

Fish YF8506 (75.25 cm FL) was caught near S FAD at 0630. Unlike the other FAD-associated yellowfin, it immediately began to move steadily away, maintaining a constant southwest course for the next 17.5 hours, at which time the track was terminated (Fig. 5).
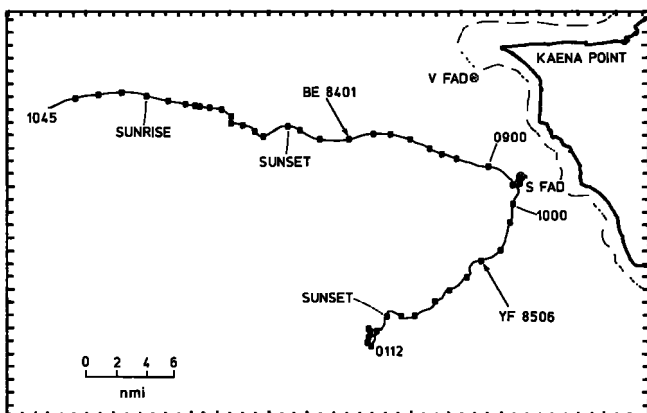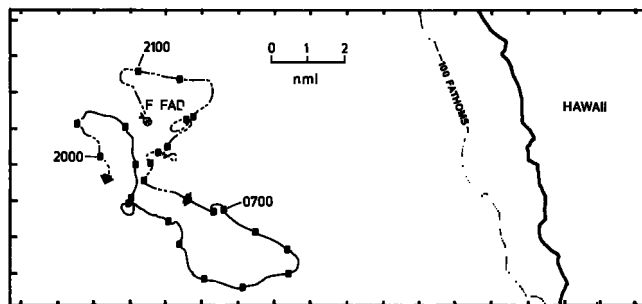
Figure 5

Bigeye BE8401 and yellowfin tuna YF8506 both departed S FAD almost immediately upon release and maintained quite straight azimuths at constant speeds. During darkness, both fish slowed down, and YF8506 became more variable in swimming direction.
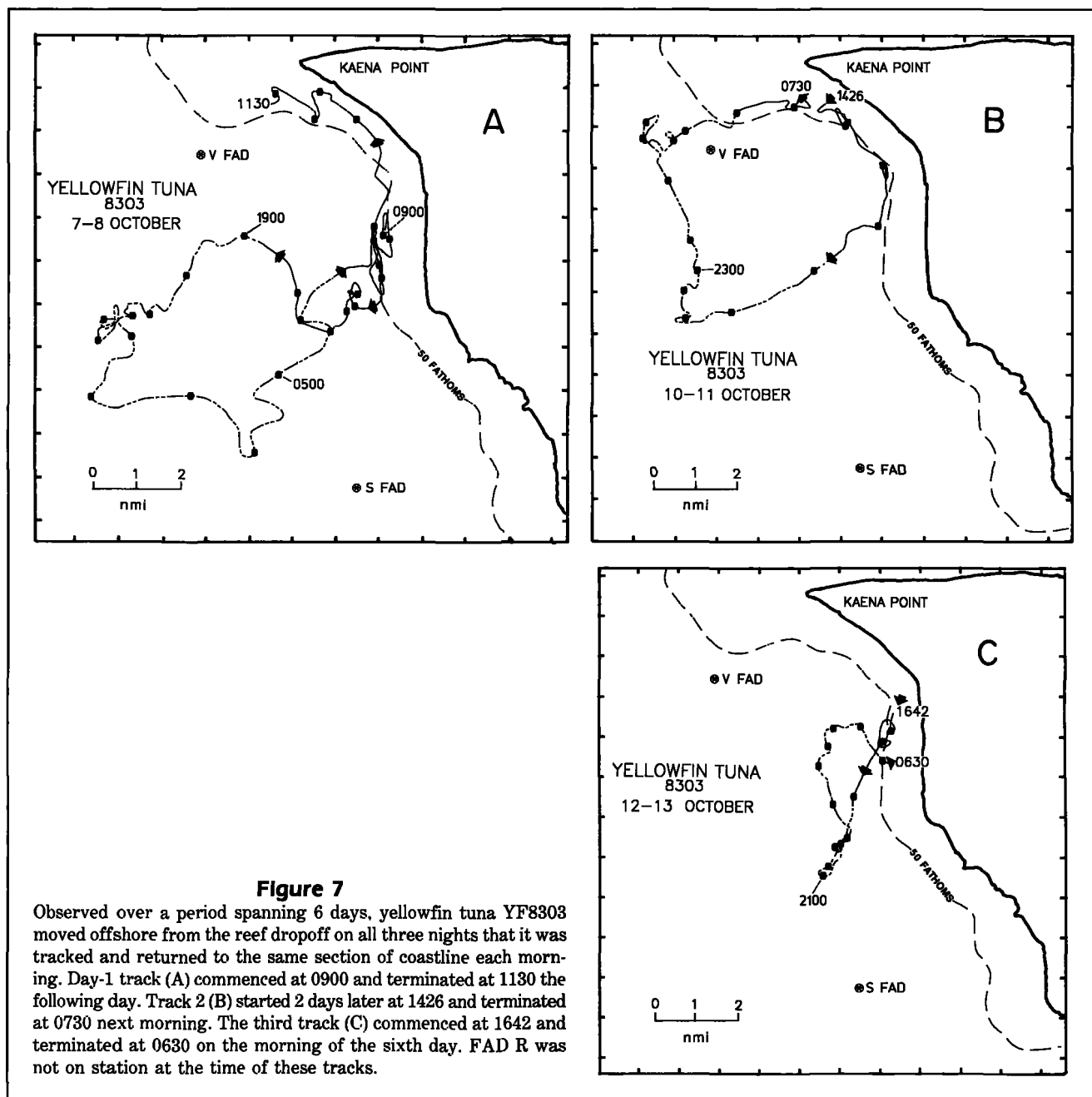

Figure 6

Caught and released after sunset at F FAD off the Kona coast of Hawaii, bigeye tuna BE8205 made a 24-nmi overnight loop before returning to the FAD by late afternoon of the following day.

FAD-associated bigeye tuna   Four tracks were made of bigeye tuna caught near FADs. Of these four, one was lost after a few hours and before any diurnal patterns became apparent, one moved continuously away from the FAD (Fig. 5), and two displayed diurnal on-FAD and off-FAD behavior similar to that exhibited by the yellowfin tuna. The following is a synopsis of these two tracks.

Bigeye tuna BE8205 (74.5 cm FL) was caught and tagged 200 m from F FAD off Kona, Hawaii, about 1 hour after sunset (Fig. 6). Upon release, it proceeded on a 24.0-nmi overnight excursion which took it away from the FAD, before gradually reapproaching the FAD in the afternoon of the next day. The maximum distance it moved away from the FAD was 5.75 nmi. This track was then terminated after 24.0 h.

Fish BE8706 (72.0 cm FL) was caught at first light within 50 m of C FAD located off Kealakekua, Hawaii. The fish remained extremely close to the bouy throughout the day until 1 hour after sunset, when it made a 2-nmi excursion that lasted approximately 3 hours. The fish then returned to the immediate vicinity of the buoy, where it remained for the rest of the night and at least through noon of the following day, when the track was terminated after 30.0 hours.

Coastline-associated yellowfin tuna   Three tracks were made of yellowfin tuna caught on the reef dropoff on the west coast of Oahu in water between 40 and 50 fathoms (75–95 m) deep. These fish were in the same size range as those caught around the FADs, and tracks spanning 6 days, 36 hours, and 37 hours were obtained, which encompassed a total of six day-night transitions. Two of the three fish displayed offshore excursions

every night that they were tracked (a total of five nights). These tracks were as follows.

Fish YF8303 (70.0 cm FL) was caught and tagged at 0855 about 0.75 nmi off the leeward coast of Oahu on the 40-fathom dropoff (Fig. 7A). For the next 7 hours, the fish remained on or near the 40-fathom dropoff, before moving slightly further offshore in the late afternoon. During the subsequent 12 hours of darkness, the fish made a 17-nmi offshore excursion before returning to the 40-fathom contour in the second hour of daylight on the following day. The maximum distance away from the point at which it reencountered the dropoff was approximately 8.25 nmi. The fish remained on the reef slope for the remaining daylight hours until contact was lost at 1130, after 26 hours of tracking.

Forty-eight hours after contact was lost, a hydroacoustic search of the 40-fathom contour reestablished contact with the fish, and the track was resumed at 1426 of the third day (Fig. 7B). The fish spent the remaining daylight hours moving back and forth along the dropoff before moving offshore in late afternoon. The fish spent all night on a 13-nmi excursion before returning to the 40-fathom contour at first light on the next day. The greatest distance from the point of return to the dropoff was approximately 5.25 nmi. The track was suspended at 0730 on the fourth day. The fish was relocated on the 40-fathom isobath on the afternoon of the following (fifth) day at 1642 (Fig. 7C). Again, the fish moved offshore in the late afternoon and spent all night in deeper water on a 7.5 nmi excursion. Maximum distance from the point of return to the dropoff was 3.3 nmi. The time of arrival back at the 40-fathom contour was within 1 minute of the time of arrival on the previous day (Fig. 7B,C). The track was terminated at 0630 on the sixth day because of an impending storm. In summary, this fish was tracked over three day-night-day cycles spanning 6 days and, on each occasion, it made a nighttime off-
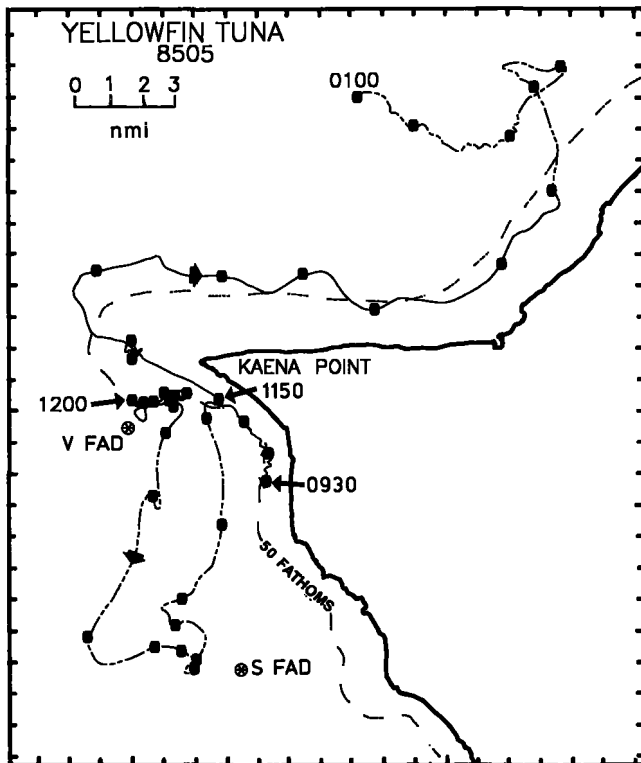
Figure 7
Observed over a period spanning 6 days, yellowfin tuna YF8303 moved offshore from the reef dropoff on all three nights that it was tracked and returned to the same section of coastline each morning. Day-1 track (A) commenced at 0900 and terminated at 1130 the following day. Track 2 (B) started 2 days later at 1426 and terminated at 0730 next morning. The third track (C) commenced at 1642 and terminated at 0630 on the morning of the sixth day. FAD R was not on station at the time of these tracks.

shore excursion followed by a return to the 40-fathom contour on the following morning.

Fish YF8503 (47 cm FL) was caught on the 50-fathom contour at 1200 and stayed in this vicinity for 7.0 hours before moving offshore in the late afternoon to make a 24-nmi nighttime excursion (Fig. 8). The next morning, the fish returned to within 0.5 nmi of the section of coastline it had left the previous evening, the maximum distance from the point of return being 9 nmi. The tracking was temporarily suspended at 0930 and resumed at 1150, when the fish was relocated on

the 40-fathom contour near Kaena Point. From here the fish embarked on a prolonged and constant run around the point and along the 40–50 fathom contour of the north shore of Oahu. At sunset of the second day, the fish again moved offshore. When contact was lost at 0100, the fish was 7.5 nmi offshore.

Fish YF8405 (57 cm FL) was caught on the 50-fathom contour and patroled this area for about the next 24 hours. This fish did not move offshore at night. Tracking was suspended at 0715 the second day, but resumed at 1715 the same evening when the fish was

Figure 8

Yellowfin tuna YF8503 moved offshore and made a complete loop during the first night. Tracking was suspended between 0930 and 1150 of the second day. During the second day it swam at a constant pace along the reef dropoff bordering the north shore of Oahu before again heading offshore after sunset on the second night. This demonstrates that the diurnal onshore–offshore pattern is not site-specific to the west coast of Oahu. Contact was lost at 0100.

relocated on the 40-fathom contour. At times, the fish moved into water less than 30 m deep, but was lost just after sunset when the transmitter battery failed. However, this fish was caught two weeks later by a fisherman trolling at R FAD, 7 nmi away from the initial release point.

Combining the FAD-associated and coastline-associated fish, 7 of the 11 yellowfin tuna demonstrated diurnal behavioral patterns in which daytime haunts were abandoned at night. These 7 fish were observed to make a total of 11 nighttime departures from daytime locations. Of those 11 nighttime excursions, 7 were demonstrated to be completed loops wherein the fish returned to their original starting points. In addition, two FAD-associated bigeye tuna completed two nighttime-initiated loops. For the yellowfin tuna, the average maximum distance away from the following morning's destination was 5.28 nmi (SD = 1.9, N = 7). When the two documented bigeye tuna loops are included, the average maximum distance is 4.97 nmi (SD = 2.0, N = 9).

Swimming speeds Unlike the majority of the fish, one bigeye (BE8401) and one yellowfin tuna (YF8506) almost immediately departed their respective FADs and continued to swim away along straight azimuths for the entire duration of the tracks (Fig. 5). Consequently, large sections of these tracks were included in calculations of sustained swimming speeds. Daytime sustained swimming-speed data are summarized in Table 1.

The greatest distance traveled in 1 hour was exhibited at night by YF8503 which traveled 5.0 nmi. This is equivalent to 2.57 m (4.6 body lengths) per second (Fig. 8). When YF8504 was driven away from R FAD by a porpoise school, it swam the first half-hour towards the 40-fathom contour at a rate of 1.32 m (2.4 body lengths) per second (Fig. 3).

Table 1

Daytime sustained swimming speeds of selected yellowfin (YF) and bigeye (BE) tunas.

Track number	Fork length (cm)	Segment duration (h)	Average hourly speed ($\pm$ SD)	
			m/s	Body lengths (FL)/s
YF8506	72.25	10.0	0.89 $\pm$ 0.15	1.19 $\pm$ 0.20
YF8502	74.50	7.0	0.95 $\pm$ 0.10	1.28 $\pm$ 0.14
YF8503	56.00	6.0	1.80 $\pm$ 0.38	3.20 $\pm$ 0.68
YF8305	54.50	4.0	1.32 $\pm$ 0.24	2.40 $\pm$ 0.40
		YF Mean =	1.24 $\pm$ 0.41	2.01 $\pm$ 0.96
BE8401	57.00	13.0	0.79 $\pm$ 0.20	1.38 $\pm$ 0.35
		Combined mean =	1.15 $\pm$ 0.41	1.89 $\pm$ 0.88
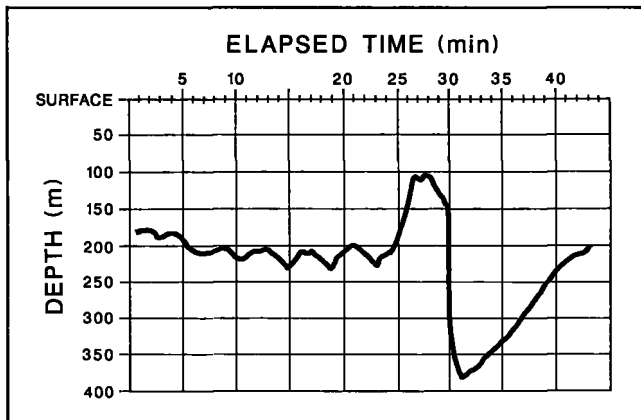
Figure 9

Figure 9

Fine-scale behavior of bigeye tuna BE8401 shown by 45-minute segment of vertical movements transcribed from data tape, including a rapid dive of 230 m in 1 minute, a rate equivalent to 6.7 body lengths/second. Ambient temperature at the maximum depth of 380 m was 9°C.
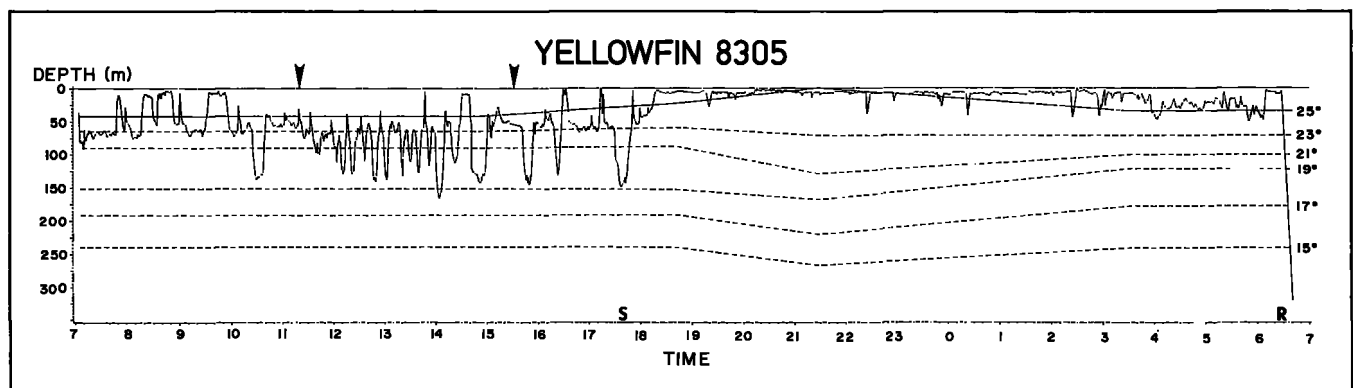
Vertical movements

The tape recordings of the pulsed signal from the transmitters resulted in detailed, continuous plots of vertical position. Rapid and small-scale changes in depth were discernible (e.g., Fig. 9), as were longer-term diurnal shifts in vertical distribution.

Day-night depth distributions In general, yellowfin tuna swam closer to the surface during darkness. For example, a dramatic change in the depth of swimming of fish YF8305 occurred exactly at sunset and lasted

until first light the following morning, when it again began to swim deeper (Fig. 10). Combining all the off-shore and off-FAD portions of the yellowfin tuna tracks yielded an average daytime depth of 71.3 m ($\pm$42.0 SD, $N = 333$), whereas the average nighttime depth was 47.3 m ($\pm$33.1 SD, $N = 444$). These daytime and nighttime depth distributions (Fig. 11A,B) are significantly different (ANOVA, $p = 0.0001$). However, this analysis also indicates significant variability among individual tracks.

Bigeye tuna swam at significantly greater daytime depths than the yellowfin tuna, and showed even greater shifts between daytime and nighttime distributions. When off-FAD, the predominant bigeye tuna daytime distribution was between 220 and 240 m, whereas the predominant nighttime depth was between 70 and 90 m (Fig. 12A,B).

On-FAD versus Off-FAD depth distributions Swimming depths of five yellowfin and one bigeye tuna that were on- and off-FAD during daytime hours support the proposition that FADs tend to bring the fish closer to the surface than they would normally be in other offshore parts of the ocean. These tracks were analyzed to determine if significant changes in depth distribution occurred when the fish were aggregated around the FADs, independant of diurnal influences. When on-FAD, three of the yellowfin tuna were closer to the surface than when off-FAD, one showed no change in depth, and one was deeper. Pooling these data for this subset of yellowfin tuna gave a mean on-FAD depth of 59.3 m ($\pm$30.7 SD, $N = 225$), which is significantly different from the mean off-FAD depth of 85.2 m ($\pm$52.0 SD, $N = 239$).

Figure 10

Plot (24-hour) of vertical movements of yellowfin tuna YF8305. In this and subsequent figures, S = sunset, R = sunrise. Arrows denote the beginning and end of time spent at V FAD. Before and after this period, the fish exhibited the "traveling" behavior of making abrupt shifts between the surface and the top layers of the thermocline. Once at the FAD, the vertical behavior became predominantly sinusoidal. All dives made both on- and off-FAD had a consistent floor around 20°C between 140 and 150 m. The rapidly descending trace at end of plot denotes the tag being shed from the fish.
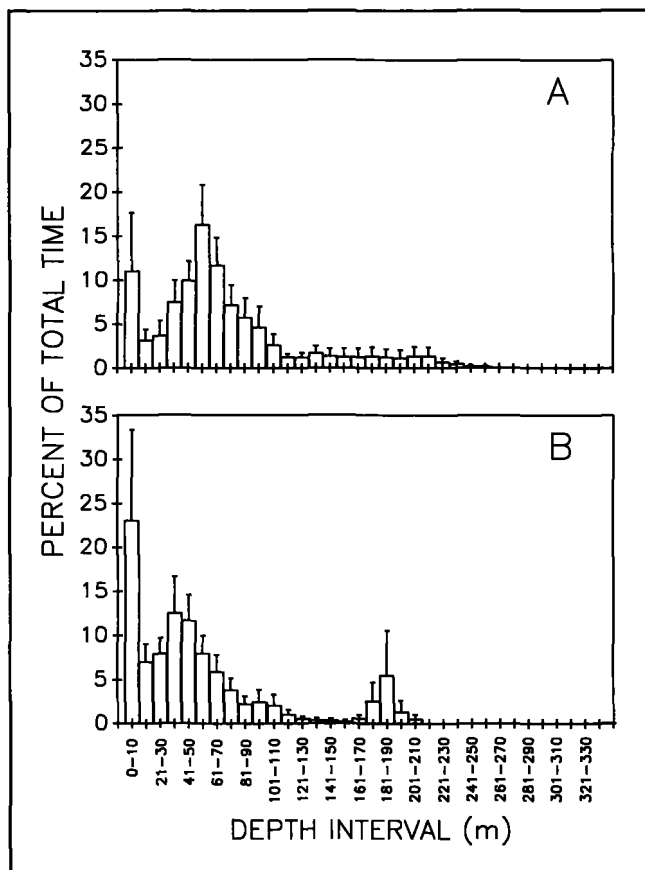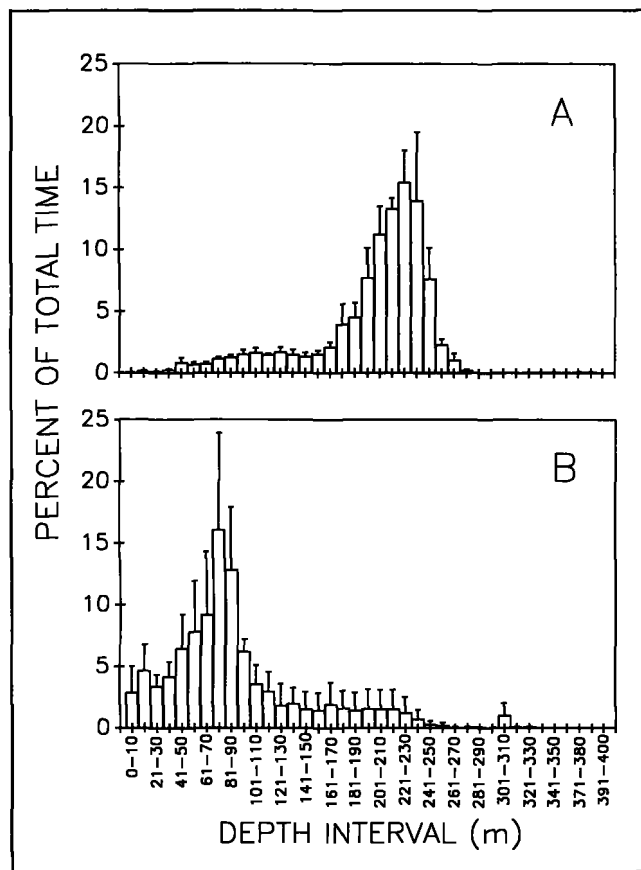
Figure 11

Yellowfin tuna daytime distribution (A) shows two modes, one at the surface and one between 60 and 90 m, which corresponds to the normal position of the interface between the mixed layer and the top layers of the thermocline. Nighttime distribution (B) reflects the tendency of these fish to swim closer to the surface at night. In this and subsequent histograms, bars = standard error.

The tendency of FADs to bring fish closer to the surface was even more apparent in the deeper-swimming
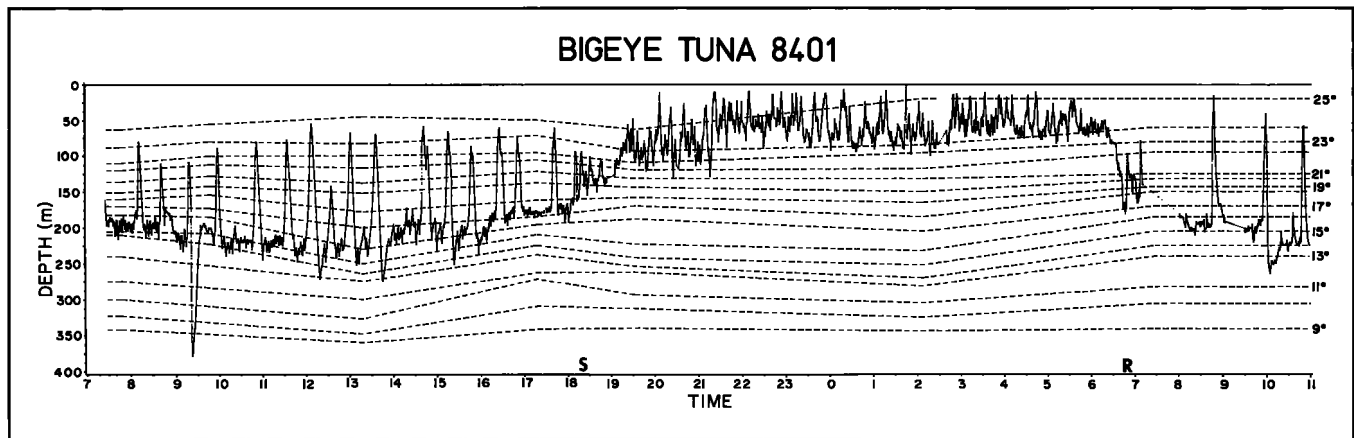

Figure 12

Daytime distribution of bigeye tuna (A) displays a major mode between 200 and 240 m, whereas nighttime distribution is much shallower (B), with the predominant distribution falling between 70 and 90 m.

bigeye tuna, as was dramatically demonstrated by BE8603 which stayed close to S FAD for 6 hours of daylight before moving away at midday. Figure 13 illustrates the rapid change of depth that coincided with
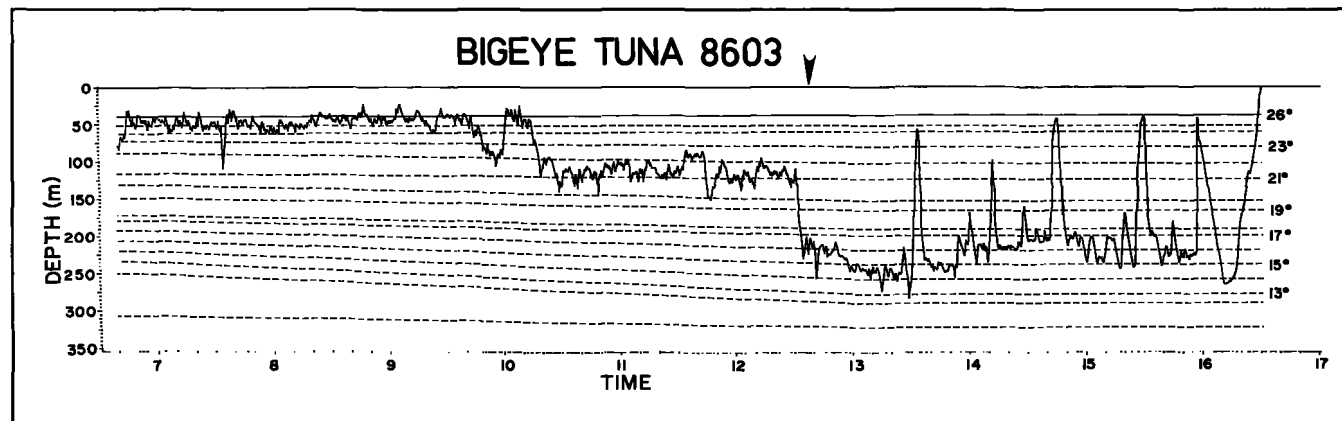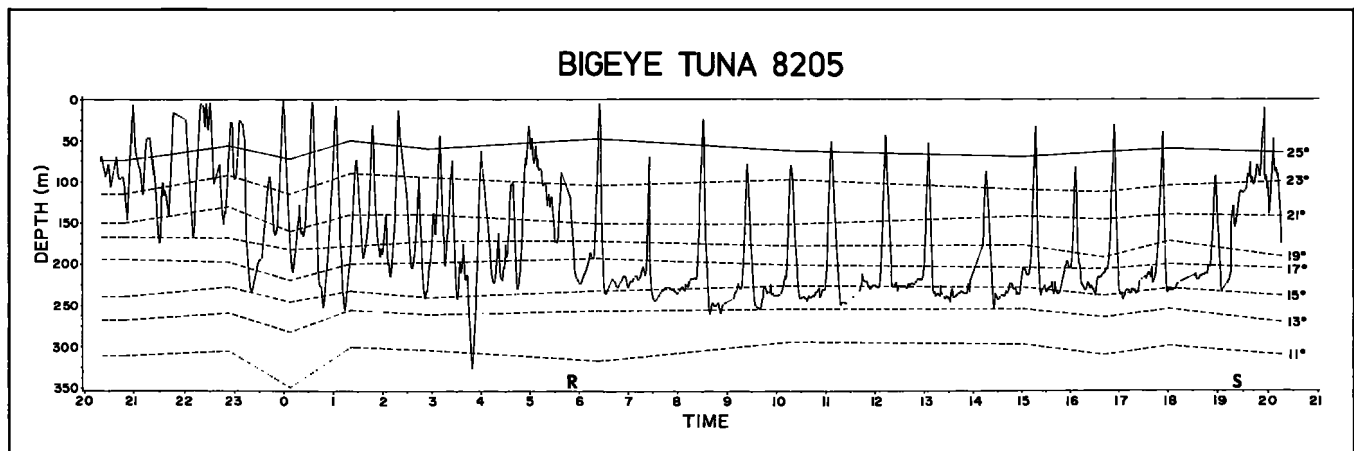

Figure 13

Plot of the on-FAD and off-FAD movements of bigeye tuna BE8603. Arrow indicates when fish departed R FAD.

BIGEYE TUNA 8401

Figure 14
Plot of day-night-day movements of bigeye tuna BE8401. The rapid dive shown in Figure 9 can be seen at 0915 on the first day.

BIGEYE TUNA 8205

Figure 15
Plot of vertical movements of bigeye tuna BE8205 showing extremely regular daytime upward excursions. These excursions consistently terminated in the zone encompassing the interface between the mixed layer and the thermocline.

the departure of this fish from the FAD. The subsequent depth and pattern of swimming were similar to those shown by the other bigeye tuna that departed their respective FADs almost immediately upon release (Figs. 14, 15). Bigeye tuna BE8706, which remained within 200 m of S FAD for 27.0 hours of the 30.0-hour track, displayed a predominant on-FAD daytime depth of between 50 and 60 m, whereas the predominant, pooled, daytime off-FAD depth of the other three bigeye tuna was 230 m.

Temperature distribution

For the yellowfin tuna, the surface mixed layer (ML) and first degree of the thermocline (ML-1) accounted for 68% of daytime distribution (Fig. 16A). After sunset, the mixed layer alone represented over 62% of the

distribution of this species, with the upper 2 degrees of the thermocline contributing an additional 26% of the yellowfin tuna's nighttime distribution (Fig. 16B). Obviously, the warmer nighttime distributions are reflective of the generally shallower depths occupied during the hours of darkness.

In the case of the bigeye tuna, daytime distribution was more dependent on absolute temperature than temperature relative to the surface mixed layer. Thus, in daytime 62.5% of the pooled off-FAD distribution occurred between 14° and 17°C (Fig. 17A). On an individual basis, the strong influence of temperature on daytime vertical distribution was demonstrated by fish BE8401 which consistently oscillated between the 15° and 17°C isotherms even though these isotherms were changing in depth over the course of the track (Fig. 14). Of this bigeye tuna's daytime movements, 68%
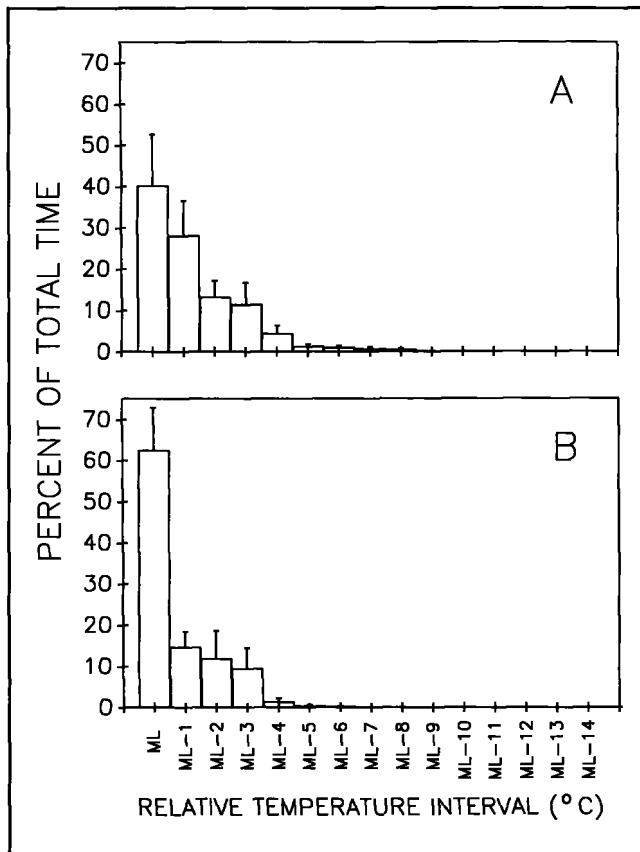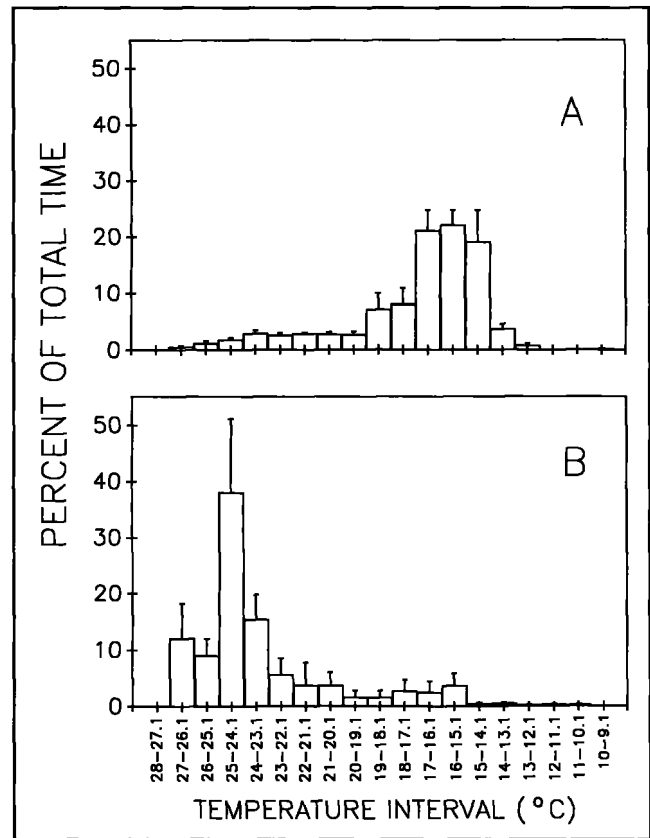
Figure 16
Yellowfin tuna temperature distributions relative to the upper mixed layer (ML). (A) day, (B) night.

Figure 17
Bigeye tuna temperature distribution. (A) day, (B) night.

occurred between 14° and 17°C. Similarly, BE8205 spent 70% of daylight hours between the 14° and 16°C isotherms (Fig. 15), and BE8603 spent 76% of off-FAD daylight hours between 14° and 17°C isotherms (Fig. 13).

As with the yellowfin, bigeye tuna occupied warmer waters at night (Fig. 17B). The difference between daytime and nighttime temperature distributions was greater for bigeye than for yellowfin tuna because of the much deeper and colder daytime distribution of the bigeye tuna and their comparatively large nocturnal upward shift.

Regular, large, upward excursions were a major feature of the daytime swimming behavior of all the bigeye tuna that were tracked in off-FAD situations (Figs. 13, 14, and 15). This behavior occurred regardless of the type of horizontal movement (e.g., meandering versus straight line). These excursions were comprised of rapid ascents and descents of uniform rate. Ascents usually peaked close to the bottom of the mixed layer and the descending phases usually terminated at the predominant daytime swimming depth. These

regular excursions did not occur at night or when on-FAD. For example, these upward excursions were exhibited by fish BE8603 only after it departed S FAD and assumed a deeper off-FAD distribution (Fig. 13). The periodicity and duration of these large excursions were quite regular. For instance, 13 daytime peaks exhibited by BE8205 had a peak-to-peak interval of 57.7 minutes (± 7.0 SD) and a duration of 12.0 minutes (± 2.6 SD).

Individual fish of both species tended to adopt consistent upper and lower limits to their movements such that, even if they were making frequent upward and downward movements, these were often terminated at consistent depths or temperatures. The most common of these turnaround points was the zone encompassing the bottom of the surface mixed layer and the uppermost layers of the thermocline. Thus, in the case of yellowfin YF8305, the top of the thermocline represented the bottom of dives made from the surface and the starting and finishing points of dives made to deeper depths, most of which had a consistent "floor" around the 20°C isotherm at approximately 130 m (Fig. 10). Similarly, in addition to the well-defined temperature confines of their smaller vertical oscillations, most

of the bigeye tunas' large upward excursions consistently terminated near the interface between the thermocline and the mixed layer (Figs. 13, 14, and 15).

Examples of possible fly-glide behavior (Weihs 1973, Carey and Olsen 1982) were observed in tracks of yellowfin and bigeye tuna, a very consistent example being BE8401, which exhibited "sawtooth" oscillations with a period of approximately 4 minutes and an amplitude between 35 and 45 m for the entire 11-hour daylight segment of the track. Similar, persistent oscillating daytime behavior was exhibited by fish YF8506 as it moved on a direct course away from S FAD (Fig. 18). For instance, between 0930 and 1815 this fish swam on a straight southwesterly course at an apparently constant horizontal speed of 1.02 m/second (Fig. 5). Assuming this constant speed, the descending angles during this period averaged 6.06° (±0.7 SD, $N = 11$), and the climbing angles averaged 9.55° (±1.4 SD, $N = 11$) with 100% of the climbing angles being greater than the descending angles. Also, of the measurable oscillations occurring between 0915 and 1815, 39 out of 46 (85%) displayed longer falling than rising phases, suggesting active upward swimming followed by a comparatively passive downward glide. These oscillations were characterized by constant rates of ascent and descent, with abrupt changes in direction linking the falling and rising phases (Fig. 18).

Discussion

Using two tie wraps appears to be a satisfactory way of attaching transmitters to tunas. Transmitters attached in this way were carried successfully by four captive fish for several weeks, and one of the tracked fish was caught in good health (and still carrying the transmitter) by a fisherman 2 weeks after we terminated the track. The similarity of vertical and horizontal movements across tracks also suggests minimal alteration of normal behavior.

The association of these tuna with a daytime range, whether FAD or reef perimeter, was extremely strong. In the case of FADs, several fish spent many hours within a few meters of the mooring line. Similarly, none of the reef-associated fish made significant offshore movements during daylight hours. In fact, the alongshore movements were remarkable for their fidelity to the outer reef contour. Combining FAD-associated and reef-perimeter fish, 10 of the 15 fish tracked in this study moved within a well-defined home range during daylight hours and two other fish were lost before any diel patterns could be observed. Most of the fish made nocturnal excursions away from their respective daytime habitats. Similar, consistent diurnal behavior has been previously observed in a 44-cm skipjack tuna,
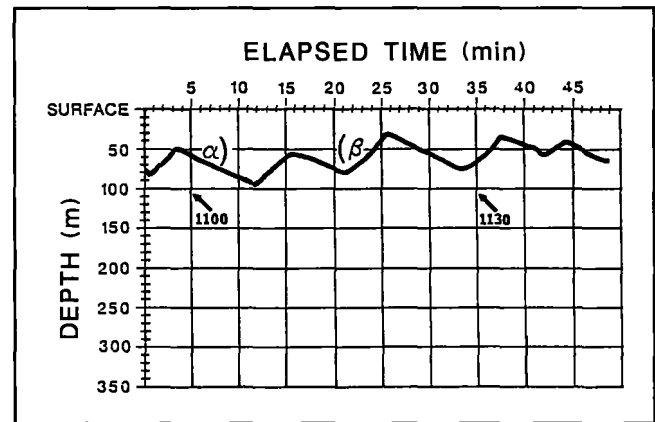
Figure 18

Yellowfin tuna YF8506 showed oscillations suggestive of "fly-glide" behavior while moving on an essentially straight course away from S FAD (cf. Fig. 5). All descending angles (a) were smaller than the climbing angles (β).

which returned to the same reef after making offshore excursions on each of six nights that it was tracked (Yuen 1970).

This skipjack tuna and the yellowfin tuna tracked in the present study represent the smaller size classes of these species. For fish of these sizes, the reef dropoff probably represents a zone of enhanced prey density where epipelagic species, such as bigeye scad *Decapturus crumenopthalmus*, mackerel scad *D. pinnulatus*, and flying fish (Exocidae), can be found in proximity to reef species which are also prey for these tunas (Hida 1973). The nighttime excursions away from the island reefs and FADs may be foraging behavior targeting on squid and shrimp, which come up from greater daytime depths and which are important components of yellowfin tuna diets (Reintjes and King 1953, King and Ikehara 1956, Brock 1985). Even though the reef-associated fish moved out into deeper water, the nighttime distribution of these yellowfin tuna was closer to the surface than their daytime depths.

The strong daytime association of yellowfin tuna with the FADs, and their nighttime excursions away from them, appears to be analogous to the behavior of island-associated fish patroling the outer reef dropoff. That is, yellowfin tuna appear to respond to FADs as outliers of the natural island topography (e.g., as offshore pinnacles). However, the FAD-associated fish may be paying an energetics penalty because the forage resource at FADs is probably considerably smaller than that available at the reef perimeter. This is indicated by the fact that yellowfin tuna caught at FAD locations have significantly smaller volumes of food in their guts and a significantly higher frequency of completely empty stomachs than do fish caught away from FADs (Brock

1985). Alternatively, it is possible that nighttime feeding excursions away from the FADs, combined with the apparently reduced daytime swimming activity at FADs as compared with reef banks, result in an energetics balance equivalent to that of better-fed, but more active, open-ocean fish or reef-perimeter fish. Even though feeding may not occur as often at FADs as in other areas, FAD-associated tuna may conserve energy normally associated with active hunting. By orienting to FADs, the fish maintain a fixed position in the current flow and may feed on current-borne prey, a situation analogous to trout holding station in a river. The predominant upcurrent orientation of FAD-associated tunas may serve to intercept incoming prey items before they can use the FAD structure for shelter. These feeding advantages would not pertain to tuna associated with logs, which drift with the current and cannot provide the function of serving as a fixed point in a stream. Thus, although logs may indicate areas of enriched forage for planktivores by marking zones of Langmuir cell convergence (Fedoryako 1982), they are unlikely to supply the high food demands of even a medium-sized school of tuna, and, in fact, small fishes found in association with logs are not an important part of the diets of tuna taken from beneath logs (Hunter and Mitchell 1967).

There are other indications that different phenomena may underlie the association of tuna with natural debris and their association with FADs. For instance, fishing techniques which take advantage of log-associated tuna indicate that in these circumstances the tuna tend to aggregate around logs at night and move away in the daytime—exactly the opposite of the behavior observed in the current study. However, in the log situations, tuna behavior may be perturbed by the use of lights placed on the logs by fishermen. Also, since tunas probably are capable of magneticaly mediated orientation (Walker 1984), and in our own study exhibited precise feats of navigation (e.g., returning to the same FAD; navigating between FADs; maintaining straight azimuths over prolonged periods of time), it is unlikely that tunas have trouble distinguishing between logs and FADs because, unlike logs, FADs are both stationary and attached to the ocean floor by visibly (and possibly, acoustically) discernible chain and rope.

The combined data yield an average nightime excursion distance of approximately 5 nmi. This would indicate that to maximize the ability of FADs to aggregate yellowfin tuna consistently, and to minimize the influence of FADs on coastline-associated populations, FADs should be placed a minimum of 5 nmi from the nearest 40-fathom bank. This interpretation is supported by the track of fish YF8504 which rapidly traversed the 3.5 nmi to the 40-fathom contour when disturbed at R FAD by a school of porpoises. Similarly, YF8405 was caught at R FAD 2 weeks after being tracked along the adjacent coastline which, at its nearest point, is between 3.5 and 4.0 nmi away. In fact, optimal FAD placement would be greater than 10 nmi offshore (or from the nearest 40-fathom bank) so that the radii of influence of the FAD and the coastline do not overlap. Frequent anecdotal observations and the impressions of Hawaiian fishermen suggest that FADs located 10 nmi offshore are more consistently productive than FADs located closer to shore.

Daytime orientation of yellowfin tuna to the top layers of the thermocline, with excursions into the mixed layer and to the surface, and a nighttime shallowing into the mixed layer, are consistent with patterns observed by Yonemori (1982) and Carey and Olson (1982). The yellowfin tuna in the current study displayed a particularly strong adherence to the interface between the surface mixed layer and the thermocline when exhibiting straight-line movements. Similar behavior has been previously noted by Carey and Olson (1982). In the present study, these "traveling" fish would often abruptly alternate between the surface and the thermocline interface, both of which might serve to assist straight-line orientation in what is otherwise a truly three-dimensional habitat. By contrast, fish orienting around FADs showed either little vertical movement or vertical movements that were sinusoidal and largely within the mixed layer.

The depth and temperature distributions derived from the bigeye tuna tracks are in good agreement with distributional data obtained by analysis of longline fishing success (Saito 1975; Hanamoto 1976, 1987). These fishery data indicate maximum abundance at depths >200 m and in temperatures between 11° and 15°C, where the dissolved oxygen is >1 mL/L. However, the tracking data suggest daytime distribution (220–240 m, 14–17°C) is influenced at least as much by temperature as by depth, and none of the catch-rate studies indicate the dramatic nighttime upward shift that the tracking data reveal.

The average sustained swimming speed derived from the straight sections of the current yellowfin tuna tracks was 4.46 Km/hour (range 3.2–6.5 Km/hour, Table 1), which is similar to the 4.27 Km/hour average (range 2.4–7.8 Km/hour) reported by Carey and Olson (1982) for fish having an average fork length 41% greater than those used in our study. This comparison would suggest that absolute traveling (sustainable) swimming speed for this species does not increase with size, at least for fish between 45 and 100 cm FL. This constancy of swimming speed, regardless of increasing fish length, is consistent with the model generated by Magnuson (1973, 1978), which predicts that increased weight associated with increasing length is

offset in this species by the allometric growth of the swim bladder, thereby precluding the need to increase hydrodynamic lift through higher swimming speeds. However, the sustained swimming speeds observed during these tracks (average of 1.24 m/second) are considerably higher than the 0.5 to 0.6 m/second predicted by Magnuson (1978) for fish of this size. Obviously, field observations of larger fish would be useful in further testing the Magnuson model.

Periods of possible fly-glide behavior were observed in sections of tracks of yellowfin and bigeye tunas. These oscillations, which in one instance (YF8506) were exhibited for the entire daylight portion of a straight azimuth track, have been hypothesized to result in a saving of energy required for locomotion between two points (Weihs 1973, Magnuson 1978). As predicted by this model, most gliding phases lasted longer than the ascending phases, and the descending and ascending legs were connected by abrupt angles, which maximize energy transfer from the gliding to the flying phase. Thus, using the "fly" angle (β) of 9.55 and "glide" angle (α) of 6.06 obtained from YF8506, and a swim/glide drag ratio (k) of 1.2 (Magnuson 1978), the equation:

$$\text{Energy saving} = 1 - \frac{\tan \alpha}{\sin \beta + (\tan \alpha \cdot \cos \beta)} \times \left(1 + \frac{1 \sin \beta}{k \sin \alpha}\right)$$

results in an energy saving of 9.4% compared with level swimming over the same distance. And, where T is the increased time to travel the same distance using a fly/glide strategy as opposed to level swimming, using the equation

$$T = \frac{\sin \alpha + \sin \beta}{\sin (\alpha + \beta)}$$

indicates that this strategy results in only a 0.9% increase in time to travel the same distance.

The extremely regular, large, upward excursions made by all the off-FAD bigeye tuna during daylight hours may represent behavioral thermoregulation. At the low (14–17°C) ambient temperatures adopted by these fish, their core temperatures possibly drop below some threshold level which requires movement into warmer water to regain optimum body temperatures. If this is the case, it would suggest that there exists a strong motivation for inhabiting the deep cold layers observed during these tracks. A possible motivation would be the opportunity to feed on deepwater fish, squid, and crustaceans which the bigeye tuna then follow into shallower depths at night when these prey

organisms migrate toward the surface. Monitoring the core muscle temperatures of bigeye tuna would indicate if, in fact, the large upward excursions are a form of behavioral thermoregulation which, when combined with physiological thermoconservation, allows these fish to exploit an otherwise unreachable resource.

Acknowledgments

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