Journal of Fish Biology (2009) **74,** 1434–1449
doi:10.1111/j.1095-8649.2009.02209.x, available online at http://www.blackwell-synergy.com

Habitat and behaviour of yellowfin tuna *Thunnus albacares* in the Gulf of Mexico determined using pop-up satellite archival tags

K. C. Weng*†, M. J. W. Stokesbury‡, A. M. Boustany§, A. C. Seitz||, S. L. H. Teo¶, S. K. Miller# and B. A. Block**

**School of Ocean and Earth Science and Technology, University of Hawaii at Manoa, Honolulu, HI 96822, U.S.A., ‡Biology Department, Dalhousie University, Halifax, NS, B3H 4J1 Canada, §Marine Science and Conservation, Duke University, Durham, NC 27708, U.S.A., ||Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, AK 99775, U.S.A., ¶Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, U.S.A., #Tag-A-Giant Foundation, Babylon, NY 11702, U.S.A. and **Hopkins Marine Station of Stanford University, Pacific Grove, CA 93950, U.S.A.*

(Received 8 July 2008, Accepted 22 January 2009)

This study presents the first data on movement, habitat use and behaviour for yellowfin tuna *Thunnus albacares* in the Atlantic Basin. Six individuals were tracked in the Gulf of Mexico using pop-up satellite archival tags. Records up to 80 days in length were obtained, providing information on depth and temperature preferences as well as horizontal movements. *Thunnus albacares* in the Gulf of Mexico showed a strong preference for the mixed layer and thermocline, consistent with findings for this species in other ocean basins. Fish showed a diel pattern in depth distribution, remaining in surface and mixed layer waters at night and diving to deeper waters during the day. The vertical extent of *T. albacares* habitat appeared to be temperature limited, with fish generally avoiding waters that were >6° C cooler than surface waters. The vertical and thermal habitat usage of *T. albacares* differs from that of bigeye *Thunnus obesus* and bluefin *Thunnus thynnus*, *Thunnus orientalis* and *Thunnus maccoyii* tunas. These results are consistent with the results of earlier studies conducted on *T. albacares* in other oceans.

Key words: by-catch; fishery management; satellite telemetry.

INTRODUCTION

Understanding the biology of an organism requires knowledge of where it lives and of its various movements between different habitats (Turchin, 1998). In the case of organisms that are hunted by humans, knowledge of movements and habitat preferences enables improvements to be made; estimates of population abundance and health, such as fishery stock assessment models (Brill & Lutcavage, 2001), and in predicting the vulnerability of a species to capture by different types

†Author to whom correspondence should be addressed. Tel.: +1 808 956 6346; fax: +1 309 423 4204; email: kevincmweng@gmail.com

of fishing gear (Sharp, 1978; Ward & Myers, 2005). Knowledge of habitat use, particularly in the vertical dimension, is also required for the interpretation of stable isotope ratio studies of diet and trophic level (Graham *et al.*, 2007).

Electronic tracking technologies have yielded new insights into the biology of teleosts (Block *et al.*, 2005), sharks (Weng *et al.*, 2005), mammals (Le Boeuf *et al.*, 2000), birds (Weimerskirch *et al.*, 2002), reptiles (Hays *et al.*, 2004) and cephalopods (Gilly *et al.*, 2006). One electronic tracking technology that provides fishery-independent data collection for submerged marine animals is the pop-up satellite archive tag (PSAT) (Block *et al.*, 1998*a*). PSATs archive data while attached to the organism, detach at a programmed date, surface and transmit data summaries to Argos satellites (Block *et al.*, 1997; Lutcavage *et al.*, 1999; Boustany *et al.*, 2001; Gunn & Block, 2001; Marcinek *et al.*, 2001; Weng *et al.*, 2007*a*). PSATs yield long records that extend far beyond the recovery behaviour that often follows the stress of capture (Holland *et al.*, 1990*a*; Block *et al.*, 1992, 1997; Boustany *et al.*, 2001) and are free of behavioural responses to tracking vessels (Carey & Olson, 1982; Block *et al.*, 1997; Dagorn *et al.*, 2001). Unlike archival tags, PSATs are not dependent on the distribution of fishing effort for the recovery of data (Gunn, 1994; Block *et al.*, 1998*b*).

The yellowfin tuna *Thunnus albacares* (Bonnaterre) occupies tropical and subtropical oceans worldwide and is the target of major fisheries throughout its range (Collette & Nauen, 1983). Vertical movements and environmental preferences of *T. albacares* have been studied by a number of investigators using acoustic and satellite telemetry as well as archival data loggers (Table I). Acoustic tracking in the Pacific and Indian Oceans has demonstrated that *T. albacares* exhibit an oscillatory diving pattern and spend the majority of their time in the surface mixed layer (where temperatures are similar across a layer of near-surface water) and thermocline (where temperatures decrease rapidly with depth), with the ability to dive below the thermocline (where temperatures are similar across a layer of subsurface waters) to several 100 m depth for brief durations (Carey & Olson, 1982; Holland *et al.*, 1990*b*; Cayre & Marsac, 1993; Block *et al.*, 1997; Josse *et al.*, 1998; Brill *et al.*, 1999). Acoustic tracking studies found that *T. albacares* did not remain in cool or oxygen-deficient waters for more than a few minutes (Cayre & Marsac, 1993; Block *et al.*, 1997). The species typically has deeper daytime and shallower night-time distributions (Holland *et al.*, 1990*b*), but diel patterns are muted at the northern extent of the species' range (Block *et al.*, 1997). Archival tagging studies have corroborated the findings of acoustics telemetry studies but have also revealed that *T. albacares* do display impressive diving abilities, sometimes to depths exceeding 1000 m and temperatures cooler than 5° C (Dagorn *et al.*, 2006; Schaefer *et al.*, 2007).

Oxygen concentration is a limiting factor for all fishes, though a wide degree of variation exists for tolerance to hypoxic conditions (Brill, 1994). Cayre & Marsac (1993) noted that *T. albacares* rarely moved into waters with oxygen lower than 5·7 mg l^{-1}, where the maximum gradient of the oxycline occurred. In laboratory studies, *T. albacares* the first physiological response (bradycardia) to low oxygen at 5·1–6·1 mg l^{-1} (Bushnell *et al.*, 1990; Bushnell & Brill, 1992). These findings suggest that *T. albacares* may access sub-thermocline prey resources to a lesser extent than swordfish *Xiphias gladius* L. (Carey & Robison,

TABLE I. Summary of *Thunnus albacares* tracking studies providing depth and temperature data

Study	Location	*n*	L_F (mm)	Track length (days)	Greatest depth (m)	Minimum temperature (° C)	Greatest ΔT* (° C)	Modal ΔT (° C)
Carey & Olson (1982)	Clipperton Island	4	870–980	0·4–2·0	464	9	15	n/a
Holland *et al.* (1990*b*)	Hawaii	11	440–750	0·2–2·0	150	18	7	5
Cayre & Marsac (1993)	Comoros Islands	3	730–1050	0·5–1·0	170	21	6	n/a
Block *et al.* (1997)	California Bight	3	750–940	2·5–3·0	300	7	12	7
Josse *et al.* (1998)	French Polynesia	1	600	1	250	n/a	n/a	n/a
Brill *et al.* (1999)	Hawaii	5	1480–1670	0·5–3·5	250	13	11	8
Dagorn *et al.* (2006)	Seychelles	1	1340	98	1160	5·8	23·3	
Schaefer *et al.* (2007)	Eastern Pacific	20	670–1300	154–1161	1173	4·5	23·9	8
Present study	Gulf of Mexico	7	1360–1550	5–80	432	10·2		n/a

L_F, fork length; n/a, not available.
*ΔT, sea surface temperature minus minimum temperature.

1981), bigeye tuna *Thunnus obesus* (Lowe) (Holland *et al.*, 1990*b*; Josse *et al.*, 1998; Dagorn *et al.*, 2000) and bluefin tuna *Thunnus thynnus* (L.) (Block *et al.*, 2001).

MATERIALS AND METHODS

The movements and environmental preferences of *T. albacares* were monitored with PSATs (PAT Tag version 2.00; Wildlife Computers; www.wildlifecomputers.com) (Block *et al.*, 1998*a*; Gunn & Block, 2001). *Thunnus albacares* were captured in the Gulf of Mexico using commercial longline gear in the spring of 2000. Longline sets occurred during day and night at depths of 40–120 m using circle hooks baited with squid *Loglio opalescens* or sardines *Sardinella aurita* Valenciennes.

The locations of tagging events were recorded using the vessel's global positioning system (GPS). Tags were attached to titanium darts with 136 kg monofilament line (*c.* 150 mm). All fish were tagged at the side of the vessel using a 2 m pole. The dart was inserted into the dorsal musculature of the fish, between the pterigiophores at the base of the second dorsal fin, such that the tag trailed behind the second dorsal fin. Following attachment of the tag, the fishing line was cut near the hook, or the hook was removed to release the fish. Because fish were not brought on deck, mass was estimated by commercial fishermen, and fork length (L_F) was derived from a L_F and M regression (Le Guen & Sakagawa, 1973).

PSATs (on-board software versions 1.06 and 1.09) were programmed to collect data at 2 min intervals, summarize the data into bins and transmit the summary information to satellites-based Argos receivers. These versions of the PSAT did not allow the estimation of longitude from the tag light sensor and clock. For this study, PSAT were programmed with bins ranging from 2 to 12 h. A tag with 2 h bins pooled data from 0600 to 0759 hours into one bin, 0800 to 0959 hours into the next bin and so on. The summary data comprised time at depth, time at temperature and a temperature profile for the deepest dive within each time bin. The temperature profile provided eight individual depth and temperature recordings spaced evenly between the shallowest and the deepest points reached during the time bin. Depth measurements were summarized as the percentage of the time bin that was spent within 12 depth ranges. These depth ranges were chosen to provide higher resolution at shallower depths where fish were expected to spend the majority of their time. Temperature measurements were summarized as the percentage of the time bin that was spent within consecutive 2° C increments. End locations were obtained when tags popped off, based on the Doppler shift of a tag's radio transmissions to the Argos satellites. Argos provides the following 1-S.D. error radii for geopositions: quality zero, unknown error; quality one, <1500 m; quality two, <500 m quality three, <250 m (Anon., 2003).

After each tagging event, a depth–temperature profile extending to *c.* 200 m depth was obtained using a depth–temperature recorder (ABT-1; Alec Electronics; www.alec-electronics.co.jp). A conductivity–temperature–depth array with an oxygen sensor (CTD, Sea-Bird Electronics; www.seabird.com) was deployed by hand if sea conditions were calm. Sea surface temperature (SST) patterns for the Gulf of Mexico were obtained *via* images taken by satellite-based advanced very high resolution radiometers (AVHRR; National Oceanic and Atmospheric Administration Washington, DC, U.S.A.).

To determine if a PSAT remained attached to the fish for the programmed duration, the depth record collected by the tag's pressure sensor was examined. If the record showed an abrupt transition to continuous zero depth readings, it was assumed that the tag had prematurely detached from the fish and was floating at the surface. For prematurely detached tags, only data prior to the premature detachment are presented. The Argos end position was considered to be incorrect for tags that detached from the fish prior to the pop-up date and thus, drifted at the surface for a period of time before transmitting. Results are presented as mean ± 1 S.E. unless otherwise stated.

RESULTS

Ten *T. albacares* were tagged with PSATs in the Gulf of Mexico in the spring of 2000 and six tags successfully reported data (Fig. 1). A cumulative total of 210 days of PSAT data on *T. albacares* distribution, depth and ambient temperature occupancy were obtained (Table II).

ENVIRONMENTAL PREFERENCES AND DAY–NIGHT DEPTH DIFFERENCES OF *THUNNUS ALBACARES*

Thunnus albacares primarily occupied the mixed layer or thermocline, spending 93·4 ± 2·0% of their time above 200 m (Fig. 2). Fish spent 72·0 ± 5·1% of their time in the upper 50 m of the water column (Fig. 2), which corresponds approximately to the mixed layer (Fig. 3). Depth distribution was shallower at night when fish spent 84·9 ± 4·6% of their time above 50 m, compared to 59·3 ± 6·1% during the day. During the night, *T. albacares* spent only 10·7 ± 3·7% of their time deeper than 50 m, compared to 34·2 ± 7·0% during the day. *T. albacares* spent 99·5 ± 0·2% of their time in waters warmer than 14° C (Fig. 2). Nocturnal distribution was warmer, with fish spending 90·7 ± 0·2% of their time in waters warmer than 22° C, compared to 64·7 ± 6·2% during the day. *Thunnus albacares* did not enter cold waters beneath the thermocline, spending only 0·7 ± 0·5% of their time in waters cooler than 14° C during the day and none during

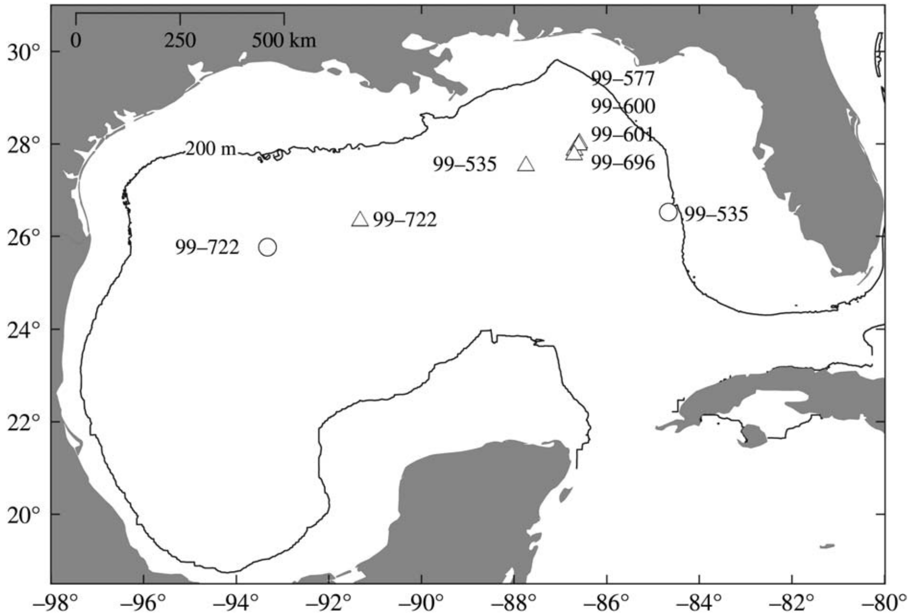

FIG. 1. Deployment and pop-up positions for pop-up satellite archival tags attached to *Thunnus albacares* in the Gulf of Mexico during 2000. Deployment locations (△) are shown for the six tags that successfully reported data to Argos satellites. Pop-up endpoint positions (○) are shown for two tags that remained on the fish for the entire track, as indicated by the depth record. The 200 m contour is shown to delineate the edge of the continental shelf.

TABLE II. Summary of *Thunnus albacares* tracks from pop-up satellite archival tags in 2000

Fish	L_F (cm)*	Date tagged	Duration (days)	Deployment position	Pop-up position	Greatest depth (m)	Lowest temperature (° C)
99-722	136	25 April	6	26°23′ N; 91°20′ W	25°47′ N; 93°20′ W	150	16·4
99-535	154	3 May	28	27°35′ N; 87°45′ W	26°24′ N; 84°39′ W	432	12·6
99-696	140	9 May	12	27°49′ N; 86°43′ W	n/a†	188	16·4
99-577	145	10 May	10	28°04′ N; 86°36′ W	n/a†	250	13·0
99-600	148	10 May	74	27°55′ N; 86°42′ W	n/a†	272	10·2
99-601	155	10 May	80	28°02′ N; 86°37′ W	n/a†	300	12·8

n/a, not available.
*Fork length (L_F) estimated by sight.
†Premature release of tags occurred, followed by a drifting phase, so pop-up position did not represent position of fish.

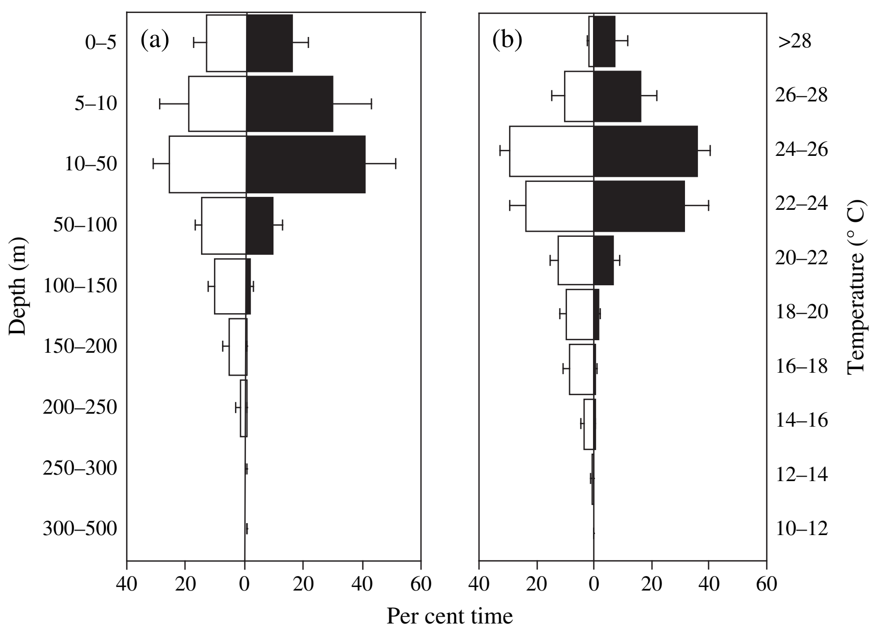

FIG. 2. (a) Time-at-depth for six *Thunnus albacares*, averaged for 208 days. Fish primarily inhabit the upper 50 m of the water column, corresponding to the mixed layer and upper thermocline. Vertical distribution is shallower and narrower during the night (■) with deeper dives occurring during the day (□). (b) Time-at-temperature for six *T. albacares*, averaged for 208 days. Fish occupied a narrower range of temperatures during the night (■) than during the day (□). Daytime diving increased the thermal range during the day, but fish avoided cold waters, spending only 0·7 ± 0·5% (mean ± S.E.) of their time in waters cooler than 14° C. Values are mean ± S.E.

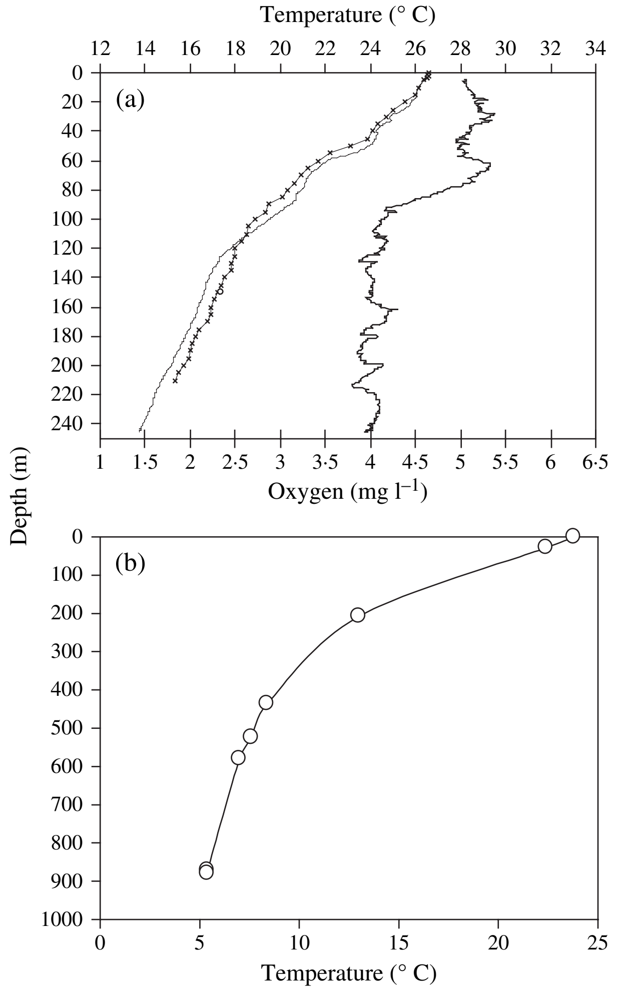

FIG. 3. (a) Temperature profiles from a conductivity, temperature and depth recorder (CTD; ——) and bathythermograph (⋆); the rightmost line shows CTD oxygen profile (——). All data taken from 10 to 13 May 2000. (b) Temperature profile from a pop-up satellite archival tag (PSAT 99-588) on a *Thunnus thynnus* in the same area on 22 April 2000, showing that thermocline extended beyond 500 m.

the night (Fig. 2). The coldest temperature recorded was 10·2° C during a dive to 272 m (fish 99–600).

Fish 99–600 provided a 74 day track, during which the deepest dive during each 12 h period varied between 60 and 312 m. Dive depths for this fish were significantly deeper during the day (*t*-test, d.f. = 66, $P < 0{\cdot}01$) when the fish spent 22·5 ± 4·0% of its time deeper than 150 m, compared to 1·0 ± 0·27% during the night. The fish experienced significantly lower temperatures during the day (*t*-test, d.f. = 66, $P < 0{\cdot}01$), spending 29·9 ± 4·6% of its time in waters cooler than 20° C, compared to 6·0 ± 1·9% during the night.

OCEANOGRAPHIC CONDITIONS DURING TRACKING

Oceanographic conditions during the cruise were characterized using a bathythermograph (http://www.jfe-alec.co.sp/html/english_top.htm) and conductivity, temperature and depth recorder (CTD) probes deployed from the fishing vessel, as well as from the depth–temperature function of the PSAT deployed on the fish. The mixed layer varied between 0 and 50 m during the cruise (Fig. 3), and this range did not change during the tracking period for the six PSAT-tagged fish based on temperature profile data from the PSAT. The CTD and ABT deployments were limited to 240 m, but a PSAT deployed on a *T. thynnus* sampled temperature to nearly 1000 m depth on 22 April 2000 (Fig. 3). This profile shows that the thermocline extended beyond 500 m where temperatures were <10° C.

The oxygen concentration during the tagging cruise was *c.* 5 mg l^{-1} from the surface to 60 m, with an oxycline to *c.* 100 m where the concentration reached an asymptote of 4 mg l^{-1}, continuing to the limit of measurement at 240 m (Fig. 3). Measurements of oxygen after the end of the cruise were not available.

DEPTH AND TEMPERATURE PREFERENCES OF *THUNNUS ALBACARES* IN DIFFERENT WATER MASSES

Measurements of the depth and temperature preferences of *T. albacares* (99–535) were made in two distinct water masses, showing that the fish changed its depth and temperature distributions upon moving to a different water mass on 15 May 2000. The track began in a cooler water mass to the north-west of the Loop Current, and the fish moved south-east into the Loop Current during the 28 day track (Fig. 4). The distribution of depth–temperature measurements falls into two distinct clusters, corresponding to the two time periods of the track. The first water mass occupied by the fish was cooler and had a shallower mixed layer, and the fish had a shallower depth distribution while in this water mass. While in the cooler watermass, the fish spent 88·9 ± 3·3% of the daytime in the upper 50 m, compared to 71·8 ± 3·2% while in the warmer watermass, and 93·5 ± 1·6% of the night-time in the upper 50 m, compared to 74·9 ± 3·2% while in the warmer watermass [Fig. 4(a), (b)]. While in the cooler watermass the fish spent 6·1 ± 2·5% of the daytime in waters 26° C or warmer, compared to 71·6 ± 3·5% while in the warmer watermass and 3·5 ± 1·5% of the night-time in waters 26° C or warmer, compared to 82·2 ± 3·2% while in the warmer watermass.

The maximum daily depths increased when the fish moved into the warmer water mass, while the temperatures it was exposed to during these dives increased. The mean maximum depth during each 2 h bin while in the warmer watermass was 108·9 ± 8·1 m and was significantly (17·3–55·5 m, 95% CI) deeper than the mean depth while in the cooler watermass (*t*-test, d.f. = 99, $P < 0{\cdot}01$). The mean daily minimum temperature experienced while in the warmer watermass was 24·5 ± 0·3° C, and was significantly (1·7–3·3° C; 95% CI) warmer than the mean temperature while in the cooler watermass (*t*-test, d.f. = 105, $P < 0{\cdot}01$).

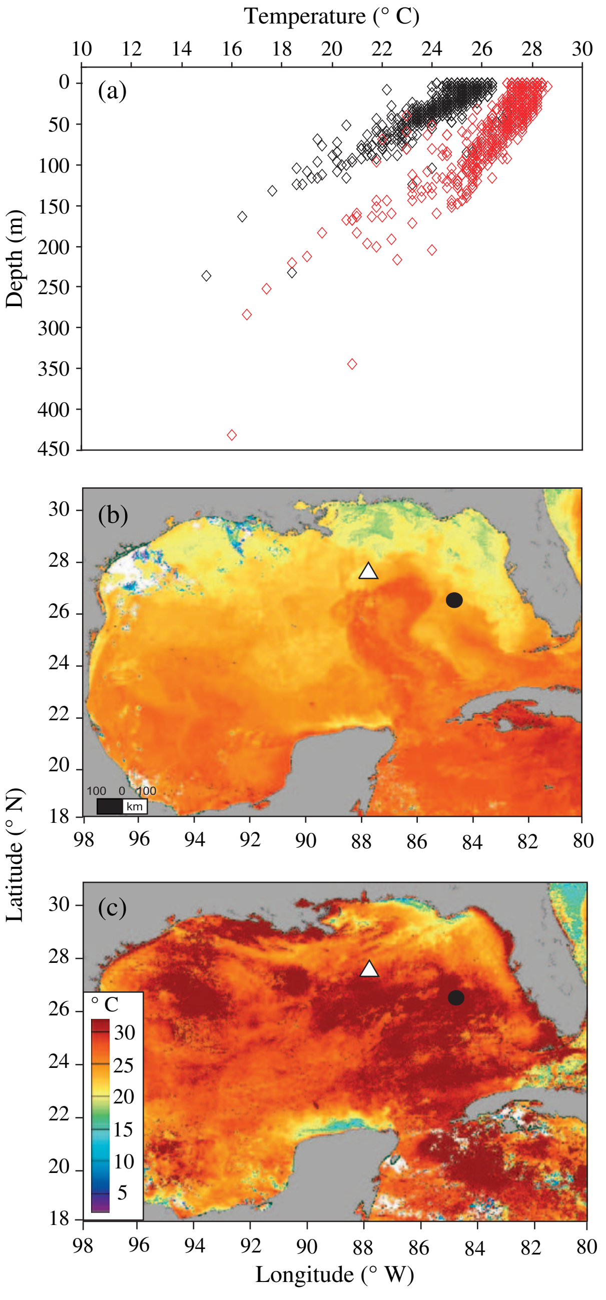

FIG. 4. (a) Distribution of temperature profiles from *Thunnus albacares* (fish 99-535) showing occupancy of two watermasses. Measurements taken prior to 15 May 2000 (◇) lie in a separate region than those taken after 15 May (◇), demonstrating that the fish occupied a cooler watermass during the first part of the track and used a shallower habitat. Upon moving into a warmer watermass the fish used a deeper but not cooler habitat. (b) Sea surface temperature (SST) image (3 day composite) of the Gulf of Mexico taken from 1 to 3 May 2000 showing the locations of tag deployment (△) and pop-up (●) for fish 99-535. The fish swam south-east from a cooler area into the warmer loop current. (c) The SST image from 29 to 31 May 2000 showing that the Gulf warmed during the track.

DISCUSSION

Tagged *T. albacares* spent the majority of their time in the mixed layer, undertook brief dives through the thermocline and oxycline, and maintained shallower distributions during night-time than daytime. These results are consistent with the results of earlier studies conducted on *T. albacares* in other oceans (Table I). Prior to the 1980s, the understanding of *T. albacares* behaviour, range and ecology were based on fishery data and conventional tagging. Acoustic telemetry yielded new information into the behaviour and ecology of *T. albacares*, but continuous observations were limited to $\leq$4 days (Carey & Olson, 1982; Holland *et al.*, 1990*b*; Cayre & Marsac, 1993; Block *et al.*, 1997; Josse *et al.*, 1998; Brill *et al.*, 1999). The acoustic studies revealed that *T. albacares* were fish of the mixed layer, rarely moving beneath the thermocline. Some authors have noted behavioural responses of acoustically tracked fish to the tracking vessel as well as altered behaviour in the hours or days after release (Carey & Olsen, 1982, Block *et al.*, 1997; Brill *et al.*, 1999). Studies employing sonic tags and listening stations yield long-term data about visitation to specific features or locations, but are not continuous as data are only acquired when the tagged animal is proximal to a listening station (Klimley & Holloway, 1999; Klimley *et al.*, 2003; Ohta & Kakuma, 2005). Studies employing archival data-logging tags enabled long records to be obtained from *T. albacares*, corroborating the finding that the species spends most of its time in the mixed layer and thermocline but also revealing impressive diving abilities. On rare occasions, *T. albacares* make dives in excess of 1000 m and to waters cooler than 5° C (Dagorn *et al.*, 2006; Schaefer *et al.*, 2007).

VERTICAL NICHE

The environmental preferences of *T. albacares* define the vertical niche of the species, and thereby its relationship with other predators and prey in the pelagic environment. *Thunnus albacares* have been studied using electronic tags over most of the species' temperature and latitudinal range and have been shown to prefer the mixed layer and thermocline (Carey & Olson, 1982; Holland *et al.*, 1990*b*; Cayre & Marsac, 1993; Block *et al.*, 1997; Josse *et al.*, 1998; Brill *et al.*, 1999). The absolute temperatures within these zones vary and depth distributions range from up to 300 m in French Polynesia (Josse *et al.*, 1998) to 20 m in the colder waters of the California Bight (Block *et al.*, 1997). Thus, the species does not appear to respond directly to depth but rather to vertical temperature structure (Brill *et al.*, 1999; Kitagawa *et al.*, 2000). While *T. albacares* have been tracked in water temperatures from 7 to 28° C, temperature changes during single dives are usually restricted to a range of *c.* 8° C based on published tracking studies (Table I). In the present study, fish spent the majority of their time in water shallower than 50 m and dives made within 2 h time periods were restricted to a variation in temperature of 6° C in 90% of all cases, which corresponds approximately to the mixed layer and thermocline (Fig. 3). More recently, *T. albacares* have been shown to enter much greater depths and cooler temperatures than those bracketed by a 6–8° C difference from surface temperatures (Dagorn *et al.*, 2006; Schaefer *et al.*, 2007), demonstrating greater cold tolerance than indicated by most studies. It is likely that these rare movements cause thermal or oxygen debts that must be repaid by returning to the mixed layer and are undertaken for reasons such as escape from predators.

Thunnus albacares 99–535 moved between two water masses with distinct thermal profiles, and upon entering into a warmer watermass, the fish increased its dives by >50 m without exposing itself to cooler waters (Fig. 4), consistent with the limitation of vertical movements by temperature. *Thunnus albacares* probably optimize their searching strategy by adjusting the vertical extent of movements within their thermal niche (Sims *et al.*, 2008). The behavioural plasticity shown by fish 99-535 is similar to that in other mega-vertebrates such as leatherback turtles, which display deep diving and diel vertical migration in some areas, but shallow diving and no diel patterns in others, probably reflecting different behaviour in their prey in different regions (Hays *et al.*, 2006).

The geographic range and diving behaviour of *T. albacares* may be related to thermal effects on cardiac performance. The heart rate, stroke volume and power output of *Thunnus* spp. hearts vary with temperature (Korsmeyer *et al.*, 1997; Brill *et al.*, 1999; Blank *et al.*, 2002), and there is a 72% decrease in *T. albacares* cardiac output when temperature falls from 25 to 10° C (Blank *et al.*, 2002). Measured Q_{10} values for cardiac output are 2·37 (18–28° C) (Korsmeyer *et al.*, 1997), 1·6 (20–25° C) and 4·6 (10–15° C) (Blank *et al.*, 2002). These results indicate that decreases in ambient temperature cause major reductions in cardiac output, particularly below 15° C, which may hamper *T. albacares*' ability to flee predators or pursue prey.

Oxygen may also be a critical factor in the habitat available to *T. albacares*. In the laboratory, the species responds to dissolved oxygen concentrations below *c.* <5 mg l^{-1} by increasing mouth gape and ventilation volume and decreasing heart rate (Bushnell *et al.*, 1990; Bushnell & Brill, 1992). Field studies have shown avoidance of waters <5·7 mg l^{-1} (Cayre & Marsac, 1993). In the present study, *T. albacares* spent >70% of their time in waters shallower than 50 m, which corresponded to the mixed layer above the oxycline. Below this depth, dissolved oxygen declined from values <5 mg l^{-1} to *c.* 4 mg l^{-1}.

Depth-based resource partitioning appears to occur between the *T. albacares* and the closely related *T. obesus*. The two species share similar geographic distributions (Collette & Nauen, 1983), but the *T. obesus* utilizes deeper waters. The larger vertical niche of *T. obesus* provides access to deeper prey, most of which undertake diel vertical migrations (Hays, 2003) and is underlain by a suite of adaptations including enhanced vision for prey perception (Brill *et al.*, 2005) as well as greater thermoregulatory and oxygen-carrying capacity. *Thunnus obesus* routinely utilize waters with low temperature and oxygen levels (Holland *et al.*, 1992), often reaching waters of 500 m, 5–10° C and <3 mg l^{-1} O_2 multiple times per day (Dagorn *et al.*, 2000; Musyl *et al.*, 2003). The ability of the *T. obesus* to inhabit this deep, cold, low-oxygen niche is based on its ability to thermoregulate (Holland *et al.*, 1992) and bind oxygen at lower concentrations (Lowe *et al.*, 2000) than other tuna species.

Thunnus thynnus and *Thunnus orientalis* (Temminck & Schlegel) do not have the tolerance to hypoxia, or the ability to vary thermal conductivity, that exists in the *T. obesus* (Holland & Sibert, 1994). The former, however, are cold tolerant and can inhabit temperate and boreal waters that are outside the geographic range of *T. obesus* and *T. albacares* (Collette & Nauen, 1983; Stokesbury *et al.*, 2004), and where SST are as low as 10·9° C (Schick *et al.*, 2004). *Thunnus thynnus*, *T. orientalis* and *Thunnus maccoyii* (Castlenau) hearts show a lesser degree of bradycardia when cooled than *T. albacares* hearts, indicating that they can maintain oxygenation of their tissues at lower temperatures (Blank *et al.*, 2004).

DAY–NIGHT DIFFERENCES IN VERTICAL DISTRIBUTION

Thunnus albacares inhabited deeper waters during day than during night. Previous tracking studies of *T. albacares* have shown similar diel patterns (Carey & Olson, 1982; Holland *et al.*, 1990*b*; Josse *et al.*, 1998). Josse *et al.* (1998) showed that *T. albacares* in the South Pacific associated with the deep scattering layer (DSL) both day and night, and that the DSL was *c.* 100 m deeper during the day. In this study *T. albacares* were, on average, significantly deeper during the day, accessing *c.* 100 m more of the water column than during the night [Figs. 2(a) and 4], a pattern that is consistent with the diel movements of DSL organisms. The depth of the highest density of the DSL in the Loop Current region of the Gulf of Mexico may be deeper than the daytime depths of *T. albacares* (Kaltenberg, 2005), suggesting that they are feeding in the lower density margins of the DSL. Diet studies of *T. albacares* show that they feed on a wide variety of teleost and crustacean prey that exhibit diel vertical migrations (Buckley & Miller, 1994; Menard *et al.*, 2000; Graham *et al.*, 2007).

Diel vertical migration, with deeper movements during daytime, has been observed in a wide variety of pelagic fishes, including *T. orientalis* (Kitagawa *et al.*, 2004), *T. obesus* (Holland *et al.*, 1992), *X. gladius* (Carey & Robison, 1981), bigeye thresher sharks *Alopias superciliosus* (Lowe) (Weng & Block, 2004), white sharks *Carcharodon carcharias* (L.) (Weng *et al.*, 2007*a*, *b*) and hammerhead sharks *Sphyrna lewini* (Griffith & Smith) (Klimley, 1993). The vertical movements of DSL organisms are thought to occur largely to avoid visual predators that are effective hunters in the photic zone (Hays, 2003). The diel patterns shown by *T. albacares* and other pelagic predators are consistent with them preying on DSL organisms (Marchal *et al.*, 1993) and studies that track both predators and prey will help in understanding this relationship (Josse *et al.*, 1998).

MANAGEMENT AND CONSERVATION

Detailed knowledge of behaviour and habitat enables management actions and fishing techniques to be tailored to target particular species more accurately (Brill & Lutcavage, 2001). In the Gulf of Mexico, *T. thynnus* are taken as by-catch in the *T. albacares* longline fishery (Block *et al.*, 2005). *Thunnus thynnus* in the western Atlantic have declined precipitously in the past half-century (Safina & Klinger, 2008) and are managed by the International Commission for the Conservation of Atlantic tunas under a quota system (ICCAT, 1999). The Gulf of Mexico is one of only two spawning areas for *T. thynnus*, and this by-catch is taking spawning individuals (Teo *et al.*, 2007). The data presented in this paper provide a foundation for research into ways to reduce *T. thynnus* by-catch in *T. albacares* fisheries.

This research was supported by grants from the National Marine Fisheries Service, the National Fish and Wildlife Federation and the Packard Foundation. The authors wish to thank D. Price and crew of the F.V. *Allison*, R. Davis and crew of the F.V. *Last Deal*, and wiremen M. Rice and B. Toney. We also thank C. Farwell and T. Sippel for support. This research was conducted in compliance with U.S. law under Scientific Research Permit TUNA-SRP-2000-002, issued by the Office of Sustainable Fisheries, National Marine Fisheries Service, Silver Spring, MD 20910, U.S.A. and the Institutional Animal Care and Use Committee of Stanford University (protocol 6957–6).

References

Anon. (2003). *Argos User Manual*. Largo, MD: Service Argos Inc.

Blank, J., Morrisette, J., Davie, P. & Block, B. A. (2002). Effects of temperature, epinephrine and Ca 2+ on the hearts of yellowfin tuna (*Thunnus albacares*). *Journal of Experimental Biology* **205,** 1881–1888.

Blank, J. M., Morrissette, J. M., Landeira-Fernandez, A. M., Blackwell, S. B., Williams, T. D. & Block, B. A. (2004). *In situ* cardiac performance of Pacific bluefin tuna hearts in response to acute temperature change. *Journal of Experimental Biology* **207,** 881–890.

Block, B., Booth, D. & Carey, F. (1992). Depth and temperature of the blue marlin, *Makaira nigricans*, observed by acoustic telemetry. *Marine Biology* **114,** 175–183.

Block, B., Dewar, H., Farwell, C. & Prince, E. (1998*a*). A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proceedings of the National Academy of Sciences of the United States of America* **95,** 9384–9389.

Block, B., Dewar, H., Williams, T., Prince, E., Farwell, C. & Fudge, D. (1998*b*). Archival tagging of Atlantic bluefin tuna (*Thunnus thynnus thynnus*). *Marine Technology Society Journal* **32,** 37–46.

Block, B., Dewar, H., Blackwell, S., Williams, T., Prince, E., Farwell, C., Boustany, A., Teo, S., Seitz, A., Walli, A. & Fudge, D. (2001). Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* **293,** 1310–1314.

Block, B. A., Keen, J. E., Castillo, B., Dewar, H., Freund, E. V., Marcinek, D. J., Brill, R. W. & Farwell, C. (1997). Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. *Marine Biology* **130,** 119–132.

Block, B. A., Teo, S. L. H., Walli, A., Boustany, A., Stokesbury, M. J. W., Farwell, C. J., Weng, K. C., Dewar, H. & Williams, T. D. (2005). Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* **434,** 1121–1127.

Boustany, A. M., Marcinek, D. J., Keen, J., Dewar, H. & Block, B. A. (2001). Movements and temperature preference of Atlantic bluefin tuna (*Thunnus thynnus*) off North Carolina: a comparison of acoustic, archival and pop-up satellite tagging. In *Electronic Tagging and Tracking in Marine Fishes* (Sibert, J. R. & Nielsen, J. L., eds), pp. 89–108. Dordrecht, Netherlands: Kluwer Academic Publishers.

Brill, R. (1994). A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. *Fisheries Oceanography* **3,** 204–216.

Brill, R. W. & Lutcavage, M. (2001). Understanding environmental influences on movements and depth distributions of tunas and billfishes can significantly improve population assessments. *American Fisheries Society Symposium* **25,** 179–198.

Brill, R. W., Block, B. A., Boggs, C. H., Bigelow, K. A., Freund, E. V. & Marcinek, D. J. (1999). Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry:

implications for the physiological ecology of pelagic fishes. *Marine Biology* **133,** 395–408.

Brill, R. W., Bigelow, K. A., Musyl, M. K., Fritsches, K. A. & Warrant, E. J. (2005). Bigeye tuna (*Thunnus obesus*) behaviour and physiology and their relevance to stock assessments and fishery biology. *ICCAT Collected Volume of Scientific Papers* **57,** 142–161.

Buckley, T. W. & Miller, B. S. (1994). Feeding habits of yellowfin tuna associated with fish aggregation devices in American Samoa. *Bulletin of Marine Science* **55,** 445–459.

Bushnell, P. G. & Brill, R. W. (1992). Oxygen transport and cardiovascular responses in skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) exposed to acute hypoxia. *Journal of Comparative Physiology* **162,** 131–143.

Bushnell, P., Brill, R. & Bourke, R. (1990). Cardiorespiratory responses of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*) to acute reductions of ambient oxygen. *Canadian Journal of Zoology* **68,** 1857–1865.

Carey, F. & Olson, R. (1982). Sonic tracking experiments with tuna. *ICCAT Collected Volume of Scientific Papers* **XVII,** 458–466.

Carey, F. & Robison, B. (1981). Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fishery Bulletin* **79,** 277–292.

Cayre, P. & Marsac, F. (1993). Modelling the yellowfin tuna (*Thunnus albacares*) vertical distribution using sonic tagging results and local environmental parameters. *Aquatic Living Resources* **6,** 1–14.

Collette, B. B. & Nauen, C. E. (1983). *FAO Species Catalogue, Vol. 2. Scombrids of the World*. Rome: FAO.

Dagorn, L., Bach, P. & Josse, E. (2000). Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Marine Biology* **136,** 361–371.

Dagorn, L., Josse, E. & Bach, P. (2001). Association of yellowfin tuna (*Thunnus albacares*) with tracking vessels during ultrasonic telemetry experiments. *Fishery Bulletin* **99,** 40–48.

Dagorn, L., Holland, K. N., Hallier, J. P., Taquet, M., Moreno, G., Sancho, G., Itano, D. G., Aumeeruddy, R., Girard, C., Million, J. & Fonteneau, A. (2006). Deep diving behaviour observed in yellowfin tuna (*Thunnus albacares*). *Aquatic Living Resources* **19,** 85–88.

Gilly, W. F., Markaida, U., Baxter, C. H., Block, B. A., Boustany, A., Zeidberg, L., Reisenbichler, K., Robison, B., Bazzino, G. & Salinas, C. (2006). Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Marine Ecology Progress Series* **324,** 1–17.

Graham, B. S., Grubbs, D., Holland, K. & Popp, B. N. (2007). A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. *Marine Biology* **150,** 647–658.

Gunn, J. (1994). Computer tuna tag becomes a reality. *Australian Fisheries* **53,** 12–14.

Gunn, J. & Block, B. (2001). Advances in acoustic, archival and satellite tagging of tunas. In *Tunas: Physiology, Ecology and Evolution* (Block, B. & Stevens, E., eds), pp. 167–224. San Diego, CA: Academic Press.

Hays, G. C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* **503,** 163–170.

Hays, G. C., Houghton, J. D. R. & Myers, A. E. (2004). Endangered species – pan-Atlantic leatherback turtle movements. *Nature* **429,** 522.

Hays, G. C., Hobson, V. J., Metcalfe, J. D., Righton, D. & Sims, D. W. (2006). Flexible foraging movements of leatherback turtles across the north Atlantic Ocean. *Ecology* **87,** 2647–2656.

Holland, K. & Sibert, J. (1994). Physiological thermoregulation in bigeye tuna, *Thunnus obesus*. *Environmental Biology of Fishes* **40,** 319–327.

Holland, K., Brill, R. & Chang, R. (1990*a*). Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. *Fishery Bulletin* **88,** 397–402.

Holland, K., Brill, R. & Chang, R. (1990*b*). Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. *Fishery Bulletin* **88,** 493–507.

Holland, K., Brill, R., Chang, R., Sibert, J. & Fournier, D. (1992). Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* **358,** 410–412.

ICCAT (1999). *International Commission for the Conservation of Atlantic Tunas. Report for Biennial Period, 1998–89*, Part 1. Madrid: ICCAT.

Josse, E., Bach, P. & Dagorn, L. (1998). Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. *Hydrobiologia* **371–372,** 61–69.

Kaltenberg, A. M. (2005). 38-kHz ADCP investigation of deep scattering layers in sperm whale habitat in the northern Gulf of Mexico. Master's Thesis, Texas A & M University, College Station, TX, U.S.A.

Kitagawa, T., Nakata, H., Kimura, S., Itoh, T., Tsuji, S. & Nitta, A. (2000). Effect of ambient temperature on the vertical distribution and movement of Pacific bluefin tuna *Thunnus thynnus*. *Marine Ecology Progress Series* **206,** 251–260.

Kitagawa, T., Kimura, S., Nakata, H. & Yamada, H. (2004). Diving behaviour of immature, feeding Pacific bluefin tuna (*Thunnus thynnus orientalis*) in relation to season and area: the East China Sea and the Kuroshio–Oyashio transition region. *Fisheries Oceanography* **13,** 161–180.

Klimley, A. & Holloway, C. (1999). School fidelity and homing synchronicity of yellowfin tuna, *Thunnus albacares*. *Marine Biology* **133,** 307–317.

Klimley, A. P. (1993). Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Marine Biology* **117,** 1–22.

Klimley, A. P., Jorgensen, S. J., Muhlia-Melo, A. & Beavers, S. C. (2003). The occurrence of yellowfin tuna (*Thunnus albacares*) at Espiritu Santo Seamount in the Gulf of California. *Fishery Bulletin* **101,** 684–692.

Korsmeyer, K. E., Lai, N. C., Shadwick, R. E. & Graham, J. B. (1997). Heart rate and stroke volume contributions to cardiac output in swimming yellowfin tuna: response to exercise and temperature. *Journal of Experimental Biology* **20,** 1975–1986.

Le Boeuf, B. J., Crocker, D. E., Costa, D. P., Blackwell, S. B., Webb, P. M. & Houser, D. S. (2000). Foraging ecology of northern elephant seals. *Ecological Monographs* **70,** 353–382.

Le Guen, J. C. & Sakagawa, G. T. (1973). Apparent growth of yellowfin tuna from the Eastern Atlantic Ocean. *Fishery Bulletin* **71,** 175–187.

Lowe, T. E., Brill, R. W. & Cousins, K. L. (2000). Blood oxygen-binding characteristics of bigeye tuna (*Thunnus obesus*), a high-energy-demand teleost that is tolerant of low ambient oxygen. *Marine Biology* **136,** 1087–1098.

Lutcavage, M. E., Brill, R. W., Skomal, G. B., Chase, B. C. & Howey, P. W. (1999). Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Canadian Journal of Fisheries and Aquatic Sciences* **56,** 173–177.

Marchal, E., Gerlotto, F. & Stequert, B. (1993). On the relationship between scattering layer, thermal structure and tuna abundance in the Eastern Atlantic equatorial current system. *Oceanologica Acta* **16,** 261–272.

Marcinek, D., Blackwell, S., Dewar, H., Freund, E., Farwell, C., Dau, D., Seitz, A. & Block, B. (2001). Depth and muscle temperature of Pacific bluefin tuna examined with acoustic and pop-up satellite archival tags. *Marine Biology* **138,** 869–885.

Menard, F., Stequert, B., Rubin, A., Herrera, M. & Marchal, E. (2000). Food consumption of tuna in the Equatorial Atlantic ocean: FAD-associated versus unassociated schools. *Aquatic Living Resources* **13,** 233–240.

Musyl, M. K., Brill, R. W., Boggs, C. H., Curran, D. S., Kazama, T. K. & Seki, M. P. (2003). Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. *Fisheries Oceanography* **12,** 152–169.

Ohta, I. & Kakuma, S. (2005). Periodic behaviour and residence time of yellowfin and bigeye tuna associated with fish aggregating devices around Okinawa Islands, as identified with automated listening stations. *Marine Biology* **146,** 581–594.

Safina, C. & Klinger, D. H. (2008). Collapse of bluefin tuna in the Western Atlantic. *Conservation Biology* **22,** 243–246.

Schaefer, K. M., Fuller, D. W. & Block, B. A. (2007). Movements, behaviour, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the northeastern Pacific Ocean, ascertained through archival tag data. *Marine Biology* **152,** 503–525.

Schick, R. S., Goldstein, J. & Lutcavage, M. E. (2004). Bluefin tuna (*Thunnus thynnus*) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994-96). *Fisheries Oceanography* **13,** 225–238.

Sharp, G. D. (1978). Behavioural and physiological properties of tunas and their effects on vulnerability to fishing gear. In *The Physiological Ecology of Tunas* (Sharp, G. D. & Dizon, A. E., eds), pp. 397–450. New York, NY: Academic Press.

Sims, D. W., Southall, E. J., Humphries, N. E., Hays, G. C., Bradshaw, C. J. A., Pitchford, J. W., James, A., Ahmed, M. Z., Brierley, A. S., Hindell, M. A., Morritt, D., Musyl, M. K., Righton, D., Shepard, E. L. C., Wearmouth, V. J., Wilson, R. P., Witt, M. J. & Metcalfe, J. D. (2008). Scaling laws of marine predator search behaviour. *Nature* **451,** 1098–1103.

Stokesbury, M. J. W., Teo, S. L. H., Seitz, A., O'Dor, R. K. & Block, B. A. (2004). Movement of Atlantic bluefin tuna (*Thunnus thynnus*) as determined by satellite tagging experiments initiated off New England. *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 1976–1987.

Teo, S. L. H., Boustany, A., Dewar, H., Stokesbury, M. J. W., Weng, K. C., Beemer, S., Seitz, A. C., Farwell, C. J., Prince, E. D. & Block, B. A. (2007). Annual migrations, diving behaviour, and thermal biology of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. *Marine Biology* **151,** 1–18.

Turchin, P. (1998). *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sunderland, MA: Sinauer Associates, Inc.

Ward, P. & Myers, R. A. (2005). Inferring the depth distribution of catchability for pelagic fishes and correcting for variations in the depth of longline fishing gear. *Canadian Journal of Fisheries and Aquatic Sciences* **62,** 1130–1142.

Weimerskirch, H., Bonadonna, F., Bailleul, F., Mabille, G., Dell'Omo, G. & Lipp, H. P. (2002). GPS tracking of foraging albatrosses. *Science* **295,** 1259.

Weng, K. & Block, B. (2004). Diel vertical migration of the bigeye thresher shark (*Alopias superciliosus*), a species possessing orbital *retia mirabilia*. *Fishery Bulletin* **102,** 221–229.

Weng, K. C., Castilho, P. C., Morrissette, J. M., Landiera-Fernandez, A., Holts, D. B., Schallert, R. J., Goldman, K. J. & Block, B. A. (2005). Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science* **310,** 104–106.

Weng, K., Boustany, A., Pyle, P., Anderson, S., Brown, A. & Block, B. (2007*a*). Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Marine Biology* **152,** 877–894.

Weng, K. C., O'Sullivan, J. B., Lowe, C. G., Winkler, C. E., Dewar, H. & Block, B. A. (2007*b*). Movements, behaviour and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. *Marine Ecology Progress Series* **338,** 211–224.