Abstract—Thirty-three skipjack tuna (*Katsuwonus pelamis*) (53–73 cm fork length) were caught and released with implanted archival tags in the eastern equatorial Pacific Ocean during April 2004. Six skipjack tuna were recaptured, and 9.3 to 10.1 days of depth and temperature data were downloaded from five recovered tags. The vertical habitat-use distributions indicated that skipjack tuna not associated with floating objects spent 98.6% of their time above the thermocline (depth=44 m) during the night, but spent 37.7% of their time below the thermocline during the day. When not associated with floating objects, skipjack tuna displayed repetitive bounce-diving behavior to depths between 50 and 300 m during the day. The deepest dive recorded was 596 m, where the ambient temperature was 7.7°C. One dive was particularly remarkable because the fish continuously swam for 2 hours below the thermocline to a maximum depth of 330 m. During that dive, the ambient temperature reached a low of 10.5°C, and the peritoneal cavity temperature reached a low of 15.9°C. The vertical movements and habitat use of skipjack tuna, revealed in this study, provide a much greater understanding of their ecological niche and catchability by purse-seine fisheries.

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Vertical movement patterns of skipjack tuna (*Katsuwonus pelamis*) in the eastern equatorial Pacific Ocean, as revealed with archival tags

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Limited information on the vertical movements of skipjack tuna (*Katsuwonus pelamis*) is available from analyses of catch data for tuna longline gear (Yabe et al., 1963), ultrasonic telemetry (Dizon et al., 1978; Schaefer and Fuller, 2005; Matsumoto et al.[1]), and archival tags (Ogura[2]). These studies have indicated that skipjack tuna inhabit predominantly the mixed layer but make occasional brief dives below the thermocline.

Skipjack tuna are distributed throughout the world's tropical and subtropical oceans (Collette and Nauen, 1983; Matsumoto et al., 1984). In the eastern Pacific Ocean (EPO), catches of this species have occurred from about 34°N off southern California to about 27°S off northern Chile. The species is limited to surface temperatures of about 17° to 30°C (Wild and Hampton, 1994). Skipjack tuna are one of three principal targets of a large-scale purse-seine fishery in the EPO and are caught mostly in association with floating objects between about 10°N and 15°S. The purse-seine catch of skipjack tuna in the EPO during 1995–2004 averaged 197 thousand metric tons (t) (range: 129 to 295 thousand t), which is 160% greater than the average of 76 thousand t (range: 51 to 95 thousand t) during the previous 10-year period (Anonymous, 2005).

The anatomical and physiological adaptations of skipjack tuna characterize them as highly efficient opportunists for exploiting their oceanic vertical habitat. Their body shape, fin configurations, and musculature are close to optimum for relatively fast, sustained, and burst swimming (Magnuson, 1978; Altringham and Shadwick, 2001). They lack a swim bladder (Godsil and Byers, 1944), are capable of physiological thermoregulation (Dizon and Brill, 1979), and have relatively rapid gastric evacuation rates (Magnuson, 1969).

Skipjack tuna possess a well-developed large central rete, in addition to epaxial and hypaxial vessels and retia (Stevens et al., 1974; Graham and Dickson, 2001). The counter-current retia provide a thermoconserving mechanism enabling metabolic heat to be retained within the muscles and thus elevate body temperatures above that of ambient water temperatures (Graham, 1975; Stevens and Neill, 1978). The anatomical specializations enhance the thermal inertia of this species and

[1] Matsumoto, T., H. Okamoto, and M. Toyonaga. 2006. Behavioral study of small bigeye, yellowfin and skipjack tunas associated with drifting FADs using ultrasonic coded transmitter in the central Pacific Ocean. Information Paper 7, 25 p. Second regular session of the scientific committee. Western and Central Pacific Fisheries Commission, P.O. Box 2356, Kolonia, Pohnpei FM 96941.

[2] Ogura, M. 2003. Swimming behavior of skipjack, *Katsuwonus pelamis*, observed by the data storage tag at the northwestern Pacific, off northern Japan, in summer of 2001 and 2002. Working Paper SKJ-7, 10 p. Sixteenth meeting of the standing committee on tuna and billfish, Sec. Pac. Comm., Noumea, New Caledonia, B.P. D5 Noumea Cedex, New Caledonia.

enable this species to slow the cooling rate of the body. Thermal inertia allows skipjack tuna to undertake brief dives into cooler waters below the thermocline to exploit deep prey resources or to escape predators (Neill et al., 1976; Stevens and Neill, 1978).

The objectives of this investigation were to elucidate vertical movement patterns of and habitat use by skipjack tuna in the equatorial EPO. By examining the behavioral and physiological constraints and environmental variables that define skipjack tuna vertical habitat, we can improve our ecological understanding and provide useful data for inclusion in stock assessments.

Materials and methods

Tag releases

Thirty-three skipjack tuna were captured, tagged, and released during 9–10 April 2004 in close proximity to a Tropical Atmosphere-Ocean (TAO) mooring at 1°59′N 95°19′W in the equatorial EPO. The estimated depth of the seafloor at the TAO mooring was 3091 m. Tagging was conducted on the chartered FV *Her Grace*, a 17.7-m pole-and-line fishing vessel. The tagged fish (tagged from an aggregation estimated at 10 t of skipjack tuna), remained associated with the tagging vessel as it drifted away from the TAO mooring at 0520 h on 11 April 2004 until 0940 h and about 15 km west of the mooring, when the aggregation dispersed as the vessel departed at about at a cruising speed of 8 kt.

The archival tags (ATs) used in this study were model LTD_1100 (Lotek Wireless Inc., St. John's, Newfoundland, Canada). The tag is a rectangular solid, measuring 8 mm × 16 mm × 27 mm, and weighing 5 g in air. Information on how to report the recovery of the tag and how to claim the associated reward (US$50) was printed in Spanish on a label encased in the epoxy of the tag.

Depth and temperature data were stored in the memory of the ATs at 28-s intervals. At this sampling rate, the memory of each AT (64 KB) was capable of storing 10.7 days of data. The maximum depth sensing was 1000 m (with a resolution of 0.4%, and an accuracy of ±1%). The temperature sensing range was from −5° to 35°C, with a resolution of 0.2°C and an accuracy of better than 0.3°C.

Skipjack tuna were captured with fishing rods and reels (n=18) and handline gear (n=9) equipped with chrome jigs and barbless hooks during the night, and with pole-and-line gear (n=6) and by chumming live bait during the day. Each fish was lifted directly into a padded aluminum cradle that was covered with wet smooth vinyl. The fish were placed ventral side up, their eyes 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 an AT was initiated. An incision about 2 cm long was made with a sterile surgical scalpel blade in the abdominal wall about 1/3 of the distance between the anus and the base of the pelvic fins and about 2 cm to the left of the centerline of the fish. Special care was taken to cut through the dermis and only 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 in Betadine solution, was inserted through the incision into the peritoneal cavity, and a 13-cm length of 64-kg spectra line was tied to the tag that protruded outside. The incision was closed with three staples, by using a surgical staple gun.

After implantation of the AT, each fish was also tagged with one numbered 12.5-cm green plastic dart tag (Hallprint, Victor Harbor, 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 either side of the fish.

The 33 skipjack tuna released with ATs were measured to the nearest centimeter (mean=66.9 cm fork length (FL), range: 53–73 cm). The fish were then picked up by hand from the cradle and released back into the ocean. The total time that fish were out of the water was less than 1 min. All fish released with ATs were observed to swim away from the vessel after release, and all appeared to be in good condition.

Tag recoveries

Six of 33 skipjack tuna released in 2004 were recaptured (18.2%), but just five of the archival tags were recovered. Data on the fish lengths, release and recapture dates and locations, numbers of days at liberty, and linear displacements of the six fish are given in Table 1. Recapture locations ranged from 341 km to 2548 km and 123° (southeast) to 260° (west) of the release location. Of the six fish recaptured, four were initially caught by using fishing rods and reels, one by using handline gear, and one by using pole-and-line gear.

Data processing

Data were downloaded from the tags, and initial exploratory data analyses were conducted with software provided by the tag manufacturer. For the five skipjack tuna, the behavior for each day at liberty was classified as associated or unassociated with floating objects, on the basis of behavioral characteristics from ultrasonic telemetry observations of skipjack tuna associated with floating objects (reported by Schaefer and Fuller [2005]). For each day at liberty, surface-oriented and deep diving behavior were also classified. Behavior associated with floating objects was characterized by tunas remaining primarily at depths of less than 50 m during the day. Behavior unassociated with floating objects was defined as the behavior of fish that made 10 or more dives to depths greater than 150 m during the daytime within

Table 1

Release and recapture information for six skipjack tuna (*Katsuwonus pelamis*) from which five archival tags were recovered. Archival tag 6553 was not recovered. The lengths given for each skipjack tuna were those recorded at the time of tagging. The release and recapture locations are given in decimal degrees. The linear displacements, in kilometers and directions (degrees), from the release to the recapture locations are given.

		Release		Recapture		Linear displacement		
Tag no.	Length (cm)	Date	Location	Date	Location	Days at liberty	Kilometers	Direction
4881	67	10 Apr 2004	1.98°N 95.32°W	18 Oct 2004	0.17°S 103.18°W	190	906	255°
4885	68	9 Apr 2004	1.98°N 95.32°W	30 Aug 2004	3.33°S 106.07°W	142	1332	244°
4908	67	9 Apr 2004	1.98°N 95.32°W	14 Nov 2004	2.42°S 117.82°W	218	2548	260°
4930	66	10 Apr 2004	1.98°N 95.32°W	6 May 2004	1.25°S 92.35°W	25	487	137°
6553	68	9 Apr 2004	1.98°N 95.32°W	25 May 2004	4.25°S 92.25°W	45	772	153°
6740	69	9 Apr 2004	1.98°N 95.32°W	21 June 2004	0.33°N 92.73°W	72	341	123°

a 24-h period. Surface-oriented behavior was defined as the behavior of fish that remained less than 10 m below the surface for periods greater than 10 minutes. Deep-diving behavior was defined as the behavior of fish that whose dives exceeded 500 m in depth. The quantitative characteristics describing the different types of behavioral events were derived from the AT records for the five fish.

The AT data sets were separated into periods of nighttime and daytime by the times of nautical twilight. Nighttime was classified as the period between the time of the first evening record after nautical twilight until the time of the last morning record before nautical twilight. The individual data sets for night and day were used in evaluations of diel differences in behavior and in habitat use.

The depth data obtained from the archival tags were analyzed in conjunction with ambient ocean temperatures, as measured by a calibrated Sea-Bird SBE 39 time-temperature-depth probe (Sea-Bird Electronics, Seattle, WA) deployed on 9 April 2004 to about 500 m depth near the TAO mooring at which the fish were tagged and released. For ambient temperatures at depths greater than 500 m we utilized the temperatures measured by a CTD (conductivity-depth-temperature) probe deployed off the National Oceanic and Atmospheric Association (NOAA) ship *Ka'imimoana* by the TAO Project Office (NOAA/Pacific Marine Environmental Laboratory) on 15 April 2004 to 1000 m depth near the same TAO mooring. These two temperature-depth profiles to depths of about 500 m, obtained from hydrocasts conducted six days apart, were virtually identical.

Results

Behavior patterns

Evaluations of the complete AT depth records, which ranged from 9.3 to 10.1 days, for the five skipjack tuna (Table 1; tag numbers: 4881, 4885, 4908, 4930, 6740) indicated that all five fish remained associated with the drifting vessel, following separation from the TAO mooring, until the vessel departed the area at 0940 h on 11 April 2004. Within 48 h of the time of separation, all five fish demonstrated distinct behavior unassociated with a floating object, including repetitive bounce diving during the day, and for each of the six subsequent days of the AT depth records. The variability in the daytime unassociated behavior patterns for each of the five fish during the approximate 8 days of AT depth records, following separation from the vessel, indicated that all five fish did not remain together.

The depth records for two representative fish (Fig. 1) showed similarities for both day and night for the first 48-h period, including a change in behavior when the vessel departed. The following day, both fish showed deeper average swimming depths, and the day after that both fish began to show repetitive bounce-diving behavior which continued for the remaining 7 days. The first day in which bounce diving occurred for a skipjack tuna (tag no. 4930), included the deepest dive, to a depth of 596 m, recorded for any of the five fish. During the last 3 days of depth records, in addition to the distinct diel differences seen for both fish, the average depth after a dive for the fish with tag 4930 (mean=47.1 m, 95% confidence interval (CI)=1.1) was significantly deeper (ANOVA: F=3.9, P<0.05) than for the fish with tag 4885 (mean=20.3 m, 95% CI=3.7). These depth differences and behavior patterns indicate that these two similar-size skipjack tuna did not remain together for long after their separation from the vessel.

Evaluations of the depth records for the five skipjack tuna carrying ATs in the equatorial EPO resulted in the discrimination of four distinct behaviors: 1) behavior associated with floating objects (abbreviated to "associated behavior" in this article; 2) behavior unassociated with floating objects (abbreviated to "unassociated behavior", 3) deep diving behavior, and 4) surface-oriented behavior. For the five archival tag data

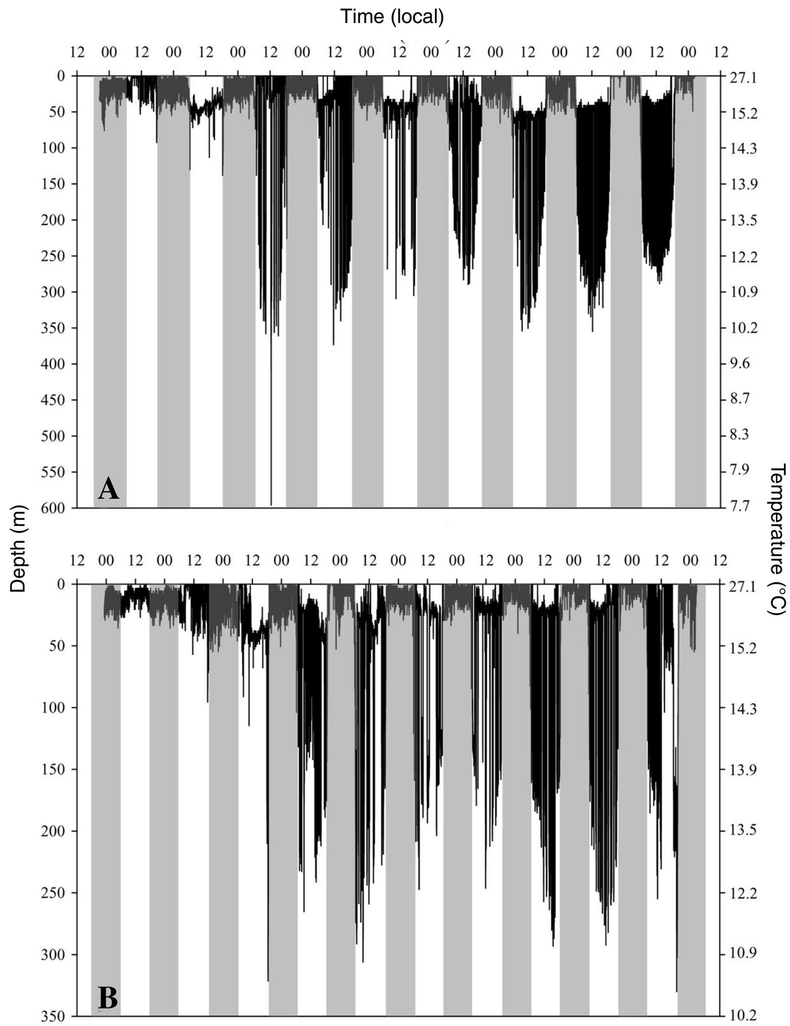

Figure 1

Depth and temperature records for skipjack tuna (*Katsuwonus pelamis*) with implanted archival tags after release. (**A**) Skipjack tuna (tag no. 4930) during April 10–20, 2004. (**B**) Skipjack tuna (tag no. 4885) during April 9–20, 2004. Time periods shaded gray indicate nighttime.

sets, behavior types 1, 2, 3, and 4 were evaluated for each day at liberty, and the descriptive characteristics presented.

Behavior associated with floating objects

The behaviors of the skipjack tuna released at the TAO mooring were distinct and discernible from the behaviors 48 h after the tuna separated from the mooring and the vessel. When the fish were associated with the mooring and the vessel, they remained primarily between the surface and 50 m during the night and day (Fig. 2A). The mean swimming depths were 13.6 m (range: 1–57.4 m) at night and 10.8 m (range: 1–92.3 m) during the day. Shortly before dusk, several dives to about 90 m were recorded, which were followed by an apparent change in the vertical movements during the night. The greater frequency of vertical movements observed during the night (1900 h to 0700 h) within the mixed layer probably represented foraging activity on prey organisms of the deep-scattering layer (DSL).

The delta T values, differences between the peritoneal cavity temperatures and the ambient temperatures (Fig. 2B), corresponding to the simultaneous depth records (Fig. 2A), showed an average of 2.2°C (95% CI=0.1°C, range:−0.4 to 14.1°C) during the day, and an average of 1.8°C (95% CI=0.1°C, range: −0.9 to 12.9°C) during the night. The depths of the mixed layer and the thermocline (depth of the 20°C isotherm) (Fiedler, 1992) were approximately 15 and 44 m, respectively. Whenever skipjack tunas made dives in excess of the thermocline depth, the delta T values were observed

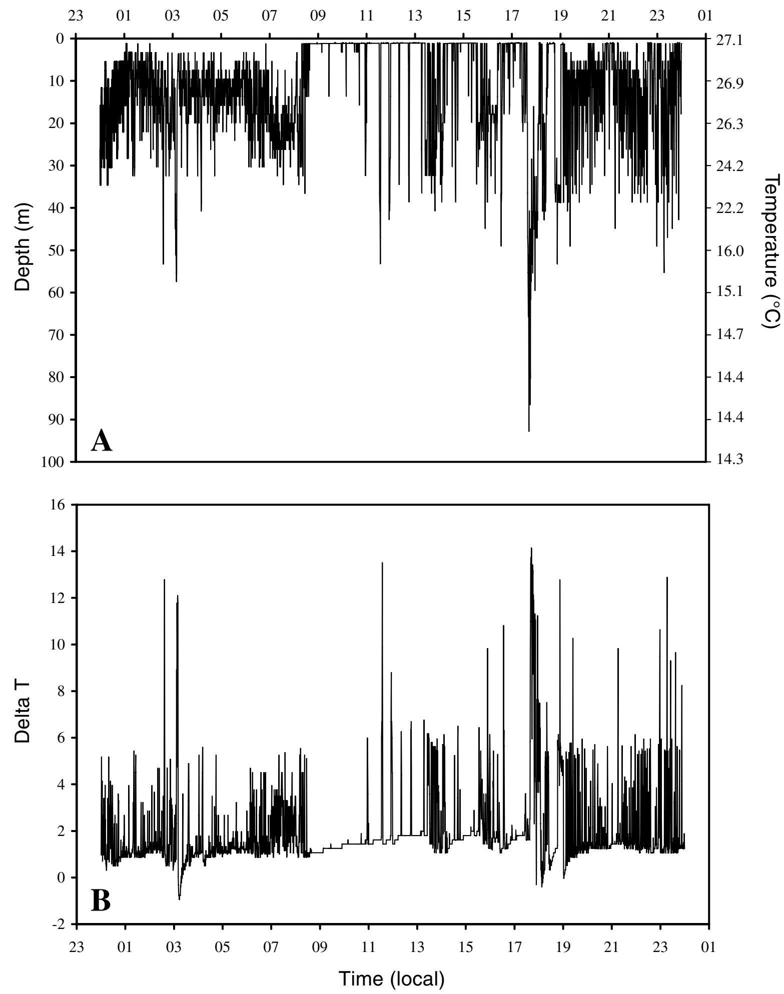

Figure 2

Depth and temperature records for a skipjack tuna (*Katsuwonus pelamis*) with an implanted archival tag (no. 4930) on 11 April 2004. (**A**) Skipjack tuna exhibiting behavior associated with floating objects. (**B**) Delta T's (differences between peritoneal cavity and ambient temperature) for the same time period as in (A).

to spike upward, indicative of the thermal excess of the peritoneal cavity in relation to the ambient temperature.

Behavior unassociated with floating objects

Within 48 hours after the skipjack tuna were unassociated with the vessel, they showed a distinct change in their vertical movements and behavior, exhibiting repetitive bounce diving between about 50 and 300 m during the day (Figs. 1 and 3A). They remained close to the surface at night, primarily within 50 m, showing distinct diel differences in behavior. Figure 3A shows 50 dives in excess of 150 m, and an average duration of 6.8 min (range: 3 to 17 min). The mean depth of these dives was 257 m (range: 153–355 m). During ascents following dives the fish returned to an average depth of 44 m, the approximate depth of the thermocline, before undertaking another dive. The delta T values (Fig. 3B), corresponding to the simultaneous depth records (Fig. 3A), showed an average of 1.9°C (95% CI=0.09°C, range: 0.8–13.5°C) during the night when the fish were primarily in the mixed layer. The delta T values during the day corresponding to the maximum depths of bounce dives were an average of 12.2°C (95% CI=0.3°C, range: 10.2–13.9°C). At the maximum depths of these bounce dives, the mode of the minimum ambient temperature experienced was 11.7°C and the peritoneal cavity temperature was 25.1°C.

For the five skipjack tuna, during days of unassociated repetitive bounce diving behavior, the mode for the time the first dive of the day occurred was 07:10 h (95%

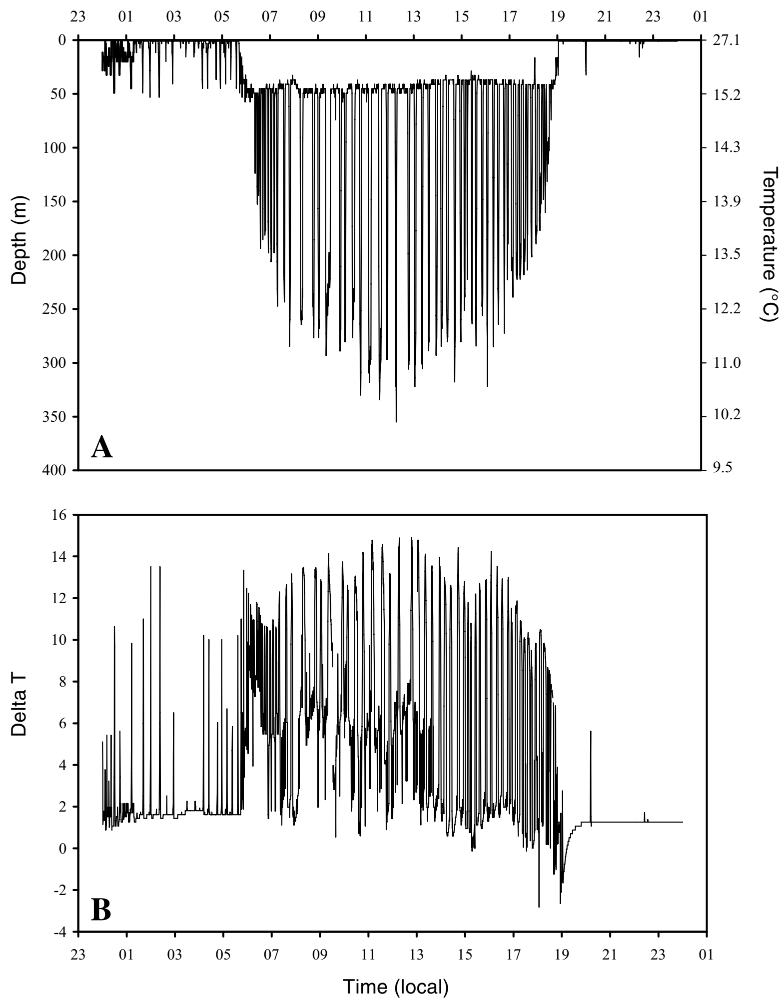

Figure 3

Depth and temperature records for a skipjack tuna (*Katsuwonus pelamis*) with an implanted archival tag (no. 4930) on 18 April 2004. (**A**) Skipjack tuna exhibiting unassociated repetitive bounce diving behavior. (**B**) Delta T's (differences between peritoneal cavity and ambient temperature) for the same time period as in (A).

CI=00:25 h) (Fig. 4A), the mean number of dives made per day was 21.2 (95% CI=4.9) (Fig. 4B), the mean duration of dives was 10.0 min (95% CI=0.9 min), and the mean depth of all dives was 230 m (95% CI=5.7) (Fig. 4C).

One skipjack tuna (tag no. 4885) made an extraordinary dive below the thermocline that lasted 119 min at 1700 h on 19 April 2004. From a depth of 36 m (22.3°C) with a peritoneal cavity temperature of 24.1°C, the fish dived to about 180 m (13.7°C) where it presumably foraged for 1 h 12 min. The fish then dived fairly rapidly to a maximum depth of 330 m (10.5°C) from which it gradually ascended toward the surface, remaining below the thermocline for another 47 min. From echosounder data collected aboard the vessel, it appeared that this fish was tracking the slowly ascending DSL and foraging on prey during this period. The minimum peritoneal cavity temperature observed in this study of 15.9°C was recorded continuously over a period of 7 mintes as this skipjack tuna ascended from 197 to 105 m depth.

Deep diving behavior

Only one of the five skipjack tuna (tag no. 4930) dived in excess of 500 m on 13 April 2004, beginning at 12:16 (Fig. 5). The maximum depth was 596 m, with a duration of 14 min in excess of 300 m (11.0°C), and 1 min 52 seconds in excess of 500 m (8.3°C). The dive profile shows that the fish dived initially to about 300 m where it remained for 4 minutes before continuing to 596 m and returning after about 2 minutes to between

300 m and 250 m, where it remained for about 12 minutes before returning to depths within the mixed layer. The peritoneal cavity temperature and delta T were 28.7°C and 3.8°C, respectively, at the beginning of the dive, 26.1°C and 18.4°C at the bottom of the dive, and 21.8°C and 9.8°C before the quick ascent at 12:38 h from 271 m to above the thermocline.

Surface-oriented behavior

For unassociated behavior, the mean number of surface-oriented events per day ranged from 5 to 23 (grand mean=9.4, 95% CI=2.4). The greatest number and longest duration of surface-oriented events occurred between 01:00 and 12:00 h (Fig. 6, A and B). The duration of events ranged from 10 to 214 min (mean=48.8 min, 95% CI=6.2 min) (Fig. 6 C).

Vertical habitat use

The vertical habitat use by the five skipjack tuna, for unassociated behavior, is presented as composite distributions by night and day along with the thermal profile in Figure 7. The vertical habitat-use distributions indicated that the fish remained above the depth of the thermocline (44 m) during the night 98.6% of the time but spent 37.7% of their time below the thermocline during the day.

Discussion

The results obtained in our study are useful for evaluating vertical movement patterns and habitat use for skipjack tuna on temporal scales previously undocumented. Knowledge about skipjack tuna movements, behavior, and habitat use, when tuna are associated and unassociated with floating objects, specifically in oceanic regions where large-scale industrial purse-seine fisheries operate, are important for understanding the ecology of this species, assessing catchability of the species for inclusion in stock assessments, and for evaluating potential modifications in fishing techniques for reduction of the bycatches of nontarget species.

In the present study, the vertical movement patterns of skipjack tuna when associated with floating objects were similar to those reported by Schaefer and Fuller (2005) for both skipjack and bigeye (*Thunnus obesus*) tunas associated with floating objects in the equatorial EPO. In both studies, the behavior of skipjack tuna was characterized by swimming depths predominantly shallower than the depth of the thermocline, throughout the day and night, and average nighttime depths were slightly deeper than those during the day. A plausible explanation for the greater average depths at night than during the day in these studies is the observed nighttime vertical distribution of the DSL and the foraging behavior of these tunas while associated with the moored buoys and the drifting vessel in this study area (Schaefer and Fuller, 2005). Ultrasonic telemetry

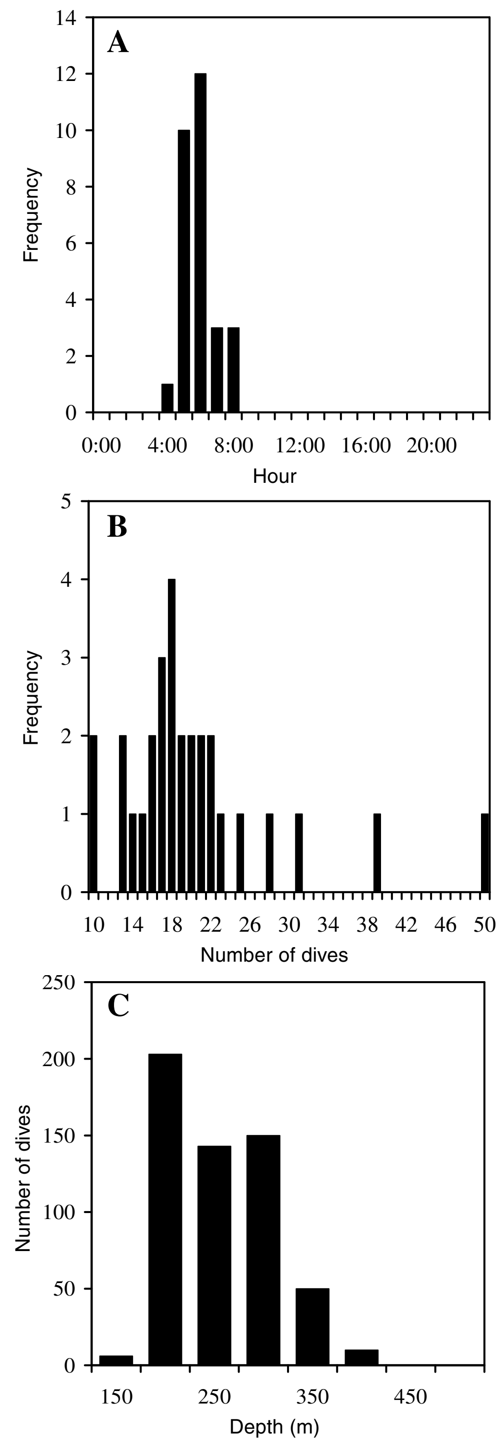

Figure 4

Summary of frequency data for repetitive bounce diving behavior not associated with floating objects for five skipjack tuna (*Katsuwonus pelamis*) over all dives. (**A**) Time the first dive of the day occurred. (**B**) Total number of dives for each day. (**C**) Depth of all dives.

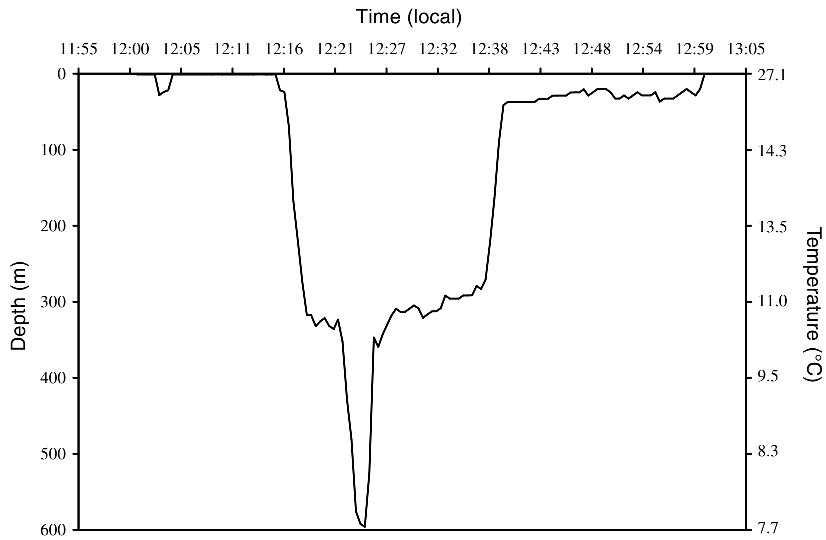

Figure 5

Depth and temperature data for a skipjack tuna (*Katsuwonus pelamis*) (tag no. 4930) exhibiting deep-diving behavior.

studies on the simultaneous behavior of skipjack, bigeye, and yellowfin (*Thunnus albacares*) tunas associated with drifting fish aggregation devices in the central Pacific Ocean also revealed that skipjack tuna swimming depths are predominantly shallower than the thermocline depth, about 115 m, throughout the day and night, but average nighttime depths are shallower than those during the daytime (Matsumoto et al.[1]).

The vertical movement patterns observed in this study for unassociated behavior of skipjack tuna, seen mostly as relatively high frequency repetitive bounce diving between dawn and dusk, was unexpected on account of the data from previously published studies (Matsumoto et al., 1984). There are, however, most likely other vertical movement patterns for skipjack tuna when unassociated with floating objects, from that observed in the present study. This pattern is probably dependent on the spatial and temporal habitat as well as forage availability. In the first published paper on acoustic tracking of tunas (Yuen, 1970), ultrasonic transmitters were used to study the behavior and movements of skipjack tuna off Hawaii. One individual, tracked for 8 days, undertook daily cyclical movements away from and back to a bank at consistent times, and from these movements Yuen (1970) first suggested that skipjack tuna can navigate and have a sense of time. The method Yuen (1970) used was suitable only to conclude that the fish remained close to the surface at night but could be found at various depths during the day. In a subsequent tracking study in Hawaiian waters, three skipjack tuna tagged with ultrasonic transmitters spent time between the surface (23.5°C) and 263 m (13.5°C) during the day, but remained above 75 m (22°C) depth at night (Dizon et al., 1978). Vertical positions of the skipjack tuna were determined only every 3 minutes, but indicated many rapid vertical movements, including some to depths below the thermocline. Although the three tracked skipjack tuna spent 85% of the time in water above 20°C (about 160 m), there were brief dives to temperatures between 12° and 14°C. The data retrieved from seven archival tags recovered from skipjack tuna released off northern Japan indicated that their nighttime movements were normally between the surface and depths of about 30 m, but during the daytime they exhibited frequent dives to depths below the thermocline and below ambient temperatures of 12°C; the greatest depth was reported to be 267 m (Ogura[2]). The lowest peritoneal cavity temperatures recorded in that study were around 17°C, whereas in the present study it was about 16°C. Skipjack tuna held in land-based tanks in Hawaii subjected to gradually lowered temperatures resulted in one mortality at 17°C, and none survived at 15°C for more than a few hours (Dizon et al., 1977).

A relatively dense DSL was observed at night on the echosounder during the time the skipjack tuna were associated with the vessel in this study. Skipjack tuna associated with a TAO mooring in this study area have been documented to be feeding at night near the surface on prey organisms of the DSL (Schaefer and Fuller, 2005). The repetitive bounce diving observed in the present study for unassociated skipjack tuna during the day apparently reflects foraging activity on prey organisms of the diurnally migrating DSL (Kuznetsov et al., 1982). The profile in Figure 3A of repetitive bounce diving shows a higher frequency of dives during the first hour at around dawn when the DSL is descending and during the 1.5 h period preceding dusk during the ascent of the DSL. Sonic tracking studies have also shown that the diel vertical migrations of bigeye tuna are closely associated with vertical movements of organisms of the DSL (Josse et al., 1998; Dagorn et al., 2000). When in areas with a high density DSL it appeared that skipjack tuna were also commonly foraging on DSL prey organisms near the surface at night and at depths well below the thermocline during the day. Depths of the DSL in the eastern tropical Pacific have been reported to be 300–400 m during the day and 0–100 m at night (Fiedler et al., 1998). 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 depths and temperatures to which skipjack tuna were repetitively bounce diving during the day in this study were mostly between 200 to 300 m and 10.9° to 13.5°C, respectively. In the same general area of the equatorial EPO, bigeye tuna unassociated with floating objects have been reported to undertake prolonged dives to similar depths and temperatures during the day to forage on DSL prey organisms (Schaefer and Fuller, 2002). A recent study of yellowfin tuna behavior off northern Mexico in the EPO, based on archival tag data, has revealed that yellowfin tuna are also capable of exploiting the vertical habitat below the thermocline by repetitively bounce diving during the day between about 150 and 250 m and between 11°C and 13.5°C, respectively (Schaefer et al., in press).

An ecological benefit of endothermy in tunas is an expanded thermal niche, including exploitation of vertical habitat by skipjack tuna (Block, 1991; Graham and Dickson, 2001). There are several anatomical and physiological differences between skipjack and bigeye tunas (Brill and Bushnell, 2001; Graham and Dickson, 2001) that would explain why skipjack, unlike large bigeye (Holland and Sibert, 1994), are unable to remain for extensive periods at optimal foraging depths below the thermocline. Instead they exhibit repetitive bounce diving behavior to employ both behaviorally and physiologically induced thermoregulation for partial independence from cold water effects on temperature-dependent functions (Graham and Dickson, 2004). Thermal inertia also helps stabilize body temperatures during dives, and larger bigeye tuna have been shown to have slower cooling rates than smaller individuals (Schaefer and Fuller, 2002). The heart rates of tunas are reduced by lower temperatures and hypoxia; therefore excursions below the thermocline may be limited by the diminished capacity of the heart to supply the oxygen requirements of the endothermic tissues (Brill and Bushnell, 2001; Blank et al., 2004).

Skipjack tuna surface-oriented behavior was observed in this study to occur primarily between 0100 h and 1200 h. Skipjack tuna within large multispecies aggregations associated with floating objects have previously been reported to show monospecific horizontal separation and "breezing" (rippling of the water surface) behavior near dawn (Schaefer and Fuller, 2005). Informa-

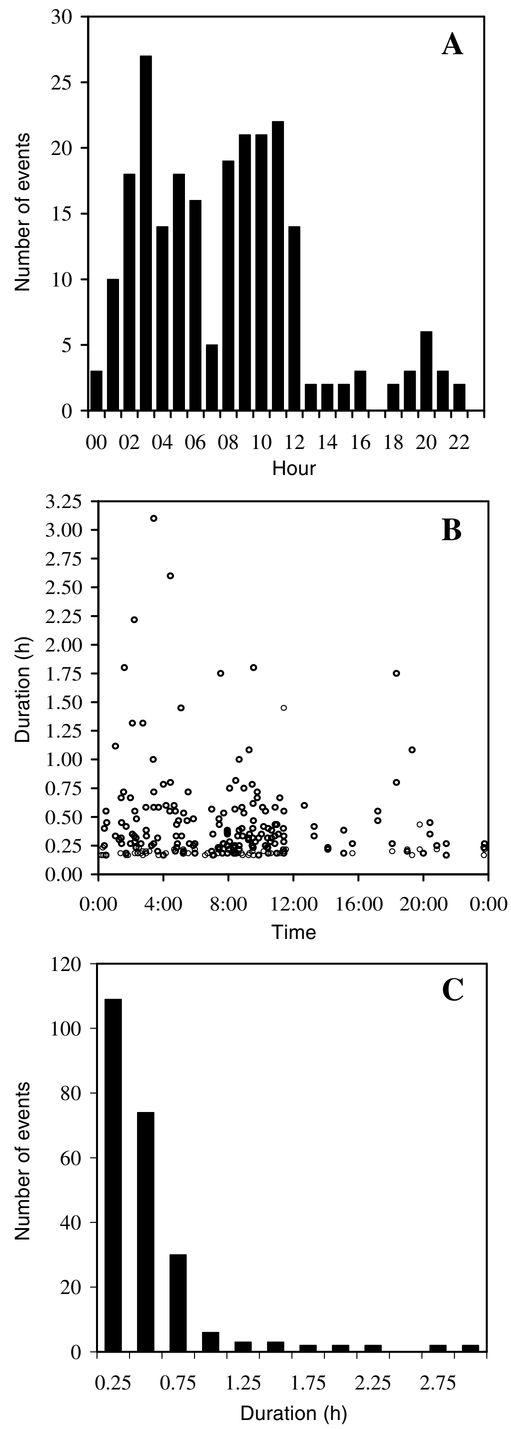

Figure 6

Summary of surface-oriented events for skipjack tuna (*Katsuwonus pelamis*). (**A**) Hour of the day at which the events occurred. (**B**) Beginning time and duration of each event. (**C**) Duration of events.

tion on surface-oriented behavior of skipjack is relevant to understanding catchability (vertical vulnerability plus spatial vulnerability) by purse-seine vessels and may be useful to incorporate into the standardization of catch and effort data. In addition, this information on occurrence and duration of surface-oriented behavior is useful for evaluating optimal detection periods for the use of remote-sensing techniques for conducting fisheries-independent abundance estimation of this species with the use of airborne optical equipment, including LIDAR (light detection and ranging) (Gauldie et al., 1997).

Large-scale studies with archival tags are needed to improve our understanding of skipjack tuna movements, behavior, and habitat use, all of which, in turn, will provide useful information for stock assessments of this valuable resource. Elucidating skipjack tuna behavior may also permit the design of optimal fishing strategies for this species, including the reduction of current bycatch levels associated with purse-seine fishing around floating objects. Archival tags are now capable of storing data for multiple years; this capacity provides a remarkable opportunity to evaluate ontogenetic changes and the influence of seasonal and annual environmental variability on the behavioral characteristics of tuna.

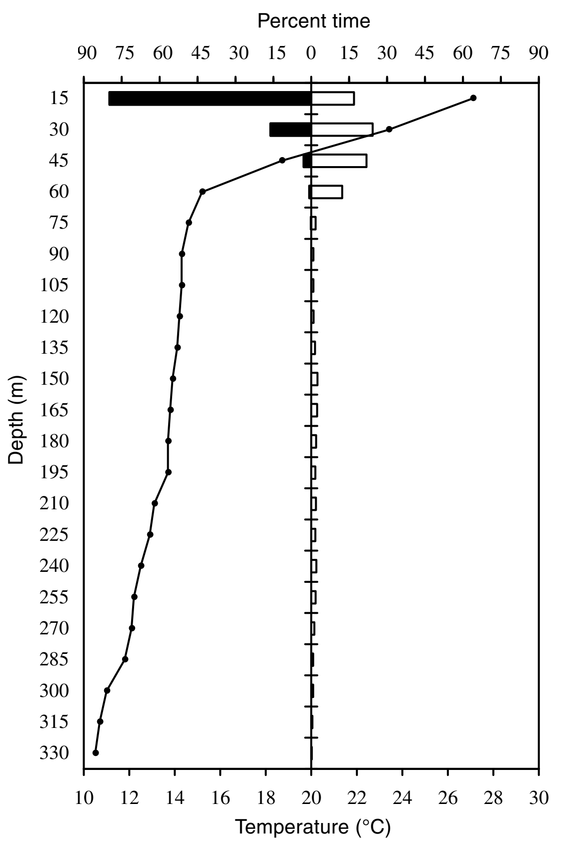

Figure 7

Composite vertical habitat-use distribution for five skipjack tuna (*Katsuwonus pelamis*) for all days of behavior unassociated with floating objects. Depth frequencies during the night are represented by the black bars and depth frequencies during the day are represented by open bars; the average ambient temperatures (line of connected dots) are shown within depth intervals.

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