

**Abstract**—Ninety-six bigeye tuna (88–134 cm fork length) were caught and released with implanted archival (electronic data storage) tags near fish-aggregating devices (FADs) in the equatorial eastern Pacific Ocean (EPO) during April 2000. Twenty-nine fish were recaptured, and the data from twenty-seven tags were successfully downloaded and processed. Time at liberty ranged from 8 to 446 days, and data for 23 fish at liberty for 30 days or more are presented. The accuracy in geolocation estimates, derived from the light level data, is about 2 degrees in latitude and 0.5 degrees in longitude in this region. The movement paths derived from the filtered geolocation estimates indicated that none of the fish traveled west of 110°W during the period between release and recapture. The null hypothesis that the movement path is random was rejected in 17 of the 22 statistical tests of the observed movement paths. The estimated mean velocity was 117 km/d. The fish exhibited occasional deep-diving behavior, and some dives exceeded 1000 m where temperatures were less than 3°C. Evaluations of timed depth records, resulted in the discrimination of three distinct behaviors: 54.3% of all days were classified as unassociated (with a floating object) type-1 behavior, 27.7% as unassociated type-2 behavior, and 18.7% as behavior associated with a floating object. The mean residence time at floating objects was 3.1 d. Data sets separated into day and night were used to evaluate diel differences in behavior and habitat selection. When the fish were exhibiting unassociated type-1 behavior (diel vertical migrations), they were mostly at depths of less than 50 m (within the mixed layer) throughout the night, and during the day between 200 and 300 m and 13° and 14°C. They shifted their average depths in conjunction with dawn and dusk events, presumably tracking the deep-scattering layer as a foraging strategy. There were also observed changes in the average nighttime depth distributions of the fish in relation to moon phase.

## Movements, behavior, and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags

Kurt M. Schaefer

Daniel W. Fuller

Inter-American Tropical Tuna Commission

8604 La Jolla Shores Drive

La Jolla, California 92037-1508

E-mail address (for K. M. Schaefer): kschaefer@iattc.org

Bigeye tuna (*Thunnus obesus*) occur in subtropical and tropical oceanic waters throughout the world, except in the Mediterranean Sea (Collette and Nauen, 1983; Collette et al., 2001). They are captured by longliners operating in the eastern Pacific Ocean (EPO) from about 40°N to 40°S and by purse seiners from about 5°N to 10°S (Miyabe and Bayliff, 1998; Bayliff, 2000). They are economically the most important species of tuna harvested by longline fisheries in the EPO. The estimated average catch of bigeye tuna by the longline fleets of Japan, Taiwan, and the Republic of Korea in the EPO has declined from an average of about 79 thousand metric tons (t) during 1985–94 to about 40 thousand t during 1995–98 (Bayliff, 2000). The longline fishery targets medium to large bigeye tuna. There is a growing purse-seine fishery that catches primarily small to medium bigeye tuna, most of which are associated with drifting fish-aggregating devices (FADs). The purse-seine catch in the EPO has dramatically increased from an estimated annual average of about 5 thousand t during 1964–93, to about 45 thousand t during 1994–98 (Bayliff, 2000; Lennert-Cody and Hall, 2000). There is concern that the longline fishery is being adversely affected by the purse-seine fishery and that current catch rates are not sustainable (Watters and Maunder, 2001).

Elucidating the environmental variables that define bigeye tuna habitat can be used to adjust gear vulnerability, to standardize catch and effort data, and thus improve bigeye tuna stock assessments (Brill, 1994; Hinton

and Nakano, 1996; Brill and Lutcvage, 2001; Hampton et al.<sup>1</sup>). It is also necessary to understand the affinity of bigeye tuna to drifting FADs, now a common feature of their habitat in the equatorial EPO, and to quantify the effect of FAD densities on vulnerability to capture. Sonic tracking studies (Holland et al., 1990; Holland et al., 1992; Daggorn et al., 2000), along with studies of catches per unit of effort (CPUEs) by longlines (Suzuki and Kume, 1982; Hanamoto, 1987; Boggs, 1992; Nakano et al., 1997) have provided information on differences in depth and temperature distributions for bigeye tuna by size and time of day.

Studies of fine-scale movements and short-term behavior, based on data from acoustic tags, have been reported for bigeye tuna associated with anchored FADs (Holland et al., 1990) and in the open ocean (Dagorn et al., 2000), but not for fish associated with drifting FADs. Bigeye tuna tend to stay within close proximity of anchored FADs during the day, move away at night, and return the next morning (Holland et al., 1990). When not associated with FADs, they swim within the mixed layer above the thermocline at night and well below the thermocline during

<sup>1</sup> Hampton, J., K. Bigelow, and M. Labelle. 1998b. Effect of longline fishing depth, water temperature and dissolved oxygen on bigeye tuna (*Thunnus obesus*) abundance indices. Working Paper 17, 18 p. Eleventh meeting of the standing committee on tuna and billfish, Sec. Pac. Comm., Noumea, New Caledonia. Oceanic Fisheries Programme, SPC, B.P. D5, 98848 Noumea Cedex, New Caledonia.

the day (Holland et al., 1990; Dagorn et al., 2000). They are capable of exploiting cold, deep waters below the thermocline because of their unique anatomy (Graham and Dickson, 2001), which enables them to physiologically and behaviorally thermoregulate by making vertical forays into the warm mixed layer throughout the day to increase their body temperatures (Holland et al., 1992, Holland and Sibert, 1994). Apparent differences in behavioral patterns of tunas around anchored FADs versus drifting FADs have been discussed, but almost no empirical results have been reported (Holland et al., 1990; Dagorn et al., 2000).

Although conventional and sonic tagging studies, and those on depth, temperature, and time of capture with longline gear, have provided valuable information on bigeye tuna biology and ecology, the present generation of archival (electronic data storage) tags can further our understanding of bigeye tuna movement, behavior, and habitat selection. Archival tags record swimming depth, internal and external temperatures, and ambient light levels. The light data can be processed to provide daily estimates of latitudes and longitudes (Hill, 1994; NMFS, 1994; Welch and Eveson, 1999; Hill and Braun, 2001).

This study presents results from analyses of data recorded by archival tags recovered from bigeye tuna that were released in the equatorial EPO during April 2000. An evaluation of the accuracy and precision of the geolocation estimates derived from the archival tag data is provided. Descriptions of movement and behavioral patterns, and also habitat characteristics of bigeye, are presented.

## Materials and methods

### Tag releases

Bigeye tuna were captured, tagged, and released at three FADs in the equatorial EPO between 0°52' and 2°01'N and between 95°24' and 97°06'W, during the period of 15–22 April 2000. Tagging was conducted on the chartered FV *Her Grace*, a 17.7-m, 99 gross-t, United States west-coast-style live-bait pole-and-line vessel. The FADs were taken out of the water before the vessel left the tagging area in order to minimize the probability of short-term recaptures, and to permit the fish to disperse.

The archival tags used in this study were model Mk7 manufactured by Wildlife Computers (Redmond, WA) (Wildlife Computers, 2002). The total weight of a tag in air is about 32 g. The Mk7 tag is designed for implantation into the peritoneal cavity of the fish so that the sensor stalk protrudes outside the fish through an incision in the abdominal wall. A label, printed in Spanish, with information about reporting the recovery of the tag and the associated reward (US\$500) was encased in the epoxy of the main body of the instrument.

The depth, internal and ambient temperatures, and light level were stored in the memory of the tag every 4 minutes. At this sampling rate, the memory of each tag (2 MB) was capable of storing 3.8 years of data. The pressure sensors measured over a range of –40 to 1000 m with 0.5-m resolution. The temperature sensors measured over

a range of –40° to 60°C with 0.05°C resolution. The light sensors had a logarithmic range from  $3 \times 10^{-10}$  W.cm<sup>-2</sup> to  $1 \times 10^{-2}$  W.cm<sup>-2</sup>. Bright sunshine is approximately  $2 \times 10^{-3}$  W.cm<sup>-2</sup>. Light-level readings of about 200 and 50 are observed in bright sunshine and in complete darkness, respectively. Exploratory analyses of our data indicated that the light sensor is able to identify dawn and dusk events at 300 m.

Each tag was rigorously tested and evaluated at sea before deployment in bigeye tuna. Tags were programmed to collect data from all four sensors at one-second intervals, placed in a nylon mesh bag with a Sea-Bird SBE-39 temperature-depth probe, and sent down to approximately 300 m. After retrieval, the data were downloaded from each tag and their performance was evaluated in relation to the temperature-at-depth data collected by the Sea-Bird SBE-39.

Bigeye tuna specimens were captured by using handline gear during the day and night. Each fish was brailed with a heavy-gauge aluminum rigid-framed net of knotless webbing and landed on a wet foam pad covered with smooth vinyl. The eyes of the fish were immediately covered with a wet synthetic chamois, the hook was removed, and the condition of the fish was determined. If the fish was in excellent condition (i.e. no damage to the eyes or gills and no significant bleeding), the surgery required for implanting the archival tag was initiated. An incision about 2 cm long was made in the abdominal wall about 10 cm anterior of the anus and about 2 cm to the left of the centerline of the fish. Special care was taken to cut through the dermis only and partially through the muscle, but not into the peritoneal cavity. A gloved finger was inserted into the incision and forced through the muscle into the peritoneal cavity. The tag, sterilized by soaking it in Betadine solution, was inserted, pointed end first, through the incision into the peritoneal cavity. The tag was then manipulated to the caudal end of the incision, and two sutures were placed rostral of where the stalk protruded to close the incision by using a sterile needle and suture material (Ethicon (PDS II) size 0, cutting cp-1, 70 cm).

Fish were also tagged with two serially numbered 12.5-cm green plastic dart tags (Hallprint, Pty., Holden Hill, Australia) by using tubular stainless steel applicators. Tags were inserted into the dorsal musculature with the barbed heads passing between the pterygiophores below the base of the second dorsal fin, from both sides of the fish. Information for reporting the recovery of the fish and for receiving the reward (US\$500) for the return of the fish was printed in Spanish on these tags. Lastly, five to ten mL of 100-mg/mL oxytetracycline hydrochloride solution were injected into the dorsal musculature with a disposable automatic vaccinator.

The 96 bigeye tuna released with archival tags were measured to the nearest centimeter with a caliper (mean=109.2 cm FL, 95% CI=1.9 cm, range=88–134 cm). The fish were then picked up by hand and released back into the sea by one or more individuals standing in a rack at the stern of the vessel. The total time most of the fish were out of the water was recorded to the nearest second (mean=2:17, 95% CI=0:06, range=1:27–4:19, n=86). All

**Table 1**

Release and recapture information for 28 bigeye tuna from which archival tags were recovered. The fish lengths are those measured at release. The locations are given in decimal degrees (dd).

Tag no.	Fish length (cm)	Release			Recapture			Days at liberty
		Location (dd)		Date	Location (dd)		Date	
99-787	115	0.87 N	97.10 W	15 Apr 00	1.72 N	83.08 W	22 Aug 00	128.7
99-792	126	0.87 N	97.10 W	15 Apr 00	1.35 N	95.82 W	15 Oct 00	182.7
99-793	114	0.87 N	97.10 W	15 Apr 00	2.25 N	97.25 W	21 Mar 01	339.7
99-801	112	1.47 N	96.97 W	17 Apr 00	1.47 N	90.72 W	06 Jul 00	79.8
99-803	113	2.02 N	95.40 W	22 Apr 00	2.20 N	102.72 W	26 Jul 00	94.1
99-804	104	1.47 N	96.97 W	17 Apr 00	4.80 N	105.42 W	23 Dec 00	249.6
99-810	120	2.02 N	95.40 W	22 Apr 00	1.65 S	93.17 W	18 Jun 00	56.0
99-812	116	2.02 N	95.40 W	22 Apr 00	0.55 N	109.00 W	29 Sep 00	159.1
99-814	120	2.02 N	95.40 W	22 Apr 00	1.42 N	88.93 W	13 Jul 01	446.1
99-816	122	2.02 N	95.40 W	22 Apr 00	1.78 N	97.60 W	30 May 00	37.1
99-817	106	1.47 N	96.97 W	17 Apr 00	1.12 S	95.87 W	18 Jun 00	61.7
99-826	119	1.47 N	96.97 W	17 Apr 00	0.50 N	101.52 W	14 Jan 01	271.8
99-835	109	2.02 N	95.40 W	22 Apr 00	1.20 N	99.68 W	18 Jun 00	56.1
99-839	109	1.47 N	96.97 W	17 Apr 00	2.33 S	95.75 W	12 Jun 00	55.8
99-847	102	1.47 N	96.97 W	17 Apr 00	1.77 N	97.23 W	29 May 00	41.7
99-853	103	2.02 N	95.40 W	22 Apr 00	1.20 N	99.68 W	18 Jun 00	56.1
99-860	104	1.47 N	96.97 W	17 Apr 00	2.18 S	97.87 W	10 Jun 00	53.7
99-861	110	1.47 N	96.97 W	17 Apr 00	2.23 S	96.67 W	04 May 00	16.8
99-862	93	1.72 N	96.80 W	18 Apr 00	1.77 S	94.80 W	21 Jun 00	63.7
99-864	110	2.02 N	95.40 W	22 Apr 00	2.70 N	97.87 W	17 May 00	24.1
99-865	101	1.47 N	96.97 W	17 Apr 00	2.67 S	99.05 W	15 Jun 00	58.6
99-869	113	1.08 N	97.08 W	16 Apr 00	4.85 N	103.18 W	07 Aug 00	112.4
99-874	108	1.47 N	96.97 W	17 Apr 00	2.70 N	97.87 W	17 May 00	29.8
99-877	88	1.08 N	97.08 W	16 Apr 00	2.77 S	99.20 W	08 May 00	21.4
99-883	116	1.93 N	96.55 W	19 Apr 00	1.60 S	95.55 W	18 Jun 00	59.7
99-884	102	0.87 N	97.10 W	15 Apr 00	1.12 N	86.18 W	01 Jul 01	441.7
99-889	112	1.08 N	97.08 W	16 Apr 00	0.37 N	98.58 W	02 Jul 00	76.4
99-891	124	2.02 N	95.40 W	22 Apr 00	0.25 S	92.88 W	01 May 00	8.1

fish released with archival tags were observed to swim rapidly down and away from the vessel after release, and all appeared to be in excellent condition.

### Tag recoveries

Twenty-nine of the 96 bigeye released with archival tags were recaptured by 4 October 2001. Twenty-eight archival tags were recovered, and the data from twenty-seven were successfully downloaded and processed. The fish lengths, release and recapture positions, and number of days at liberty of the twenty-eight fish from which archival tags were recovered are given in Table 1. Twenty-five of the tags were recovered from fish caught by purse-seine vessels during sets on FADs. Scientific observers were aboard these purse-seine vessels, thus providing verification of recapture information. Three fish, from which archival tags (99-793, 99-812, and 99-865) were recovered, were recaptured by longline vessels without scientific observers aboard.

### Data processing

Data were downloaded, decoded, and processed by using software provided by the tag manufacturer (Wildlife Computers, 2002). Light-level data were used to obtain daily position estimates for each fish and ranges of uncertainty about those estimates (Hill, 1994; Hill and Braun, 2001). The accuracy and precision of the position estimates were evaluated by calculating the differences between the known recapture locations for 21 bigeye tuna, determined by global-positioning systems (GPS) aboard the fishing vessels, and the corresponding geolocation estimates.

Two criteria were used for filtering (accepting or rejecting) daily geolocation estimates. The first was based on the uncertainty associated with estimates of latitude for the days of recapture, and the second was based on the distance between geolocation estimates for consecutive days. Those daily estimates in which the range between the north and south errors was greater than 6° or the location was farther than 4° in latitude from that for the

previous day were considered improbable and excluded from further analyses. For the 22 bigeye tuna at liberty for at least 30 days, this filtering procedure retained an average of 48.8% (95%CI=7.8%, range=15.3% to 76.5%) of the daily geolocation estimates. This procedure provided data sets of geolocation estimates throughout the period of time at liberty for each fish, about which we have a high level of confidence based on the expected accuracy and precision of these data (accuracy being the closeness of geolocation estimates to the actual position and precision the closeness or dispersion of repeated estimates [Kendall and Buckland, 1982]).

Each set of filtered geolocation estimates for individual bigeye tuna was integrated into a Geographic Information System (GIS). The animal movement analyst extension (AMAE) (Hooge and Eichenlaub, 1997; Hooge, et al.<sup>2</sup>) and the ArcView (Environmental Systems Research Institute, Inc., Redlands, CA) GIS program were used for mapping movement paths and for performing various spatial analyses of the data. The site-fidelity test in AMAE, employing 1000 random walks, was used to test the null hypothesis of random movement. The test is a modified Monte Carlo random walk, starting at the location of release, constrained by the coastline, and uses the actual sequence of distances between geolocation estimates to determine walk points. The fixed kernel home range model in the AMAE, which incorporates a least-squares cross-validation smoothing function, was used to assess probabilistic home ranges of fish for which the null hypothesis was rejected in the site-fidelity test. The 95% and 50% utilization distributions (probability contours) were chosen to describe the areas probably used (95%) and the probable core areas (50%) of activity, respectively, of individual fish.

For fish at liberty for 30 d or more, the behavior for each day at liberty was classified as unassociated (with a floating object) type-1, unassociated type-2, or associated with a floating object. Type-1 behavior is defined as that in which the fish primarily occupies the mixed layer during the night, descends at dawn below the thermocline to depths greater than 100 m and remains below 100 m throughout the day (aside from vertical forays into the mixed layer with a frequency of no more than 12 per day) and then ascends back into the mixed layer at dusk. This basic pattern has been described by Holland et al. (1990) and Dagorn et al. (2000), based on sonic tracking studies of bigeye tuna. Data from periods immediately after release at FADs until the time the FADs were removed and the data immediately preceding recapture at FADs were evaluated to determine criteria for classifying behavior of fish associated with floating objects. The percentages of time that 19 bigeye tuna spent at depths greater than 50 m, within 24-h intervals, for a total of 74 days, ranged from

0.0% to 29.1%. Sixty-nine percent of the 24-h intervals indicated that 16% or less time was spent below 50 m. The days when the fish were below 50 m for 16% of the time or less were classified as behavior associated with a floating object, and the days in which that time was greater than 16% were classified as unassociated type-2 behavior. For each fish, the numbers and durations of each behavioral event were determined throughout the period at liberty. A statistical test for a difference between the spatial distributions of the geolocation estimates for unassociated and associated behavior was conducted (Syrjala, 1996).

Dives in excess of 500 m were classified as deep dives, and the time, duration, and maximum depth of each event was determined for each bigeye tuna throughout periods at liberty. For those dives in which the pressure sensor reached its limit, at approximately 1000 m, depth was estimated from the ambient temperature value recorded by the tags by using historical annual mean temperatures at depths for the area of the deep diving event (Levitus and Boyer, 1994). The light level and ambient temperature data recorded by tags from bigeye tuna making dives in excess of 500 m indicated that light was essentially nonexistent below 500 m and that the ambient temperature was less than 8.5°C.

The archival tag data sets (for each recaptured bigeye tuna at liberty for at least 30 d) were separated into periods of nighttime and daytime by using light-level records. Nighttime was classified as the period between the time of the first record after dusk when there was no recognizable light from the sun until the time of the last record (before dawn) of no recognizable light from the sun. The individual data sets for night and day were used in evaluations of diel differences in behavior and habitat selection. The data for each night were classified by the moon phase (U. S. Naval Observatory, 2001). The classification scale used was 1 through 29 for the entire moon phase cycle. We analyzed changes in average daytime and nighttime depths for 20 individual bigeye tuna in relation to the visible disk area of the moon.

## Results

### Behavior

Evaluation of the depth and temperature records for bigeye tuna carrying archival tags resulted in the discrimination of four distinct behaviors: 1) unassociated type-1, 2) unassociated type-2, 3) associated with a floating object, and 4) deep diving. For the 23 fish at liberty for 30 or more days, behavior was classified for each day at liberty, and the duration of each behavior was determined (Table 2).

The behaviors of fish released or recaptured at FADs were distinct and discernible from the behaviors after the FAD was removed until the fish associated with the FAD at which it was recaptured (Fig. 1). Fish released at FADs showed a consistent swimming depth, predominantly less than 50 m during the night and day. When the FAD was removed fish showed an erratic up-and-down swimming behavior, followed by a consistent pattern of shallow (less

<sup>2</sup> Hooge, P. N., W. Eichenlaub, and E. K. Solomon. 2001. Using GIS to analyze animal movements in the marine environment. *In* 2001, spatial processes and management of marine populations (G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith, and D. Witherell, eds.), 20 p. Univ. Alaska Sea Grant, P.O. Box 755040, Fairbanks, AK 99775-5040.

**Table 2**

Summary statistics for the classification of daily behavior of 23 bigeye tuna at liberty for 30 days or more. The definitions for the four behavioral types and the classification criteria used are given in the text. The percentage of the total days at liberty for which an individual was classified as exhibiting a behavioral type is given as % days. The total number of events observed and classified in each dataset for a behavioral type and the mean duration for those events are given. Durations are given in days, except for deep diving events, which are given in hours.

Tag no.	Unassociated type-1			Unassociated type-2			Associated			Deep diving	
	% days	events	$\bar{x}$ duration	% days	events	$\bar{x}$ duration	% days	events	$\bar{x}$ duration	events	$\bar{x}$ duration
99-787	64.7	8	10.4	22.5	8	3.6	12.8	5	3.3	1	0.9
99-792	37.6	16	4.3	41.9	15	5.1	37.5	5	7.5	14	1.5
99-793	41.0	19	7.0	49.9	24	6.5	9.2	7	4.1	4	2.2
99-801	64.5	5	10.3	13.5	3	3.6	22.0	4	4.4	5	1.2
99-803	59.2	7	8.0	15.9	6	2.5	24.9	7	3.4	2	1.1
99-804	41.9	13	5.7	45.7	14	5.7	12.3	6	3.6	5	0.5
99-810	79.0	5	8.9	2.6	2	0.7	18.4	6	1.7	6	0.7
99-812	49.9	20	4.0	34.6	19	2.9	15.4	10	2.5	10	1.7
99-814	48.5	41	4.3	43.9	43	3.7	7.6	12	2.3	22	1.7
99-816	68.1	3	8.5	30.6	3	3.8	1.3	1	0.5	5	1.1
99-817	43.4	5	5.4	33.3	6	3.4	23.3	4	3.6	1	0.7
99-826	59.5	18	9.0	33.0	18	5.0	7.5	6	3.4	10	1.0
99-835	79.5	4	11.2	1.5	2	0.4	19.0	4	2.7	0	—
99-839	70.3	5	7.9	8.9	3	1.7	20.8	3	3.9	3	1.7
99-847	35.3	6	2.5	38.0	6	2.7	26.7	3	3.7	0	—
99-860	45.4	7	3.5	40.4	5	4.4	14.2	5	1.5	0	—
99-862	50.2	5	6.4	10.8	5	1.4	39.0	7	3.6	3	0.6
99-865	52.0	5	6.1	22.3	8	1.6	25.7	5	3.0	7	1.0
99-869	42.2	8	6.0	38.6	6	7.3	19.2	5	4.3	0	—
99-874	36.0	2	5.4	35.5	4	2.7	28.5	4	2.1	1	0.3
99-883	69.6	7	6.0	14.4	7	1.2	16.0	5	1.9	5	1.0
99-884	41.4	25	5.3	40.0	31	4.1	18.6	23	2.6	10	1.0
99-889	69.6	6	8.9	20.4	7	2.2	10.0	3	2.6	3	2.3
Mean	54.3	10.4	6.7	27.7	10.7	3.3	18.7	6.1	3.1	5.1	1.2
95%CI	6.1	4.0	1.0	6.2	4.5	0.8	4.0	1.9	0.6	2.3	0.3

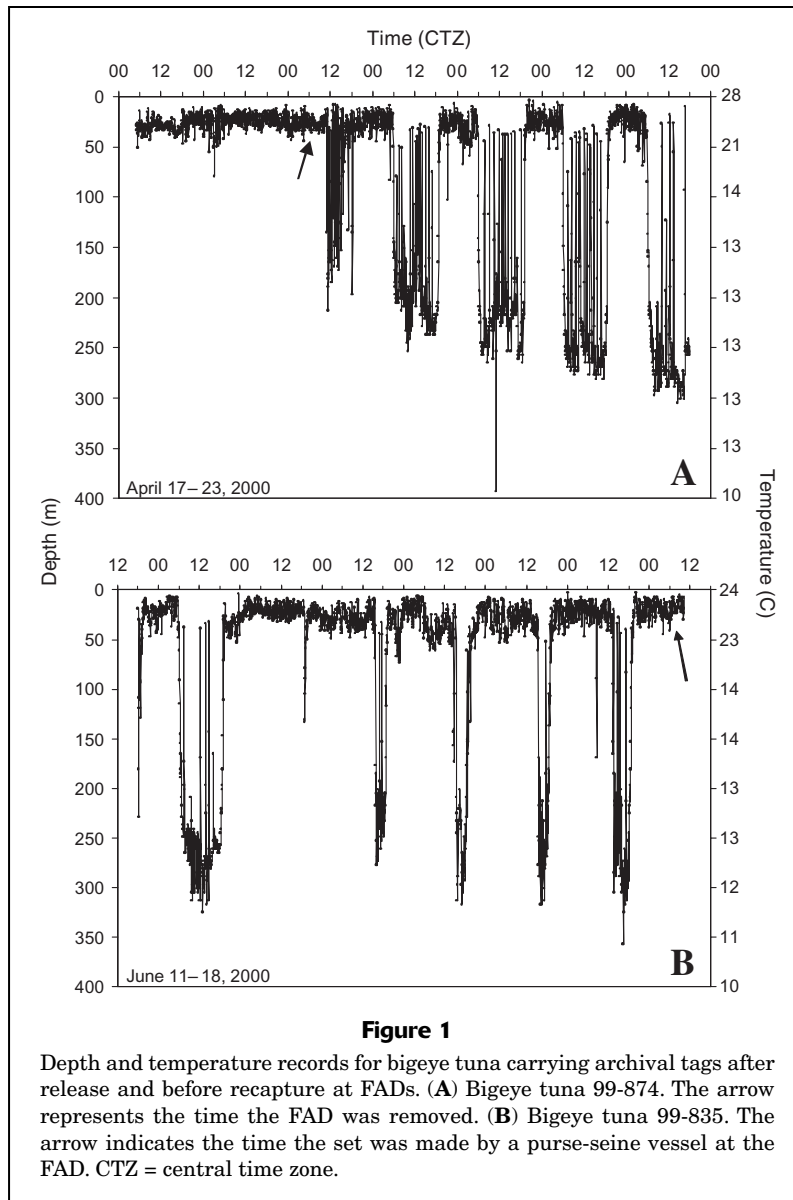
than about 50 m) depths at nighttime and depths of about 200 to 300 m during the daytime (during the latter period vertical forays were made toward the surface [Fig. 1A]). Fish at FADs prior to recapture consistently swam at less than 50 m during the day and night, but made excursions to depths of 200 to 300 m for about 2 hours in the late afternoon. It was almost always apparent when a fish associated with a FAD because there was a change in swimming depths and behavior, specifically during the daytime (Fig. 1B).

### Unassociated type-1 behavior

Type-1 behavior of bigeye tuna in the equatorial EPO was exhibited by fish not associated with FADs or other floating objects. The fish remained at 10 to 50 m at night and at 200 to 350 m during the day but undertook brief vertical forays into the mixed layer throughout the day (Fig. 2). The percentage of total days classified as type-1 behavior for individual fish ranged from 35.3% to 79.5% (mean=54.3%, 95% CI=6.1%). The mean duration of type-1

behavior ranged from 2.5 to 11.2 d (grand mean=6.7 d, 95% CI=1.0 d) (Table 2). The distribution of the durations of the 240 type-1 behaviors is shown in Figure 3A.

The differences in behavior between a 93-cm (tag 99-862) and 116-cm (tag 99-883) bigeye tuna within one week after release at the same FAD, both exhibiting type-1 behavior, are illustrated in Figure 4. Both fish showed the characteristic diel shifts in depth distribution at dawn and dusk. However, the 116-cm fish showed a shallower and less variable swimming depth at night and undertook fewer vertical forays during the daytime than did the 93-cm fish (Fig. 4A). The difference in the number of vertical forays by these two fish is explained by the more rapid rate of heat loss by the smaller individual, as indicated by the differences between the peritoneal cavity temperatures and the ambient temperatures (Fig. 4B). The 116-cm fish was able to maintain its internal temperature for longer periods of time. Thus, although these two fish were at similar maximum depth during the day, the average depth during the day for the 93-cm fish was less because of the increased time spent undergoing vertical forays.



### Unassociated type-2 behavior

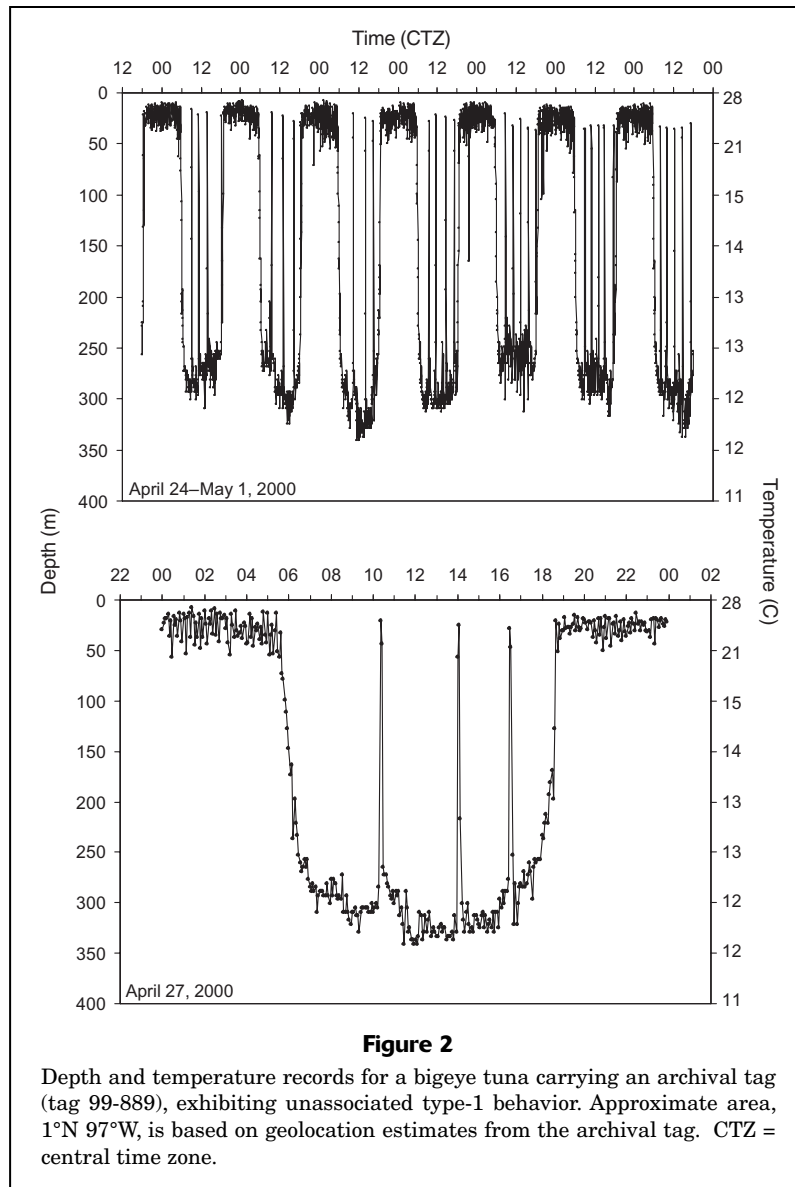
Type-2 behavior was defined as the behavior of fish that did not undergo the diel shifts in swimming depths at dawn and dusk but remained at depths in excess of 50 m for more than 16% of the time during a 24-h period (Fig. 5). The percentage of total days classified as type-2 behavior for individual fish ranged from 1.5% to 49.9% (mean=27.7%, 95% CI=6.2%). The mean duration of type-2 behavior for individual fish ranged from 0.4 to 7.3 d (grand mean=3.3 d, 95% CI=0.8 d) (Table 2). The distribution of the durations for each of the 245 type-2 behaviors is shown in Figure 3B.

### Behavior associated with floating objects

Behavior associated with floating objects was defined as the behavior of fish that remained below 50 m for no more than

16% of the time throughout a 24-h period (Fig. 6). Although bigeye tuna mostly remained in the mixed layer while associated with floating objects, there was, nevertheless, a prominent diel cycle in the average depth distribution—from shallower at night to slightly deeper during the day (Fig. 6). The mean swimming depths for the data illustrated in Figure 6 are 27.7 m at night and 33.5 m during the day. The percentage of total days classified as associated behavior for individual fish ranged from 1.3% to 39.0% (mean=18.7%, 95% CI=4.0%). The mean duration of associated behaviors for individual fish ranged from 0.5 to 7.5 d (grand mean=3.1 d, 95% CI=0.6 d) (Table 2). The distribution of the durations of the 140 associated behaviors is shown in Figure 3C.

An examination of the classification of daily behavioral types by individual fish sorted by lengths (Table 2) indicated that a greater percentage of time was spent at FADs by bigeye tuna less than 110 cm in length (mean=23.3%,



$n=9$ ), even though the larger fish (mean=16.2%,  $n=12$ ) still had an obvious affinity for floating objects.

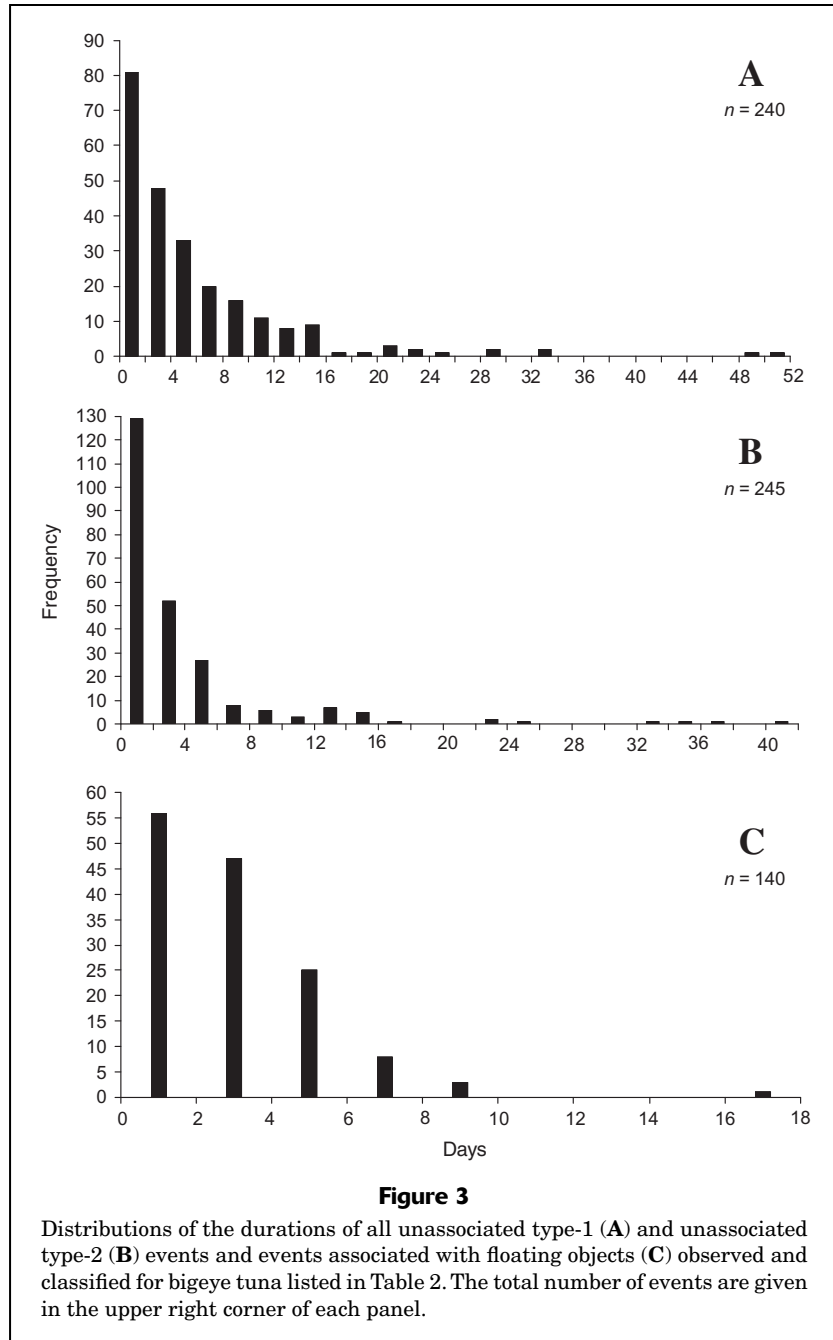
### Deep-diving behavior

Deep-diving behavior was defined as dives in excess of 500 m (Fig. 7). The mean duration of deep-diving behaviors for individual fish ranged from 0.3 to 2.3 h (grand mean=1.2 h, 95% CI=0.3 h) (Table 2). The distributions of the time of day, duration, and maximum depth of the 115 deep-diving events are shown in Figure 8. The majority of the deep dives occurred during daylight hours (mean=11:56 central time zone [CTZ]), although some deep dives were made at night. The prominent mode in the maximum depth distribution was about 650 to 850 m. The estimated maximum depth and minimum temperature reached by three bigeye tuna (99-801, 99-803, and 99-889) were 1500 m and 3°C, respectively.

### Reliability of the geolocation estimates

The estimated mean accuracy and precision in the geolocation estimates of latitude were 2.04 and 0.79 degrees, respectively (Table 3). The associated uncertainty in those estimates averaged 2.57 degrees (95% CI=0.85) for the south error and 3.40 degrees (95% CI=1.00) for the north error. The estimated mean accuracy and precision of the geolocation estimates for longitude was 0.46 and 0.26 degrees, respectively (Table 3). The associated uncertainty in those estimates averaged 0.33 degrees (95% CI=0.13) for the west error and 0.17 degrees (95% CI=0.13) for the east error.

Additional information on the accuracy and precision of the estimates from the processed archival tag light-level data was obtained by comparing the differences between estimates and actual latitudes and longitudes of recapture for tags 99-864 and 99-874 (Table 3). The two bigeye tuna

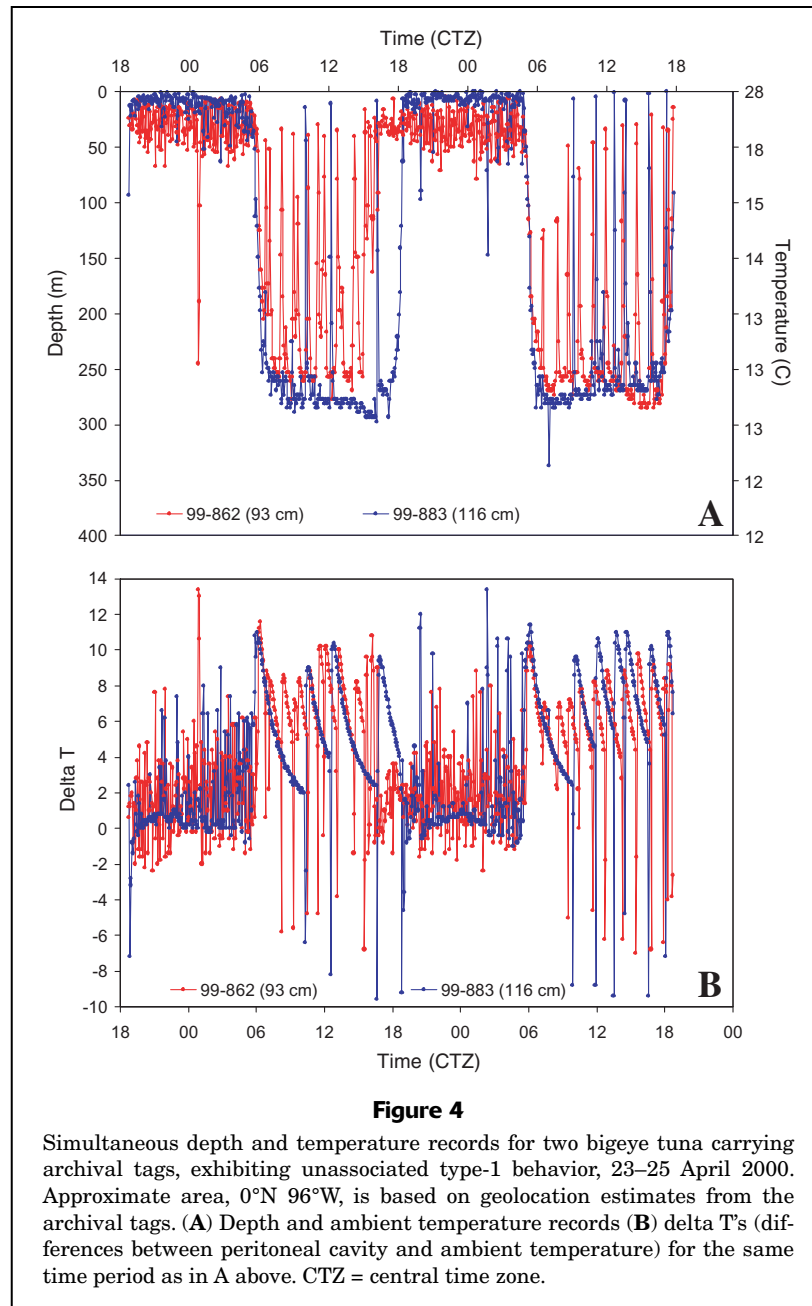


carrying these tags were recaptured at the same location in the same purse-seine set. The respective differences between estimates and actual values were 0.20 and 0.30 for latitude and 0.23 and 0.06 for longitude. We also noted that the differences between estimated and actual latitudes and longitudes were 1.95 and 0.29, respectively, for the fish with tag 99-812, and 2.67 and 0.28, respectively, for the fish with tag 99-865 (Table 3). These two fish carrying these tags were recaptured by longline vessels, and scientific observers were not aboard to verify recapture positions.

Aside from the large differences between the estimates and actual recapture latitudes in Table 3 for tag numbers 99-801, 99-847, and 99-891, the majority of the estimates were within 2 degrees of the actual latitudes. Tags 99-792, 99-835, 99-861, and 99-877 were the only tags that provided differences more than 1 degree between the estimates and actual recapture longitudes.

Fish with tags 99-792, 99-793, 99-804, and 99-826 were at liberty during the autumn equinox. The geolocation estimates for longitude were unaffected by this event, but the estimates for latitude were unreliable for a few weeks





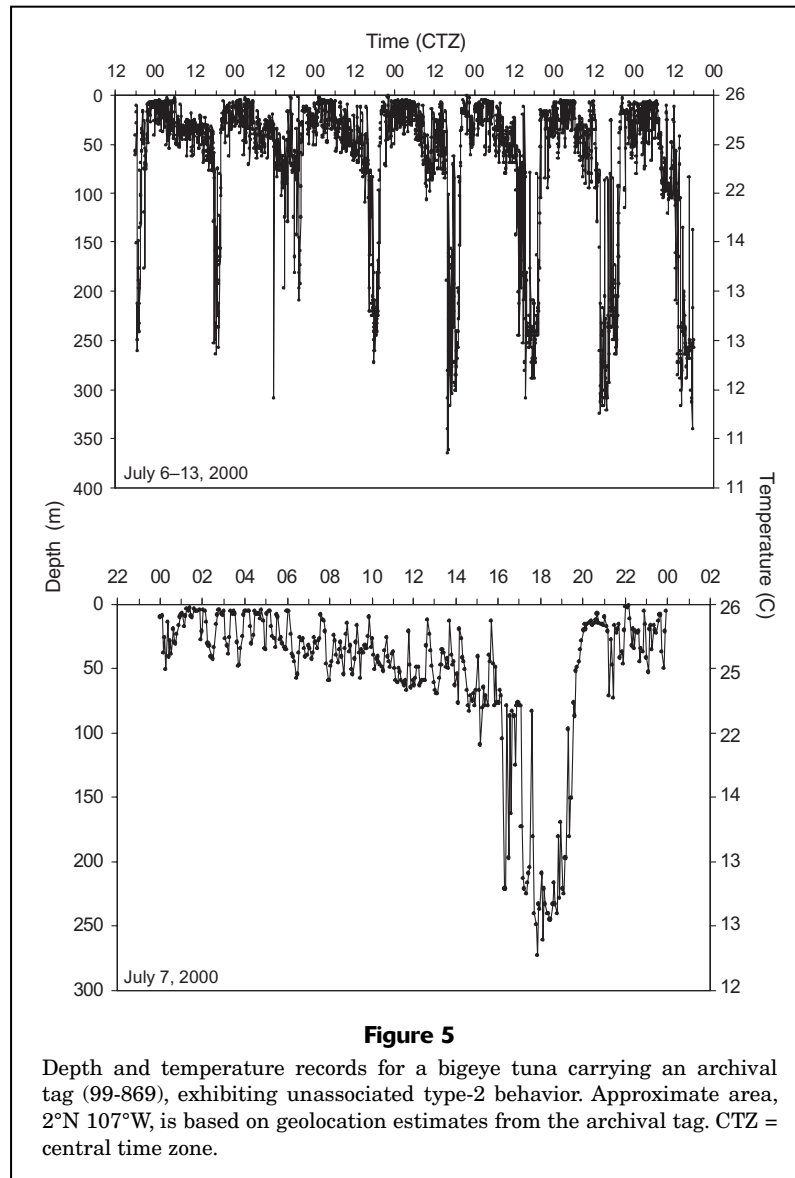
surrounding the autumn equinox because there was very little variation in day length near the spring and autumn equinoxes (Hill and Braun, 2001).

### Movements

The movements of 8 bigeye tuna at liberty for 76 to 340 days are plotted in Figure 9, A–D. No bigeye tuna went farther west than about 110°W and most spent the majority of time between 90°W to 105°W and 5°N to 5°S. Data for the estimated movement paths of 22 fish, derived from the filtered geolocation estimates, are given in Table 4. The

estimated mean speeds ranged from 76 to 165 km/d (grand mean=116.6 km/d, 95% CI=10.0 km/d). The hypothesis that the observed movement path is random was rejected for 17 of the 22 fish (Table 4). A significant positive correlation ( $r=0.61$ ,  $P<0.05$ ) was found between the number of days at liberty and their corresponding 95% utilization distributions (Tables 1 and 4).

The areas encompassed by the 95% probability ellipses for the geolocation estimates of unassociated behavior and behavior associated with floating objects (Fig. 10), for the 22 bigeye tuna at liberty for 30 d or more (Table 4), were 3.9 and  $3.1 \times 10^6$  km<sup>2</sup>, respectively. The difference between

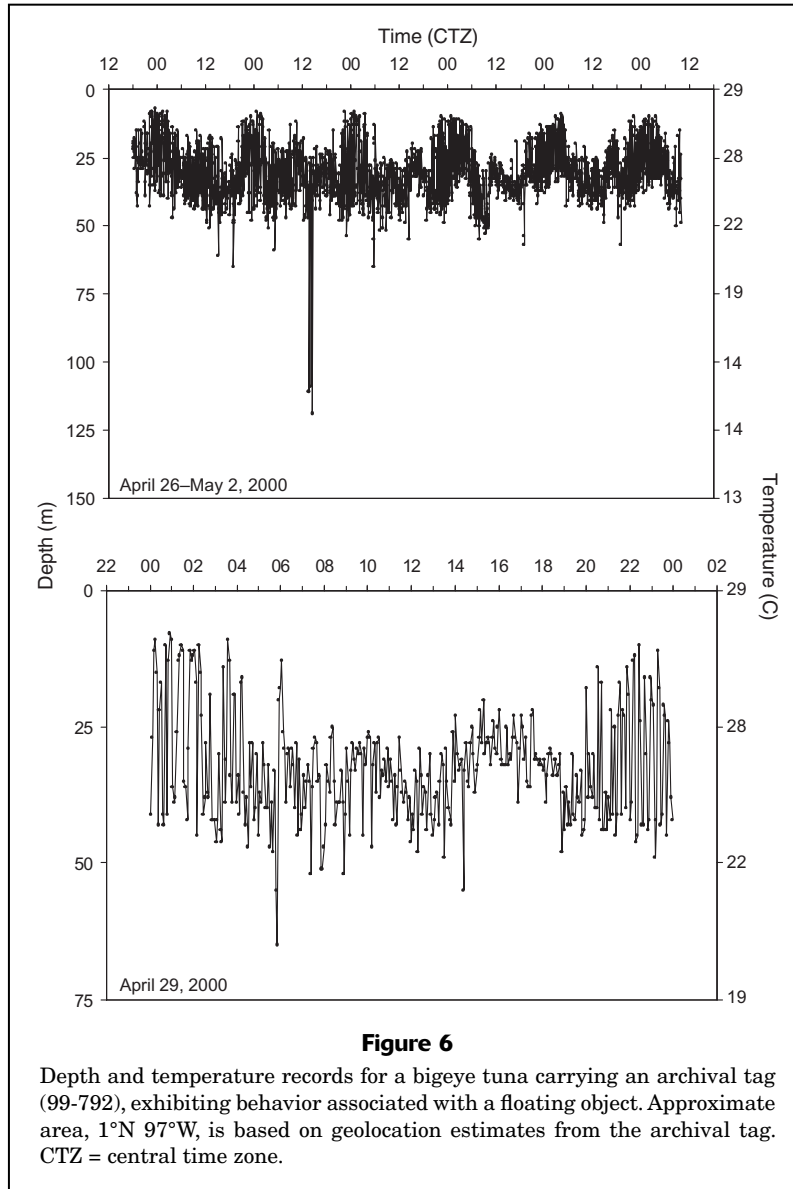


the two spatial distributions was not statistically significant ( $\Psi=0.313$ ,  $P=0.524$ ).

The fish with tag 99-793 was at liberty 340 d and exhibited behavior associated with floating objects for 9.2% of those days. It traveled initially to the east, remained for a considerable period in a relatively restricted area north of the Galapagos Islands, displayed some range in latitudinal movements between about 5°N and 5°S, and was recaptured only 83 nmi north of its release location (Fig. 9A, Tables 1, 2, and 4). The fish with tag 99-812 was released at a different FAD and was at liberty for a shorter period (159 d). It exhibited behavior associated with floating objects for 15.4% of the days at liberty. In contrast to the fish with tag 99-793, the fish with tag 99-812 traveled westward, displaying a fairly directed movement path, and was subsequently recaptured 821 nmi west of its release location (Fig. 9A, Tables 1, 2, and 4).

The fish with tag 99-826 was at liberty 272 d and exhibited behavior associated with floating objects for 7.5% of those days. It traveled the greatest total distance, displaying extensive longitudinal and latitudinal movements, and yet was recaptured only 279 nmi west of its release location (Fig. 9B, Tables 1, 2, and 4). The fish with tag 99-804 was released at the same FAD as the fish with tag 99-826 and was at liberty for a comparable period (250 d). It exhibited behavior associated with floating objects for 12.4% of the days at liberty. In contrast to the fish with tag 99-826, the fish with tag 99-804 displayed a much more constrained movement path. This fish started moving to the northwest during its last few months at liberty and was subsequently recaptured 544 nmi west of its release location (Fig. 9B, Tables 1, 2, and 4).

The fish with tag 99-792 was at liberty for 183 d and exhibited behavior associated with floating objects for 37.5%



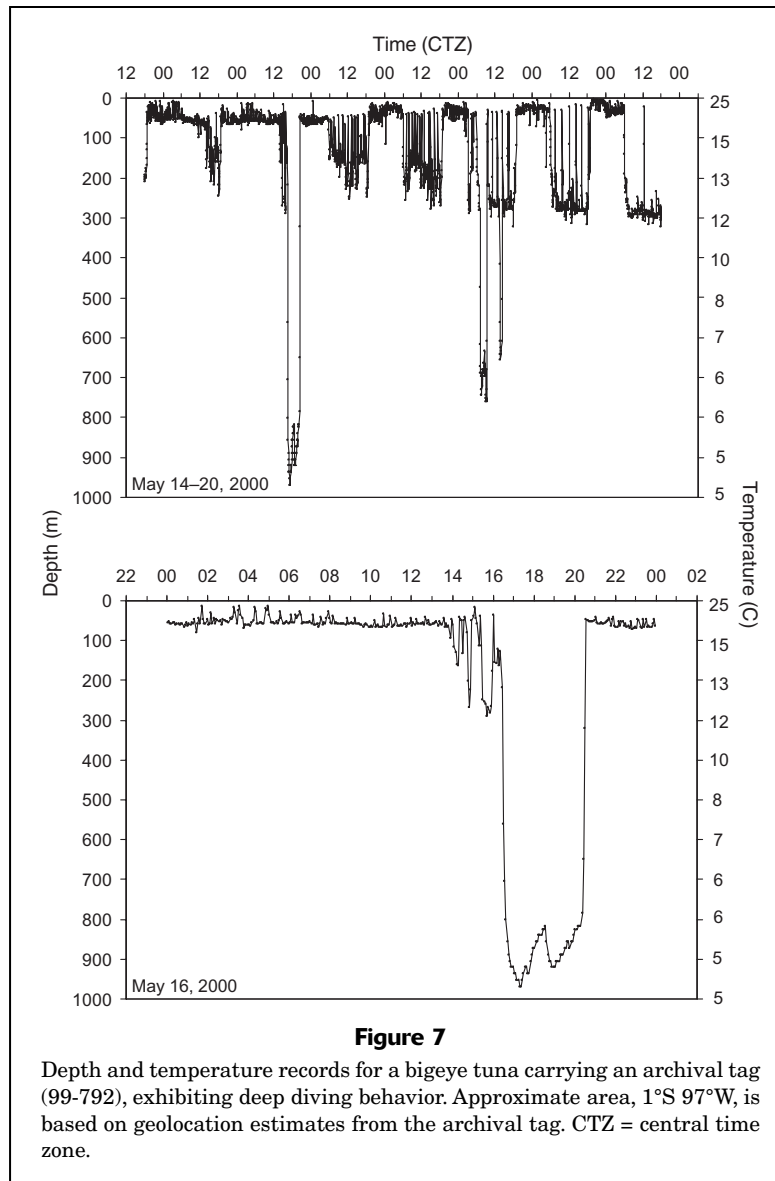
of time at liberty. The fish traveled a considerable distance west and southwest to about 5°S and 110°W, before moving back toward the east. It was recaptured only 82 nmi east of its release location (Fig. 9C, Tables 1, 2, and 4). The fish with tag 99-787 was released at the same FAD where the fish with tag 99-792 was also released. It was at liberty for 129 d and exhibited behavior associated with floating objects for 12.8% of time at liberty. In contrast to the fish with tag 99-792, the fish with tag 99-787 traveled in the opposite direction, toward the east, moving fairly rapidly to around 82°W, and then moving north and south between about 3°N and 3°S. This fish was recaptured 843 nmi east of its release location (Fig. 9C, Tables 1, 2, and 4).

The fish with tag 99-889 was at liberty 76 d and exhibited behavior associated with floating objects for 10.0% of time at liberty. This fish traveled a considerable distance south to about 7°S, before moving back northward, and

was subsequently recaptured only 100 nmi southwest of its release location (Fig. 9D, Tables 1, 2, and 4). The fish with tag 99-869 that was released at the same FAD where fish 99-889 was released, was at liberty 112 d and exhibited behavior associated with floating objects for 19.2% of time at liberty. The fish initially traveled in a similar direction as that of fish 99-889 before moving westward. It showed extensive latitudinal movements from about 5°S to 5°N, and was recaptured 430 nmi northwest of its release location (Fig. 9D, Tables 1, 2, and 4).

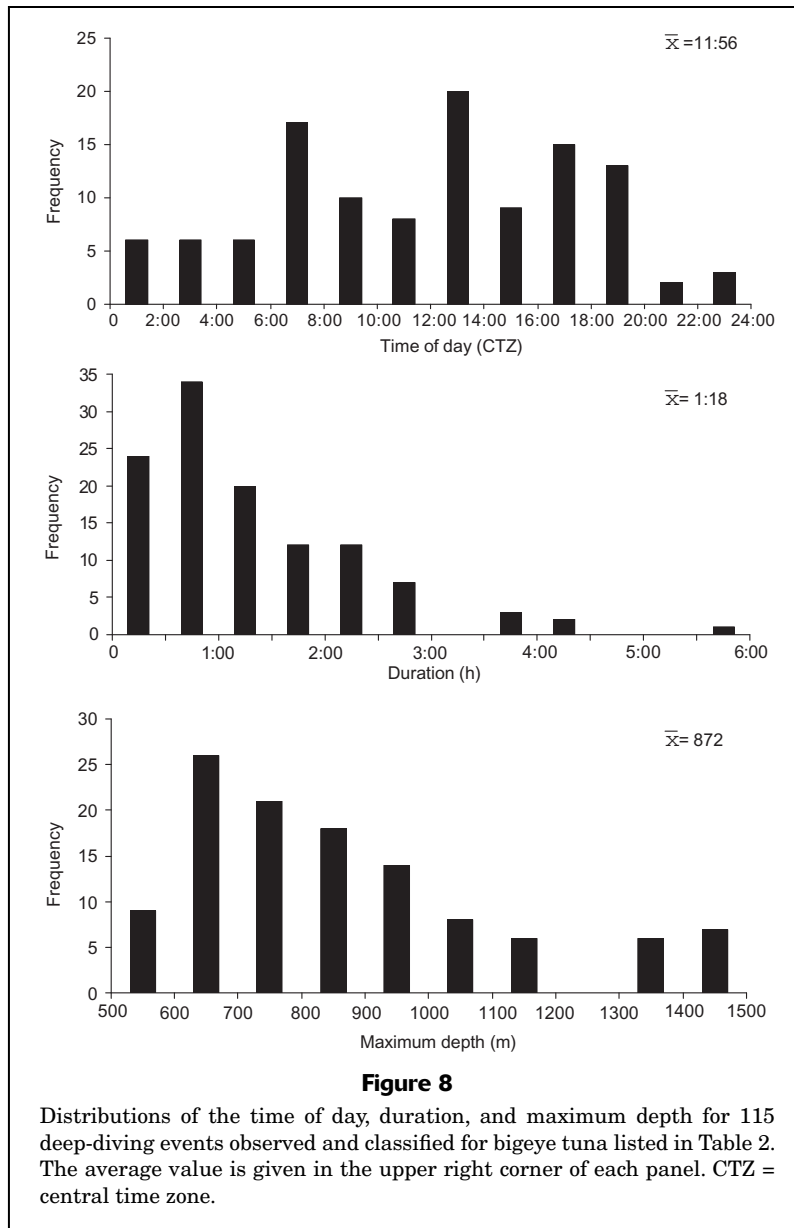
### Habitat selection

The habitat selected by bigeye tuna is presented by month in Figure 11, for days with unassociated type-1 behavior only. The nighttime and daytime depth distributions were very similar for April, May, and June. Most of the time



was spent above 50 m at night and between 250 to 300 m during the day. From April to June, the average depths of the 20°C and 15°C isotherms were 50 and 100 m, respectively. The habitat selected by the fish during July, August, and September was different and more variable during the day than that for the previous three months. Most of the time was spent above 50 m during the night. During the day the primary mode in depth in July was similar to the previous three months, but in August the primary mode shifted to about 200–275 m. In July the average depths of the 20°C and 15°C isotherms were 17 and 90 m, respectively, whereas in August and September the average depths of the 20°C and 15°C isotherms were 10 and 75 m, respectively. In September the depth distribution during the day was more uniform from about 100–350 m, with a slight mode between 175 and 250 m. The daily vertical behavior of the fish during September was highly

unusual and erratic in relation to previous months and to October; 78% of the days for five fish were classified as unassociated type-2 behavior. The habitat selected by the fish during October, November, and December was different during the night, than that for the previous six months. Most of the time was spent above 25 m during the night. During the day the primary modes in depth during October, November, and December were not as distinct as in previous months, excluding September, but were primarily between 150 and 275 m. The average depths of the 20°C and 15°C isotherms for October and December were 15 and 75 m respectively, whereas in November the average depths of the 20°C and 15°C isotherms were 25 and 50 meters, respectively. The habitat selected by the fish during the day in January, February, and March was similar, with a distinct mode in depth between about 200 and 300 m. During the night, there was a transition



during these three months from most of the time being spent above 25 m in January to a greater amount of time spent between 25 to 50 m at night in March. This transition corresponded with a downward shift in the depths of the 20°C and 15°C isotherms from an average of 30 and 80 m in January and February to 50 and 100 m in March, respectively.

The percentages of time that 13 bigeye tuna (112–126 cm in length at release) spent within 25-m depth intervals from the surface to 400 m, during each hour of each day at liberty, while exhibiting unassociated type-1 behavior, are given in Table 5. The average daytime temperatures and depths for these fish throughout their times at liberty, when exhibiting type-1 behavior, indicated that the highest concentration (about 50%) were between 13° and 14°C and 200 and 300 m depth. About 85% of the data were

distributed between 13° and 16°C and 150 and 300 m in depth.

Twelve of the twenty-two bigeye tuna showed significant correlations ( $r=0.61$  to  $0.75$ ,  $P<0.05$ ) between the visible disk area of the moon and their average nighttime depth distributions. There was a significant correlation ( $r=0.81$ ,  $P<0.05$ ) between the average nighttime depth for all 22 fish and the visible disk area of the moon (Fig. 12A). Fish occupied significantly greater depths for the 7-day period surrounding the full moon (29.0 m), in contrast to the other 22 days of the lunar cycle (21.2 m) (Fig. 12A). The average nighttime light levels indicated that the change in depth did not totally compensate for the greater light intensity during the full moon phase (Fig. 12A). Eight of the twenty-two fish showed significant correlations ( $r=0.54$  to  $0.75$ ,  $P<0.05$ ) between average daytime depth

**Table 3**

The accuracy, precision, and uncertainty in estimated latitudes and longitudes derived from archival tag light-level data from 21 bigeye tuna, processed with the geolocation programs of Wildlife Computers (Hill and Braun, 2001). The latitudes and longitudes are given as decimal degrees (dd). The error estimates are the uncertainty about the individual estimates of latitude or longitude. The differences are those between the actual latitude and longitude of recapture and the corresponding geolocation estimates.

Tag no.	Recapture latitude (dd)					Recapture longitude (dd)				
	Actual	Estimate	South error	North error	Difference	Actual	Estimate	West error	East error	Difference
99-787	1.72 N	1.0 N	2.5	2.5	0.72	83.08 W	82.97 W	0.5	0.0	0.11
99-792	1.35 N	3.0 N	3.0	4.0	1.65	95.82 W	93.93 W	0.5	0.0	1.89
99-801	1.47 N	5.0 S	1.5	4.5	6.47	90.72 W	90.62 W	0.5	0.0	0.10
99-803	2.20 N	1.0 N	2.5	2.0	1.20	102.72 W	102.12 W	0.5	0.0	0.60
99-810	1.65 S	2.5 S	1.5	2.0	0.85	93.17 W	93.21 W	0.0	0.5	0.04
99-812	0.55 N	2.5 N	0.0	2.0	1.95	109.00 W	109.29 W	0.0	0.5	0.29
99-816	1.78 N	1.5 N	3.0	3.5	0.28	97.60 W	97.40 W	0.0	0.5	0.20
99-817	1.12 S	2.0 S	3.5	5.5	0.88	95.87 W	95.47 W	1.0	0.0	0.40
99-835	1.20 N	5.0 N	2.5	2.5	3.80	99.68 W	98.48 W	0.5	0.0	1.20
99-839	2.33 S	0.0 N	6.5	0.5	2.33	95.75 W	95.54 W	0.5	0.0	0.21
99-847	1.77 N	3.0 S	2.5	5.0	4.77	97.23 W	97.17 W	0.0	0.5	0.06
99-860	2.18 S	2.0 S	3.0	2.0	0.18	97.87 W	97.20 W	0.5	0.0	0.67
99-861	2.23 S	1.5 N	6.0	6.5	3.73	96.67 W	95.56 W	0.0	0.0	1.11
99-864	2.70 N	2.5 N	1.0	3.0	0.20	97.87 W	98.10 W	0.5	0.5	0.23
99-865	2.67 S	0.0 N	1.5	6.5	2.67	99.05 W	99.33 W	0.5	0.0	0.28
99-869	4.85 N	4.0 N	2.5	2.0	0.85	103.18 W	103.35 W	0.5	0.0	0.17
99-874	2.70 N	3.0 N	1.0	2.0	0.30	97.87 W	97.81 W	0.5	0.0	0.06
99-877	2.77 S	2.0 S	7.0	3.0	0.77	99.20 W	97.37 W	0.0	1.0	1.83
99-883	1.60 S	0.5 N	0.5	0.5	2.10	95.55 W	95.67 W	0.0	0.0	0.12
99-889	0.37 N	2.5 S	1.5	2.5	2.87	98.58 W	98.57 W	0.0	0.0	0.01
99-891	0.25 S	4.5 S	1.0	9.5	4.25	92.88 W	92.74 W	0.5	0.0	0.14
Mean			2.57	3.40	2.04			0.33	0.17	0.46
95% CI			0.85	1.00	0.79			0.13	0.13	0.26

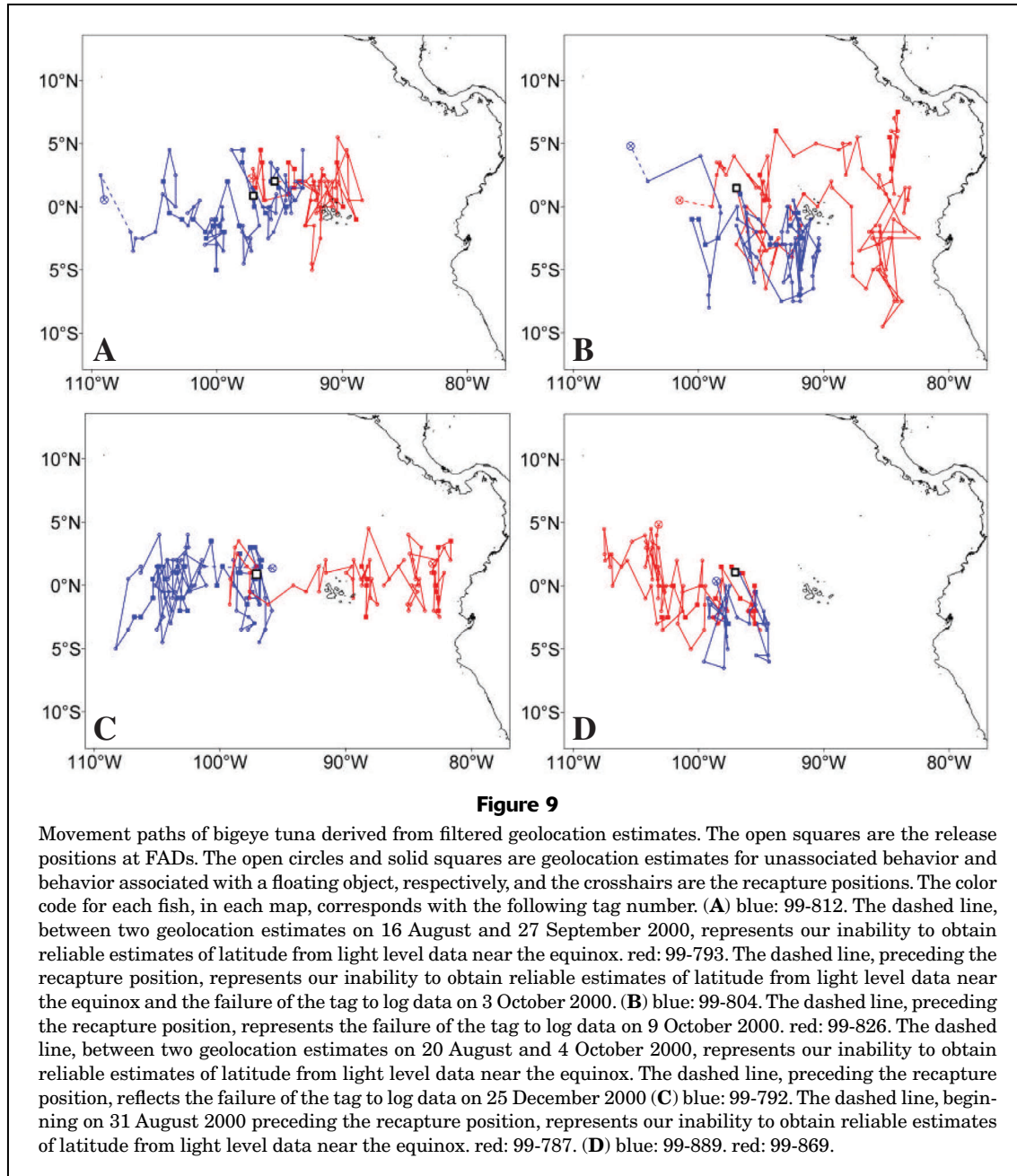
distributions and visible disk area of the moon. The patterns in average daytime depths for 5 of the 8 fish showed a significantly shallower depth distribution for a 3-day period surrounding the full moon (190 m) compared to the other 26 days of the lunar cycle (221 m). There was no apparent pattern, and the correlation coefficient ( $r=0.15$ ,  $P>0.05$ ) was not significant for the average daytime depth for all 22 bigeye tuna in relation to the visible disk area of the moon (Fig. 12B).

## Discussion

The results obtained in our study are useful for evaluating fine- to large-scale horizontal and vertical movements, behavioral patterns, and habitat characteristics on spatial and temporal scales previously undocumented for bigeye tuna. Movement paths, residence times at FADs, and habitat selection are essential for understanding the ecology of this species, and should be incorporated into stock assessment models to evaluate its vulnerability to various modes of fishing.

In addition to the 96 bigeye tuna released with archival tags, we released 101 bigeye tuna, in the same area and time period, with conventional plastic dart tags only. To date, 29 (30%) of the fish with archival tags and 22 (23%) of these with conventional tags have been confirmed as recaptured. The difference between these percentages was not significant ( $P>0.05$ ), indicating that tagging mortality was probably no greater for the fish with archival tags than the fish with conventional tags.

Several of the archival tags were removed from recaptured bigeye tuna by members of the scientific staff of the Inter-American Tropical Tuna Commission (IATTC). All but two of the tags were situated in the peritoneal cavity, in the general area where they were implanted, and were apparently encapsulated by fibrous connective tissue. Of the two other tags, one had apparently been invaginated into the lumen of the stomach and the other into the lumen of the intestine. Apparently the fish were attempting to expel these foreign bodies from their peritoneal cavities. Transintestinal expulsion of surgically implanted transmitters by fish was previously considered an exceptional phenomenon, except in the case of catfish (Marty and



Summerfelt, 1986; Baras and Westerloppe, 1999). In most specimens, the ventral region of the body wall, where the stalk protruded, did not appear to be completely healed. A small, dark, circular crater was seen at the base of the stalk—obviously a mark of irritation from the movement of the stalk even after the tag body had been encapsulated by flesh. Unless it is necessary to collect internal temperature data, the dorsal musculature is a potentially better location for implanting archival tags, of appropriate size and shape, for long-term deployment (Brill et al.<sup>3</sup>).

The long-term performance of the archival tags used in our experiment was questionable. The bigeye tuna that we studied pushed these tags to the limits of their design

specifications by undergoing regular daily vertical forays with fairly dramatic temperature and pressure fluctuations, in addition to making the unexpected deep diving events exceeding 1000 m.

Of the 27 archival tags recovered to date, four of them failed to collect light data because of apparent problems

<sup>3</sup> Brill, R. W., K. Cousins, and P. Kleiber. 1997. Test of the feasibility and effects of long-term intramuscular implantation of archival tags in pelagic fishes using scale model tags and captive juvenile yellowfin tuna (*Thunnus albacares*). NMFS Admin. Rep. H-97-11, 12 p. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396.

**Table 4**

Spatial statistics for 22 bigeye tuna at liberty for 30 days or longer, based on filtered estimates of the geographic locations derived from the archival tag light level data.  $n$  is the total number of geographic locations in the data set. Distance is the total distance traveled per data set. Linearity is the ratio of the distance between the data set endpoints and the total distance traveled. MSD is the mean squared distance from the center of activity.  $p$  is the proportion of MSD values, from a Monte Carlo simulation, higher than the MSD value from the observed data. UD is the utilization distribution, for the 95% and 50% probability levels, reported as area in km<sup>2</sup>. NA stands for non applicable because those estimates are only valid if the movement path indicates site fidelity.

Tag no.	$n$	Distance (km)	$\bar{x}$ bearing	$\bar{x}$ speed (km/d)	Linearity	MSD (km 10 <sup>9</sup> )	Site fidelity ( $p$ )	95% UD (km <sup>2</sup> )	50% UD (km <sup>2</sup> )
99-787	75	13596	11	105	0.12	408.017	59.6	NA	NA
99-792	94	20017	217	142	0.01	195.310	99.7	1,182,310	131,437
99-793	52	11996	30	86	0.06	111.726	99.9	793,555	103,429
99-801	32	7513	171	94	0.09	227.857	78.9	NA	NA
99-803	72	11721	186	123	0.08	134.198	95.3	802,037	100,354
99-804	75	17044	219	115	0.06	218.924	98.4	1,169,153	104,391
99-810	33	6975	51	122	0.05	79.566	99.9	430,586	83,410
99-812	78	14603	182	92	0.11	262.036	84.2	NA	NA
99-814	70	17671	138	143	0.02	109.497	99.9	836,649	158,936
99-816	27	4752	309	128	0.08	62.609	96.7	393,121	49,882
99-817	36	7970	158	129	0.03	83.159	99.9	478,858	50,205
99-826	108	23,085	219	113	0.03	494.010	78.9	NA	NA
99-835	37	6785	183	119	0.09	111.445	91.9	NA	NA
99-839	24	6143	267	110	0.03	90.090	99.4	501,057	107,094
99-847	11	3188	126	76	0.04	113.948	96.3	516,561	145,177
99-860	38	8893	324	165	0.02	65.013	99.9	389,426	51,713
99-865	29	6572	258	111	0.06	69.959	99.8	508,706	94,889
99-869	81	15811	335	140	0.05	221.813	95.5	1,295,394	205,956
99-874	17	4395	96	146	0.03	123.812	95.4	526,085	84,107
99-883	29	7282	58	121	0.03	83.922	99.9	564,556	103,384
99-884	149	32501	115	98	0.04	174.997	99.9	1,164,992	341,468
99-889	31	6694	252	87	0.03	85.269	99.3	609,874	154,383

with their stalks. The batteries in four of the six tags, which were in fish at liberty for 175 days or more, failed and these tags stopped collecting data. Fortunately, however, previously collected data were preserved in the non-volatile memories of the tags. Perhaps the most important feature of archival tags is their ability to collect data on the movement of tagged fish at frequent intervals from release until recapture (Hunter et al., 1986; Gunn and Block, 2001). There are, however, several factors that can affect the accuracy of the geolocation estimates. These include, but are not limited to, latitude, equinoxes, resolution of the light sensor, light attenuation, and behavior of the fish (Gunn and Block, 2001; Musyl et al., in press).

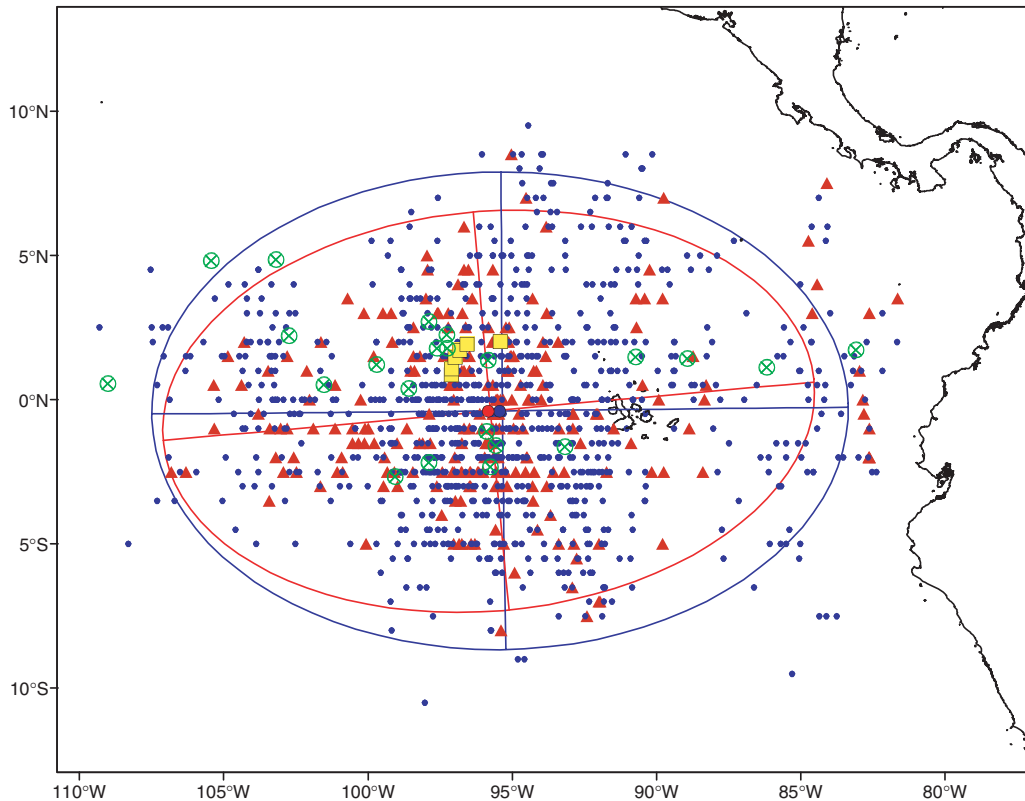
Gunn et al.<sup>4</sup> previously reported the accuracy of geolocation estimates from the light data from archival tags

attached to southern bluefin tuna (*Thunnus maccoyii*) held in cages in the Indian Ocean to be about 0.5° in longitude and 1.5° in latitude. Welch and Eveson (1999) and Musyl et al. (2001) estimated the accuracy of geolocation estimates from the light-level data recorded by archival tags by comparing the known and estimated locations of tags that were attached to oceanographic buoys in the north Pacific. The reported accuracy by Welch and Eveson (1999) was ±0.9° in longitude and ±1.2° in latitude. The reported accuracy by Musyl et al. (2001) ranged from 0.2° to 0.3° in longitude and from 1.5° to 4.4° in latitude. In our study, we estimated the accuracy of geolocation estimates (longitude: 0.5°, latitude: 2.0°) by comparing the known and estimated locations of 21 bigeye tuna on their days of recapture (Table 3).

We used our estimates of accuracy and precision as criteria for filtering the daily geolocation estimates. In other studies where archival tags were used to provide estimated movement paths, geolocation estimates derived from light data have been verified or adjusted by comparing recorded temperatures from archival tags with maps of estimated sea-surface temperatures from satellite data (Gunn and Block, 2001). In the equatorial EPO, sea-sur-

<sup>4</sup> Gunn, J. S., T. W. Polacheck, T. L. O. Davis, M. Sherlock, and A. Betlehem. 1994. The development and use of archival tags for studying the migration, behavior and physiology of southern bluefin tuna, with an assessment of the potential for transfer of the technology to groundfish research. In Proceedings of ICES mini-symposium on fish migration, 23 p. International Council for the Exploration of the Sea, Palaegade 2-4, DK-1261 Copenhagen K, Denmark.





**Figure 10**

Geolocation estimates for 22 bigeye tuna at liberty for 30 d or longer (Table 4) classified as unassociated (blue dots) or associated with floating objects (red triangles). The yellow solid squares are the release locations and the green crosshairs are the recapture locations. The larger blue and red dots, axes, and ellipses are the arithmetic means, major and minor axes, and 95% probability ellipses, respectively, for the spatial distributions of the geolocation estimates for unassociated behavior and behavior associated with floating objects.

face temperatures vary little over extremely large areas (Fiedler, 1992); therefore this technique is much less useful than in temperate regions.

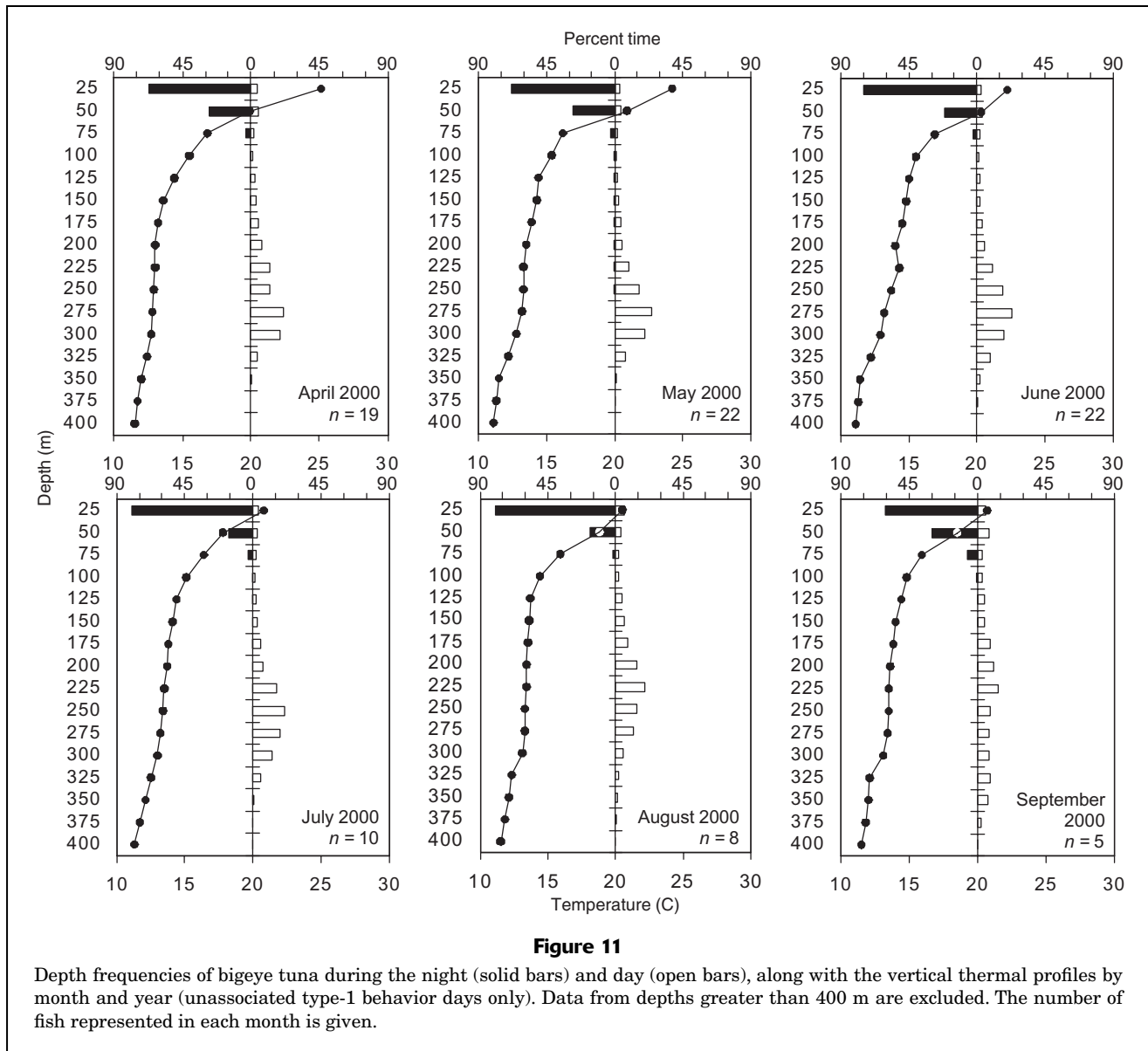
The movement paths shown for bigeye tuna in our study (Figs. 9 and 10) derived from the filtered archival tag light data indicated that the area was restricted to the equatorial EPO. No fish traveled further west than about 110°W, and most movements were constrained between about 95° and 100°W and 3°N and 5°S. However, the value of the archival tags in providing fisheries-independent information on dispersion and movement paths is apparent, especially considering the fact that 16 of the fish were recaptured within 300 nmi of where they were released. Furthermore, the minimum convex polygon for the filtered archival tag data is approximately four times the area of the minimum convex polygon surrounding the release and recapture positions. Movements of bigeye tuna inferred from large-scale conventional tagging programs in the western Pacific (Hampton and Gunn, 1998; Hampton et al.<sup>5</sup>; Kaltongga<sup>6</sup>) and Hawaii (Itano and Holland, 2000) indicate that, although there are some long-distance movements, most recoveries are near their points of release. Those data appear to indicate, as

do those of the present study, regional fidelity for bigeye tuna, and that the expected degree of mixing is quite low between the EPO and the central and western Pacific Ocean (CWPO).

The estimated mean velocity of 117 km/d or 2.6 knots (Table 4) is comparable to the estimate of 130 km/d for Pacific bluefin tuna (*Thunnus orientalis*) from archival tag data (Tsuji et al., 1999). Although this estimate should not be interpreted as actual swimming speed through the water, considering the imprecision of the movement paths and the fact that daily vertical movements were not

<sup>5</sup> Hampton, J., K. Bigelow, and M. Labelle. 1998. A summary of current information on the biology, fisheries and stock assessment of bigeye tuna (*Thunnus obesus*) in the Pacific Ocean, with recommendations for data requirements and future research. Secretariat of the Pacific Community, Oceanic Fisheries Programme, Technical Report 36, 46 p. Oceanic Fisheries Programme, SPC, B.P. D5, 98848 Noumea Cedex, New Caledonia.

<sup>6</sup> Kaltongga, B. 1998. Regional tuna tagging project: data summary. Oceanic Fish. Prog. Tech. Rept. 35, 70 p. Secretariat of the Pacific Community, Noumea, New Caledonia. Oceanic Fisheries Programme, SPC, B.P. D5, 98848 Noumea Cedex, New Caledonia.



included in the calculations of velocity. Nevertheless, this estimate should be useful for incorporation into a spatially stratified movement model that is designed to evaluate dispersion and mixing rates between large regions (see Sibert and Fournier, 2001).

Sonic tracking studies have shown that the diel vertical migrations of bigeye tuna are closely associated with vertical movements of organisms of the deep scattering layer (DSL). Bigeye tuna probably forage on squids and other mesopelagic organisms within the DSL throughout the day and night (Josse et al., 1998; Dagorn et al., 2000). As reported by Blunt (1960), squid are very important in the diet of subsurface bigeye tuna, in the eastern tropical Pacific (ETP)—70% of the stomachs examined contained squid equivalent to 60% of the total food volume. Fiedler et al. (1998) reported the depths of the DSL in the ETP as

300–400 m during the day and 0–100 m at night. Other studies have documented that bigeye tuna have evolved anatomical and physiological adaptations to enable them to exploit organisms of the DSL during the daytime in a dark, cold, and oxygen-poor environment (Kawamura et al., 1981; Holland et al., 1992; Brill, 1994; Holland and Sibert, 1994; Schaefer, 1999; Lowe et al., 2000; Graham and Dickson, 2001).

The depth distributions of bigeye tuna not associated with FADs near Hawaii and in the Coral Sea are significantly greater than those for bigeye tuna in the equatorial EPO. It seems possible that the greater daytime depths exhibited by bigeye tuna in the CWPO are related to the greater daytime DSL depths ( $\geq 400$  m) in that region (Maynard et al., 1975; Tont, 1976; Davies, 1977; Kuznetsov et al., 1982; Fiedler et al., 1998; Josse et al., 1998). For a 112-cm

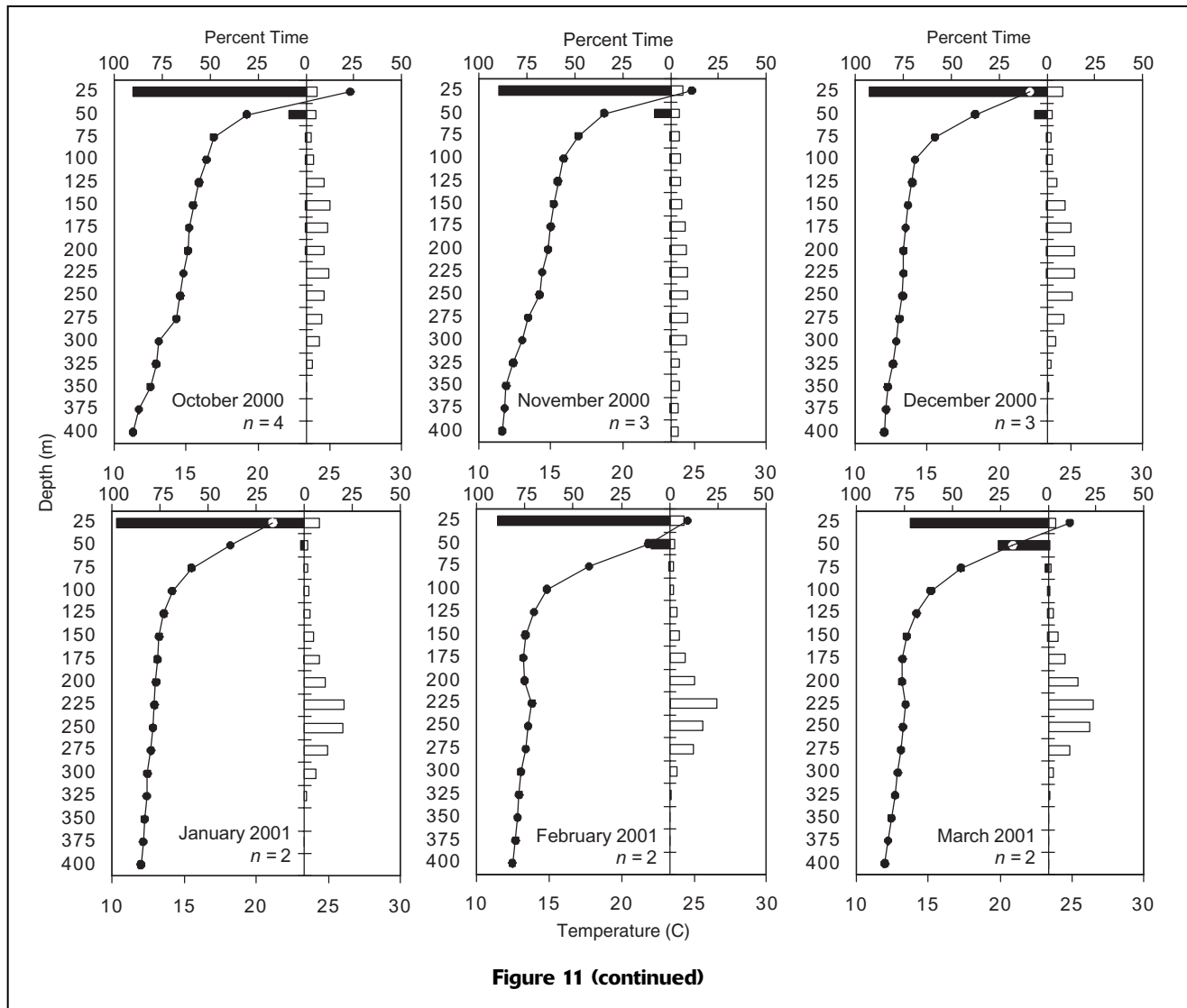
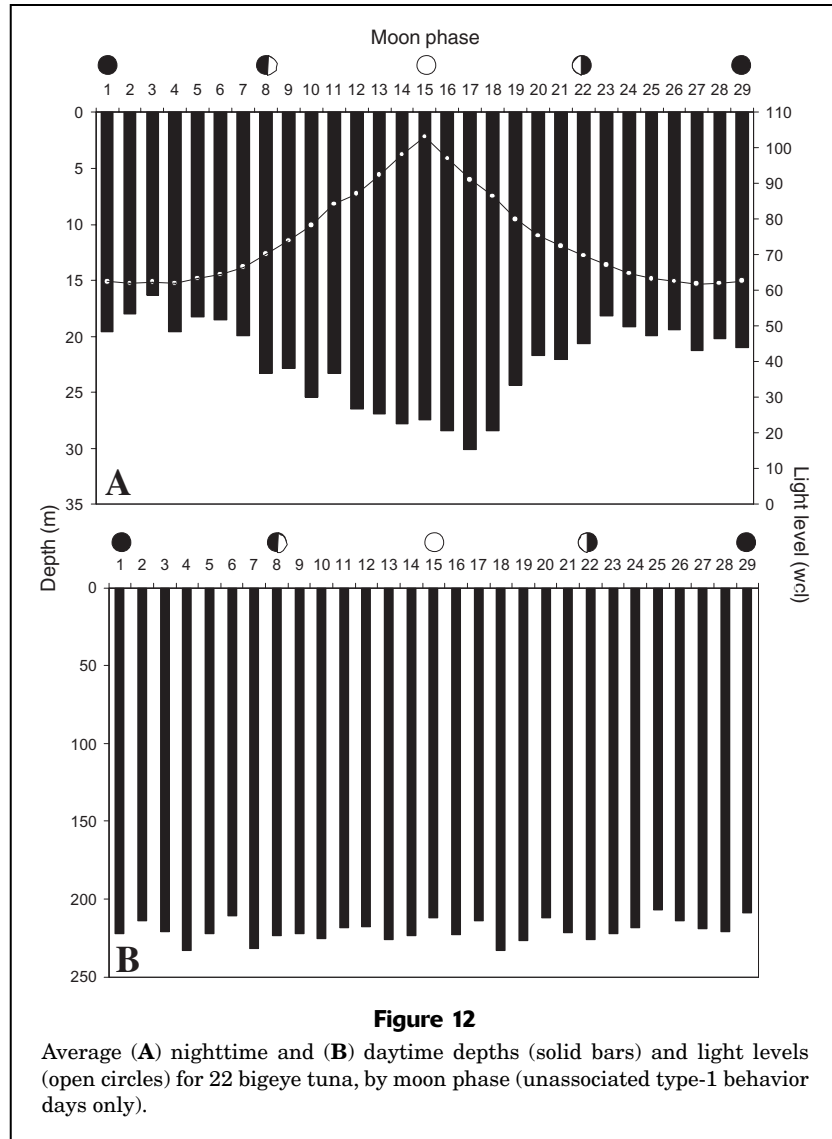


Figure 11 (continued)

bigeye tuna in the equatorial EPO not associated with a FAD (Fig. 2), the baseline daytime depth was 250 to 300 m at temperatures of 12° to 13°C. For a 131-cm bigeye tuna exhibiting similar behavior in Hawaiian waters, the baseline daytime depth was 400 to 500 m at temperatures of 7° to 10°C (Musyl et al., in press). Gunn and Block (2001) reported that bigeye tuna with archival tags in the Coral Sea showed that the mean depth of the fish at night was 50 m and that during the day they were at depths of 450 to 500 m and at temperatures of 7° to 9°C.

The average light level experienced by bigeye tuna at night (77 Wildlife Computer's light level [wcl] at 24 m), is below that experienced during the day (126 wcl at 242 m). Therefore, bigeye tuna do not occupy an isolume as has been suggested for other vertically migrating organisms (Widder and Frank, 2001). Bigeye tuna are also able to adapt to much higher light levels (195 wcl) for prolonged periods when remaining at shallow depths during daylight hours when they are associated with FADs.

Unassociated type-2 behavior observed in bigeye tuna (Fig. 5 and Table 2) may be attributed to a shift in the vertical distribution of prey items. Monospecific 100- to 200-ton schools of bigeye tuna (>100 cm length) were observed feeding at the surface on the mesopelagic fish *Vincigueria lucetia* during daylight hours on 15 December 1978 in the equatorial EPO (K. Schaefer, unpubl. data). *Vincigueria lucetia* is normally distributed at depths of 500 m or more during the day and is common in the 0–90 m layer at night (Blackburn, 1968). During the 1971–91 period, previous to the development of the drifting FAD fishery in the EPO, many purse-seine sets made during daylight hours were successful in capturing bigeye tuna schools not associated with drifting objects (Calkins et al., 1993). Atypical behavior of large schools of *Vincigueria nimbari*, present in large concentrations within the mixed layer during the day, has also been observed in the equatorial Atlantic Ocean (Marchal and Lebourges, 1996). This type of behavior has also been observed in the Coral Sea, where bigeye



**Figure 12**

Average (A) nighttime and (B) daytime depths (solid bars) and light levels (open circles) for 22 bigeye tuna, by moon phase (unassociated type-1 behavior days only).

tuna are caught throughout the day near the surface by both handline and longline fisheries between October and December (Hisada, 1973). A second explanation for some of the unassociated type-2 behavior is that the fish were still possibly associated with a FAD but were making afternoon excursions into the DSL, foraging for food.

Occasionally bigeye tuna make dives in excess of 500 m (Fig. 7 and Table 2). The durations of the deep diving events are not correlated ( $r=0.0008$ ,  $P>0.05$ ) with body size. Moreover, there appear to be two types of deep dives (Table 2). One may be for predator avoidance. The fish descend and then ascend rapidly back to the depth at which it had been previous to the dive. The second type may be a foraging behavior, where prolonged time is spent at greater depths, up to 1000 m. Deep dives to 1000 m or more have also been reported from archival tag data for bigeye tuna in the Coral Sea (Gunn and Block, 2001) and for Atlantic bluefin tuna (Block et al., 2001a; Block et al., 2001b).

Bigeye tuna exhibiting behavior associated with floating objects (Fig. 6 and Table 2) generally remain above the thermocline, but they still show a diel shift in depth distribution. They remain at about 6 m, on average, deeper during the day than at night (Fig. 6). Stomach content analysis of FAD-associated bigeye tuna in the eastern Atlantic Ocean by Ménard et al. (2000) showed that 82.7% of the stomachs were empty, whereas only 25% of the stomachs of bigeye tuna unassociated with floating objects were empty. They concluded that FADs do not have a trophic function. However, the observed excursions to depths of about 300 m for a few hours at about 1800 h for four consecutive days by a FAD-associated bigeye tuna (Fig. 1B) may be related to foraging for prey in association with the DSL.

Parin and Fedoryako (1999) stated that tunas associate with floating objects only temporarily because there are insufficient food resources in the vicinity of these devices. We found that residence times and total times spent at FADs are limited (Table 2). Our observations do not support the

hypothesis of Marsac et al. (2000) that association with FADs causes bigeye tuna to be retained within areas or transported to new areas, thus creating an ecological trap. An alternative hypothesis, suggested by Hunter and Mitchell (1966), is that FADs function by simply providing a visual stimulus in an optically void environment. An extension of their hypothesis should include the fact that FADs provide a general sensory stimulus, including sound produced by the FAD and associated fauna, which may be the mechanism by which tunas locate FADs. In addition to a general sensory stimulus, FADs may also function as reference points (Freon and Dagorn, 2000).

Archival tags have provided data on the type of habitat selected (light levels, depths, and temperatures) that should be useful for standardizing the catch per unit of effort (CPUE) of bigeye tuna by surface and longline fisheries in the EPO. The data in Table 5 indicate that bigeye tuna greater than 110 cm spend 87% or more of their time above 50 m, in the mixed layer at night and 53% or more of their time between 200 and 300 m during the day. Habitat-based stock assessment models (Hinton and Nikano, 1996; Hinton and Deriso, 1998; Hampton et al.<sup>1</sup>) have been developed for the integration of data, such as those provided in Table 5, to adjust effort based on estimated fishing depth of longline gear (Mizuno et al., 1999) in relation to the vertical distribution of target species by time of day. The fishing depth of longline gear has been shown to be an important source of variation in the CPUE for bigeye tuna (Hanamoto, 1987; Boggs, 1992); higher catch rates of bigeye tuna have been associated with greater fishing depths of the longline gear. This has been interpreted previously as a preference of bigeye tuna for 10° to 15°C water during daylight hours (Hanamoto, 1987; Holland et al., 1990; Boggs, 1992; Brill, 1994).

We suggest that bigeye tuna are most likely not selecting their daytime and nighttime habitats based on temperature, depth, or light preferences, but on the distributions of their preferred prey. Cephalopods and mesopelagic fishes also show diel vertical migrations (as do other organisms) associated with the DSL. We suggest that the depths and temperatures preferred by bigeye tuna during daylight hours when exhibiting unassociated type-1 behavior are the environmental variables associated with their preferred prey.

The greater depths and lower temperatures at which bigeye tuna are caught during the daytime in the CWPO (Hampton et al.<sup>5</sup>; Miyabe<sup>7</sup>) may be a function of the greater daytime depths of the DSL

<sup>7</sup> Miyabe, N. 1995. Follow-up study on the stock status of bigeye tuna in the Pacific ocean. Western Pacific Yellowfin Research Group 5, working paper 12; 21-23 August 1995, 15 p. Oceanic Fisheries Programme, SPC, B.P. D5, 98848 Noumea Cedex, New Caledonia.

**Table 5**  
The percentages of time 13 bigeye tuna (greater than 110 cm) spent within depth intervals by time of day (unassociated type-1 behavior days only). CTZ = central time zone.

Depth (m)	Hour (CTZ)																							
	0000	0100	0200	0300	0400	0500	0600	0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200	2300
0-25	73.4	73.0	73.0	73.9	72.6	44.0	3.6	2.2	2.5	2.8	3.1	2.9	3.2	3.0	3.0	2.9	2.8	2.3	17.3	63.2	72.6	72.0	71.7	72.6
26-50	21.9	22.0	22.2	21.9	23.4	26.7	5.7	2.4	2.9	3.0	2.9	3.1	2.7	2.8	2.8	2.7	2.5	2.1	12.0	25.2	23.7	23.5	23.4	22.7
51-75	3.1	3.1	3.3	2.7	2.9	8.3	3.4	1.0	1.0	1.1	1.2	0.9	1.1	0.9	0.9	1.1	1.0	1.1	6.6	4.5	2.7	3.3	3.8	3.3
76-100	0.5	0.4	0.5	0.5	0.4	4.5	2.8	0.8	0.9	0.8	0.7	0.7	0.7	0.8	0.7	0.6	0.8	1.2	3.6	1.2	0.4	0.3	0.4	0.6
101-125	0.2	0.3	0.3	0.2	0.2	4.2	5.1	2.6	1.9	1.3	1.6	1.2	1.3	1.3	1.5	1.6	1.7	2.1	4.9	1.1	0.2	0.2	0.1	0.1
126-150	0.2	0.3	0.2	0.2	3.3	6.3	6.3	3.9	3.1	2.4	2.5	2.3	2.3	2.7	2.5	2.9	3.1	3.5	5.7	1.0	0.2	0.2	0.1	0.2
151-175	0.2	0.2	0.1	0.2	2.7	8.8	5.4	5.1	4.7	4.7	4.7	4.6	4.0	4.8	5.3	5.0	4.6	5.0	6.7	1.1	0.1	0.1	0.2	0.1
176-200	0.2	0.1	0.1	0.1	2.1	10.8	7.1	7.6	7.4	7.1	7.1	7.1	7.1	6.5	6.4	6.8	6.5	7.1	8.0	1.0	0.1	0.2	0.1	0.1
201-225	0.2	0.2	0.1	0.1	1.9	16.9	11.7	12.1	12.9	12.7	12.7	12.9	13.4	13.0	13.3	12.0	11.9	12.1	12.9	0.8	0.1	0.1	0.1	0.1
226-250	0.1	0.1	0.1	0.1	1.1	17.2	17.3	13.9	14.5	15.0	15.0	15.8	16.7	15.7	15.4	15.0	14.8	19.0	12.1	0.4	0.1	0.1	0.1	0.1
251-275	0.2	0.2	0.1	0.1	0.8	12.5	24.5	21.2	19.6	19.6	19.6	19.3	18.4	19.1	19.0	19.4	22.3	26.1	7.0	0.2	0.1	0.1	0.1	0.1
276-300				0.1	0.4	5.1	16.3	19.5	18.8	17.9	17.9	17.8	17.7	18.1	18.5	19.7	19.8	14.0	2.4	0.1	0.1	0.1	0.1	0.1
301-325					0.1	1.7	3.9	7.1	8.6	8.5	8.5	8.3	8.5	8.8	8.4	8.7	6.8	3.9	0.7	0.1				
326-350						0.2	0.9	1.2	1.5	2.0	2.0	2.3	2.5	2.0	1.8	1.4	1.2	0.5						
351-375							0.1	0.1	0.1	0.3	0.4	0.6	0.4	0.5	0.4	0.3	0.1							
376-400										0.1	0.3	0.4	0.6	0.4	0.5	0.4	0.3	0.1						

in those regions, compared to the daytime depths of the equatorial EPO (Maynard et al., 1975; Tont, 1976; Davies, 1977; Kuznetsov et al., 1982; Fiedler et al., 1998; Josse et al., 1998). Farr and Best (1998) reported that DSL distributions are related to mesoscale oceanographic features, defined by flow and temperature variability, and are most commonly observed at the pycnocline.

Geographic variation in DSL depths throughout the Pacific are possibly related to isolines of the associated micronekton, and can potentially be estimated from the light level data recorded by the archival tags attached to bigeye tuna. Variation in daytime DSL depths is probably a function of light penetration (which is regulated by biological production) and absorption of light by chlorophyll and phaeopigments (Tont, 1976).

The behavior of bigeye tuna is strongly influenced by the presence of drifting FADs within their habitat. Because of this behavior associated with FADs, even though it is for relatively short periods, bigeye tuna are highly vulnerable to capture by purse-seine vessels. Estimates of bigeye tuna residence times and percentages of total time associated with drifting FADs, along with estimates of FAD densities, could be used to evaluate vulnerability to capture by the surface fishery. There is a critical need for conducting a large-scale tagging program in the EPO focused on bigeye tuna—a program where conventional tags are used for estimating size-specific mortality and mixing rates and archival tags are used for evaluating fine-scale movements, behavior, and habitat selection.

## Acknowledgments

We are grateful for invaluable advice and assistance provided by B. Block, T. Booth, M. Braun, R. Brill, J. Gunn, R. Hill, P. Hooge, and T. Williams. We are thankful to B. Blocker and the crew of *Her Grace* for their performance in fishing and tagging operations. We are indebted to vessel owners, captains, fishermen, unloaders, and industry representatives for returning recovered archival tags. We thank Juan Gracia for his assistance with tagging and the IATTC field office personnel for recovering archival tags. We also wish to thank B. Bayliff, R. Brill, R. Deriso, G. Watters, and two anonymous reviewers for constructive comments on drafts of the manuscript.

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