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Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range

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Abstract We used acoustic telemetry to examine the small-scale movement patterns of yellowfin tuna (*Thunnus albacares*) in the California Bight at the northern extent of their range. Oceanographic profiles of temperature, oxygen, currents and fluorometry were used to determine the relationship between movements and environmental features. Three yellowfin tuna (8 to 16 kg) were tracked for 2 to 3 d. All three fish spent the majority of their time above the thermocline (18 to 45 m in depth) in water temperatures >17.5 °C. In the California Bight, yellowfin tuna have a limited vertical distribution due to the restriction imposed by temperature. The three fish made periodic short dives below the thermocline (60 to 80 m), encountering cooler temperatures (>11 °C). When swimming in northern latitudes, the depth of the mixed layer largely defines the spatial distribution of yellowfin tuna within the water column. Yellowfin prefer to spend most of their time just above the top of the thermocline. Oxygen profiles indicated that the tunas encountered oceanic water masses that ranged most often from 6.8 to 8.6 mg O_2 l^{-1}, indicating no limitation due to oxygen concentrations. The yellowfin tuna traveled at speeds ranging from 0.46 to 0.90 m s^{-1} (0.9 to 1.8 knots h^{-1}) and frequently exhibited an oscillatory diving pattern previously suggested to be a possible strategy for conserving energy during swimming.

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Introduction

Tunas are unique among teleosts because of their ability to elevate the temperature of their aerobic locomotor muscle above that of the ambient water temperature (Carey et al. 1971; Graham 1975). Tuna endothermy results from a suite of specializations which increase heat production and reduce heat loss. Tunas' high gill-surface area, large hearts and elevated standard metabolic rates combine to enhance the oxygen and metabolite-substrate delivery to the tissues, increasing the potential for heat production (Brill 1987, 1996). Elevated muscle temperatures are facilitated by the internalization of the aerobic locomotor muscle (the primary source of heat) and the elaboration of vasculature into counter-current heat exchangers which decouple heat production in the muscle from heat loss at the gills and body surface (Carey et al. 1971).

The genus *Thunnus* (Scombridae) has seven species which all possess specializations for endothermy. They have been divided by morphologists into two subgroups: a warm-water clade (the *Neothunnus*) and a cold-water or bluefin group. The *Neothunnus* comprises the yellowfin tuna (*T. albacares*), blackfin tuna (*T. tonggol*) and longtail tuna (*T. atlanticus*). These three species possess both central and lateral heat-exchangers, although the lateral retia are relatively small. The bluefin group, bigeye tuna (*T. obesus*), albacore (*T. alalunga*), northern bluefin (*T. thynnus*) and southern bluefin (*T. maccoyii*) differ in that their lateral retia are highly developed but the central heat-exchanger has been lost or reduced (Gibbs and Collette 1967; Collette 1978). This group also possesses additional retia which function to elevate the temperature of their viscera, eyes and brains (Carey 1982). The change in retial organization is thought to be associated with differences in the capacity for heat retention and endothermy. The steady-state thermal excess for yellowfin tuna (2.2 to 6 kg) ranges from 1.4 to 4 C° (Dizon and Brill 1979; Dewar et al. 1994; Dewar and Block unpublished data). Red-muscle temperatures for albacore determined by Graham and Dickson (1981) for similar sized fish (2.8 to 6 kg) were $\simeq$6 C° above ambient. For bigeye tuna (11.4 kg), acoustic telemetry data collected by Holland et al. (1992) indicate that steady-state temperatures are close to 5 C° in excess of ambient water temperatures. Temperatures for northern bluefin (220 kg) have been recorded under steady-state swimming as >11 C° and as high as 21 C° (Carey and Lawson 1973) above water-temperature.

The anatomical differences in vascular organization and physiological capacity for heat conservation present in the genus *Thunnus* are correlated with the distribution pattern of the two subgroups (Graham 1975; Sharp and Pirages 1978; Stevens and Neill 1978). Yellowfin, blackfin and longtail tunas occur in subtropical and tropical waters primarily above the thermocline (Carey and Olson 1982; Holland et al. 1990), whereas bluefin albacore and bigeye tunas occur in cooler waters at higher latitudes or below the thermocline in tropical waters (Carey and Teal 1969; Carey and Lawson 1973; Laurs et al. 1997).

Yellowfin tuna have a cosmopolitan pantropical and warm-temperate distribution (Sund et al. 1981). Previous telemetry studies in the eastern tropical Pacific and central Pacific (Carey and Olson 1982; Holland et al. 1990) indicated that the vertical movements of yellowfin tuna are restricted predominantly to movements from the surface mixed layer to the top of the thermocline. Previous studies also indicated that yellowfin tuna occasionally make deep dives (e.g. 460 m) for short durations. Tracks of small yellowfin tuna in Hawaii indicated a marked preference for the mixed layer, with the fish occupying a temperature range between 19 and 26 °C. The vulnerability of the yellowfin tuna in the tropics to purse-seine catches has also been correlated with the strength of the thermocline, indicating temperature to be the major limiting factor in their vertical distribution (Sund et al. 1981; Brill 1994). Acoustic telemetry provides one of the few methods of discerning the subtle differences in physiology, behavior and ecology of each species in the open ocean. It is often difficult to understand clearly how the process of speciation may occur amongst closely related sympatric fishes such as tunas in the pelagic environment. The coupling of acoustic tracking data with the simultaneous profiling of the ocean environment allows a determination of the environmental preferences and marine niches unique to each species.

In this study, we examined the movements of small yellowfin tuna of the eastern Pacific in the most northern part of their range late in the fall. Yellowfin tuna move seasonally into higher latitudes during the warmest months of the year, presumably to feed. The major objective of this study was to determine if the morphological and physiological specializations evident in this species for warming of the tissues provide an obvious thermal advantage at more northern latitudes, permitting an increase in vertical movements. Our capacity to track tunas from a large research ship was greatly improved through the deployment of a new acoustic telemetry system which is described in this paper.

Materials and methods

The movements of individual tuna (*Thunnus albacares*) were monitored with acoustic telemetry techniques from the UNOLS research vessel R.V. "Point Sur" in September and October 1994. Pressure-sensitive ultrasonic transmitters (Vemco, Armdale, Nova Scotia; V22P with extra power) were attached to tunas as described below. A hydrophone with four line arrays spaced at 90° intervals in a circle was towed off the forward deck of the research ship. The array elements were resonant at 32 to 50 kHz, and each had a low-noise preamplifier and band-pass filter which removes frequencies <32 and >50 kHz. This reduced the interference from low-frequency ship noise, improving the capacity to track the acoustic signal. A 70 kg tow-body was constructed from a SCUBA tank and streamlined with fiberglass. A hairy fared Kevlar conducting cable (Cortland Cable, Cortland, New York) was used to tow the hydrophone array. A Vemco VR-28 receiver equipped with a microprocessor controller and four independent acoustic receivers was used to track the tuna and acquire the depth data. Range estimates using a buoy indicated that conventional (no extra power) 34 kHz transmitters had an $\simeq$0.8 nautical mile range, and 50 kHz tags were detectable at 0.7 nautical miles while moving at low speeds (1 to 2 knots). Transmitters (V22P-EX) with extra power typically provided ranges closer to 1.0 nautical mile. The receiver data was interfaced with a PC-based tracking software which gave an accurate bearing to the fish and continuous GPS (Global Positioning System) position data (every few seconds) from the ship's GPS. Every 3 to 5 s, there was an update of the ship's satellite position which was recorded along with the movement of each fish in the data file. The visual display of the position of the fish relative to the ship coupled with an accurate measurement of the distance from the ship greatly improved the researchers' capacity to track the fish. A visual gain feature (showing decibel output from the tag) in the software display was calibrated with an acoustic tag on a buoy prior to tracking the fish, and this permitted the researchers to accurately estimate the distance of the fish from the tracking vessel while underway. Average swimming speeds for the three fish were calculated on an hourly basis using the distance per unit time traveled between each GPS position. Acoustic tracking of fish with this system was possible at speeds of up to 7 knots.

The research ship was equipped with a Seabird conductivity-temperature-depth (CTD) array that allowed simultaneous profiling of temperature, oxygen, salinity, fluorometry and transmissivity. The CTD was deployed while underway (at 1 to 2 knots) every 2 to 4 h during the tracks, providing a continuous record of the environmental profiles. An Acoustic Doppler Current Profiler permitted examination of the movements of the fish in relation to oceanic current patterns. An echosounder was used to discern the deep scattering layers. The relationship between fish movement and simultaneously collected advanced very high resolution (AVHRR) sea-surface satellite images was also examined.

Fish movements were monitored using 34 or 50 kKHz V22P depth-transmitters. The pressure-sensitive transmitters modulate the rate of pulse transmission in relationship to water-pressure changes (depth) and are accurate to ± 1 m. All tunas were caught by hook and line from the F.V. "Shogun". The fish were reeled in close to the stern of the boat and tagged in the water in the dorsal musculature with the acoustic transmitter. External attachment of the transmitters to the tunas were made with a 3 cm stainless steel dart placed ≃4 to 6 cm deep, and connected via monofilament or teflon-coated wire leaders to a plastic tie-wrap protruding from the transmitter. After tagging, the fishing line was cut close to the hook and the fish was released. The F.V. "Shogun" was also equipped with a second tracking system, as described by Holland et al. (1992).

Results

Three yellowfin tuna (*Thunnus albacares*) were tagged and tracked with ultrasonic transmitters for 55, 72 and 54 h, respectively. Fig. 1 shows the general locations of the three tracks in the California Bight. The weight and size of tagged fish was estimated from the average of similarly-sized fish caught from the same school.

Yellowfin tuna #9401 was tagged with a 50 kHz transmitter in the vicinity of a prominent bank. Fig. 2 shows the vertical movements of the tuna in relation to temperature and oxygen. The tuna demonstrated a strong preference for the shallow, 40 m-deep mixed layer, remaining above the 19 °C isotherm for the majority of the track. It made brief dives through the thermocline, with the longest excursion lasting ≃7 min. Vertical movements were characterized by a series of continuous rapid up-and-down oscillatory dives that occurred more frequently after sunset, similar to those seen for this species in the tropics (Carey and Olson 1982; Holland et al. 1990). In the evening, depth-sounder records indicated a scattering layer at 25 m. This tuna showed a marked preference for depths in the vicinity of the scattering layer. The fish made markedly rapid ascents to the surface at first light on both mornings (Fig. 2a: arrows).

Tuna #9401 was tagged with a 50 kHz transmitter and may have been traveling in a school of similar-sized fish at the end of the second day of tracking, as the second Tuna tracked (#9402) was caught and released within 100 m of the R.V. "Point Sur" which was tracking Tuna #9401. A 34 kHz transmitter was placed on Yellowfin #9402, and the research ship began following this tuna while the fishing vessel F.V. "Shogun" deployed a fiberglass V-fin tow-body with a four-way

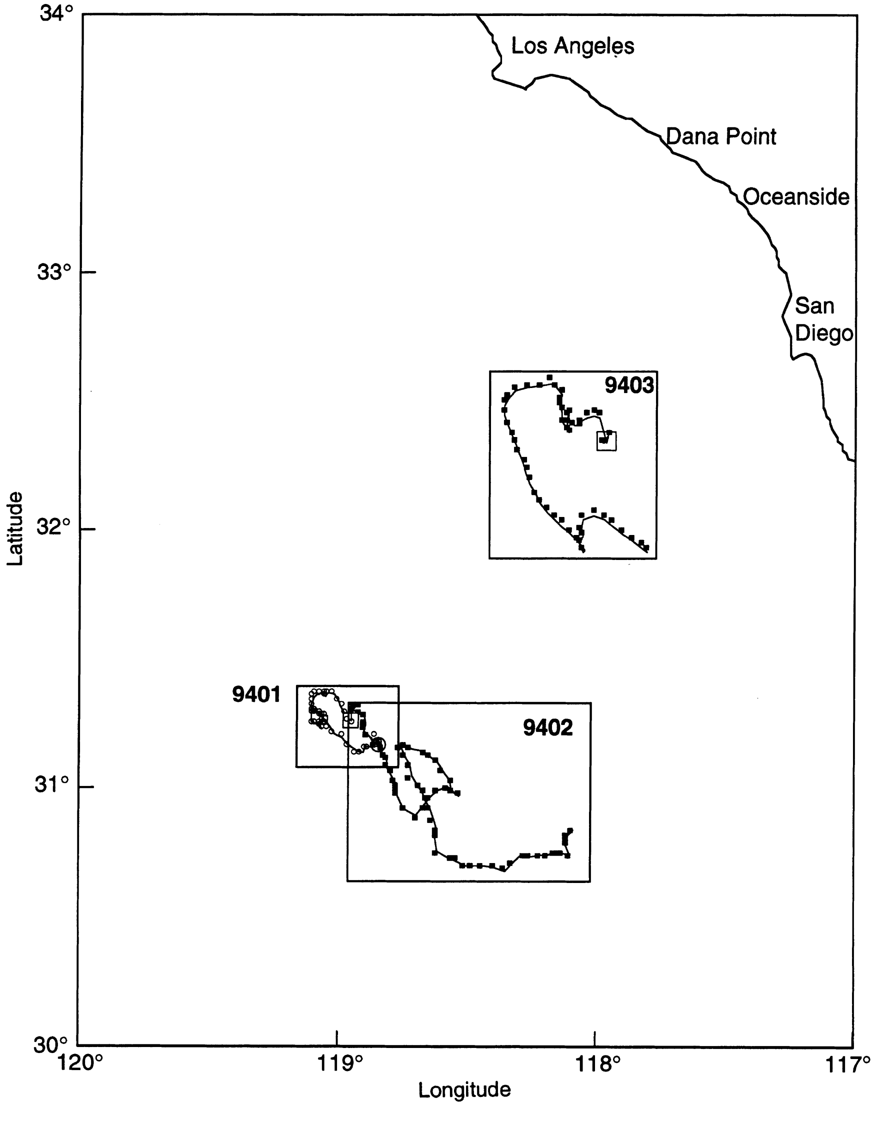

Fig. 1 *Thunnus albacares*. Geographical locations of tracks of three yellowfin tuna (*9401*, *9402*, *9403*) in southern California Bight [□, O start of tracks for 9401 and 9403 (□), and 9402 (O); ○, ■ hourly intervals along tracks of 9401 and 9402 (○) and of 9403 (■)]

Table 1 *Thunnus albacares*. Summary of tracks

Tuna No.	Estimated mass (kg)	Estimated length (cm)	Date tagged	Location of track start (Latitude; Longitude)	Track duration (h)
9401	15.7	94	28 Sep 1994	31.274°N; 118.817°W	55
9402	16.3	90	30 Sep 1994	31.334°N; 118.893°W	72
9403	8.2	75	02 Oct 1994	32.425°N; 117.913°W	54

hydrophone and continued tracking Tuna #9401. After tagging of the second fish, the two fish separated and were tracked simultaneously by the two vessels for 9 h. The two tunas had separate tracks, indicating that at least one of the fish left the school or that the school had split into two groups.

Day 1 of the 9402 track was characterized by erratic diving behavior, most likely reflecting the trauma of being caught, tagged and released (Fig. 3). There was no evident pattern of ascent or descent during the first day, and the tuna alternated between being close to the surface or close to the thermocline. During this time the fish remained at depth, encountering water temperatures as cool as 15 to 16 °C for up to 1 h. This fish spent a considerable amount of time during the first day of the track at depth in regions (70+ m) having the highest measured oxygen concentrations (8.3 mg ml^{-1}). On several occasions on the first day, the fish swam at speeds that exceeded 5.0 knots, during which the fish always stayed in the enriched oxygen region. Frequent dives into cooler waters were also evident, and in one particularly notable dive the tuna dove to almost 300 m in a matter of 1 min, encountering water as cool as 7 °C and low oxygen concentrations (< 3 mg l^{-1}). This is by far the lowest temperature occupancy recorded for a yellowfin tuna in the wild. However, this behavior occurred simultaneously with the CTD cast and the fish may have followed the instrument as it went down. During Days 2 and 3, this tuna exhibited behavior more common for the species and more characteristic of the other two tunas tracked in this study. During Day 2, #9402 stayed above the mixed layer the majority of the time, limiting most of its travels to waters above the 17.5 °C isotherm. The fish began a more oscillatory pattern of diving by Day 3, much like #9401, and displayed the same striking pattern of behavior at sunrise (Fig. 3a: arrows). Just prior to first light, the fish made a brief dive and came up to the surface.

Yellowfin Tuna #9403 was caught on Sixty Mile Bank closer to the continental shelf, and was estimated to be the smallest of the tunas tracked (8.2 kg, 75 cm). The fish exhibited a vertical diving behavior throughout the track that suggested a strong temperature-based limitation on vertical movements (Fig. 4a). CTD data indicated that the mixed layer was extremely shallow throughout the track, with the 19° isotherm at 10 to 15 m. The shallowness of the thermocline can clearly be seen as a distinct limitation to the vertical movements of this fish. This fish spent the majority of the time tracked just above the thermocline. An overlay of sea-surface satellite temperature-images demonstrated that the entire 3 d track was associated with a prominent front of cold and warm waters (Fig. 5). A similar front (not shown) had also been apparent from the sea-surface temperature (SST) images for Fish #9402. During the first day of the track, the tuna (# 9403) moved onto the cold side of the front where the thermocline was shallowest. Swimming speeds were fairly rapid (3 knots) during this time, and dives below the thermocline infrequent. After a day and a half, the fish changed its course by 180° immediately (arrowed in Fig. 5) upon encountering the warmer side of the front, and began to swim more slowly (1 to 2 knots) and dive more frequently.

Figs. 6 and 7 summarize the environmental data during the three tracks. Fig. 6 indicates the frequency of occupancy (% time) of 1 C° temperature intervals for the three tunas. The only temperatures frequented for more than 20% of the time (and thus not associated with a short descent) were the 17 to 20 °C intervals. The tunas tagged in this study displayed a decided preference for the surface layer to the top of the thermocline, the lens of warmest water in the pelagic habitat. This is clearly demonstrated in Fig. 7, in which the temperature data for the three tracks have been pooled. This figure compares the percentage of time spent at a particular depth (Fig. 7: histogram) with depth-associated changes in mean water temperature for that particular depth interval. The tunas have a vertical distribution that was temperature-dependent, with > 90% of fish-depth distribution limited to a rather narrow thermal corridor which varied by only 2.5 C° (17.5 to 20.0 °C: shaded area in Fig. 7). Oxygen on the other hand (Fig. 6b) was not a limiting factor in the environmental preference of these tuna, as the spatial distribution of the three fish was consistently in oxygen-rich waters (6.8 to 8.8 mg ml^{-1}). Depth preferences showed no regular diurnal variation, and no significant differences in depth distribution were evident over a 24 h cycle (Fig. 8).

An Acoustic Doppler Current Profiler permitted acquisition of oceanic current information simultaneously with fish movement. Fig. 9 shows the current vectors for each track. The movements of the three fish do not appear to be affected by the velocity of the currents in any predictable fashion. Velocities during all three tracks averaged less than 1 m s^{-1} (1.94 knots) and only occasionally were as high as 2.3 m s^{-1} (4.47 knots).

Swimming speeds for yellowfin tuna were estimated from straight-line calculations using positions of the tracking vessel based on GPS. Average swimming speeds for the three fish were calculated on an hourly basis, and ranged from 0.48 m s^{-1} (0.924 knots) for Tuna 9401 to

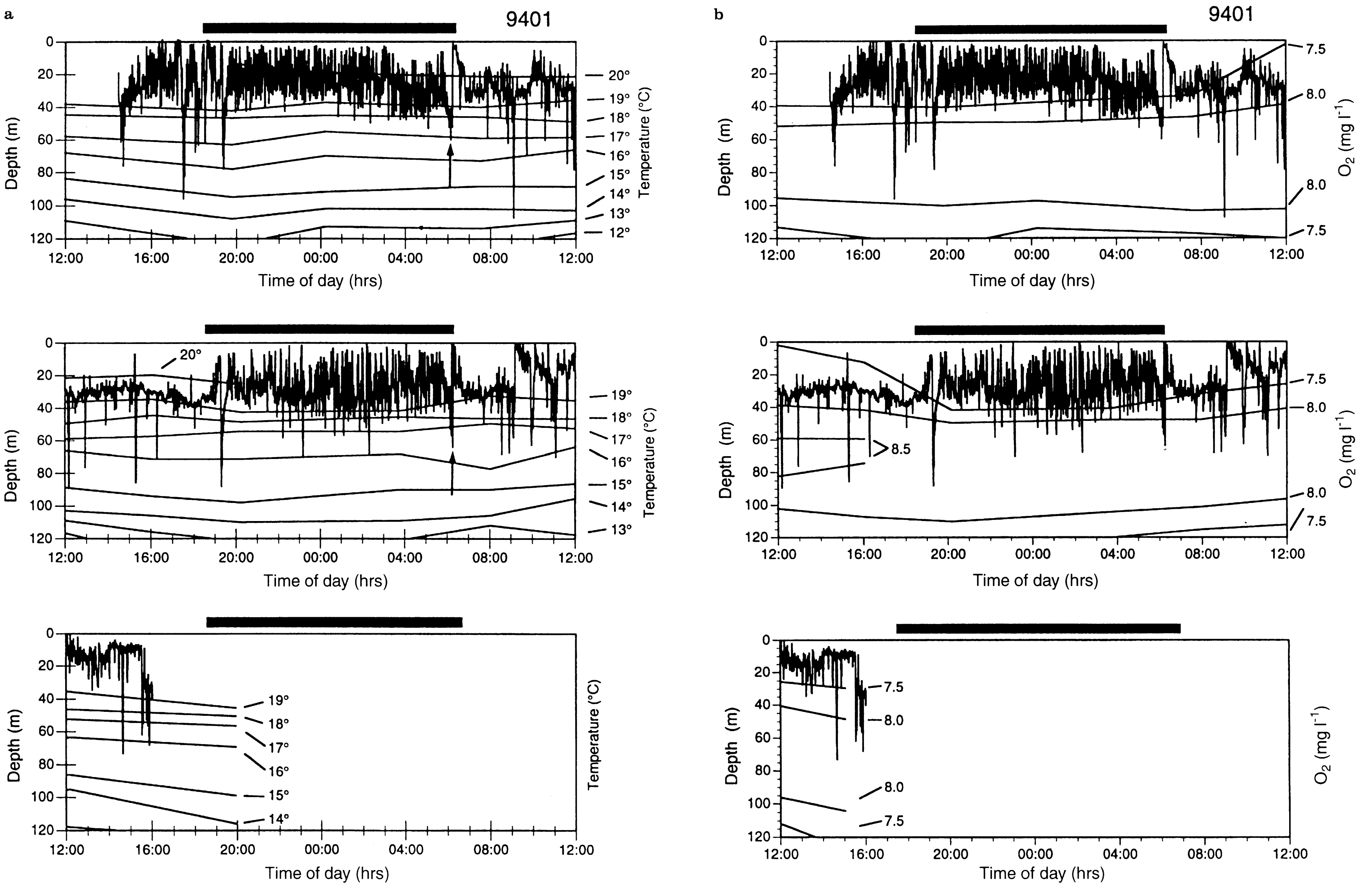

Fig. 2 *Thunnus albacares*. **a** Depth over time along track of Yellowfin Tuna #9401 [*black bar on abscissas* nighttime; *arrows at dawn* indicate unusual behavior of rising directly to surface at first light (1 C° isotherms are shown)] **b** depth movements of 9401 as a function of oxygen concentration

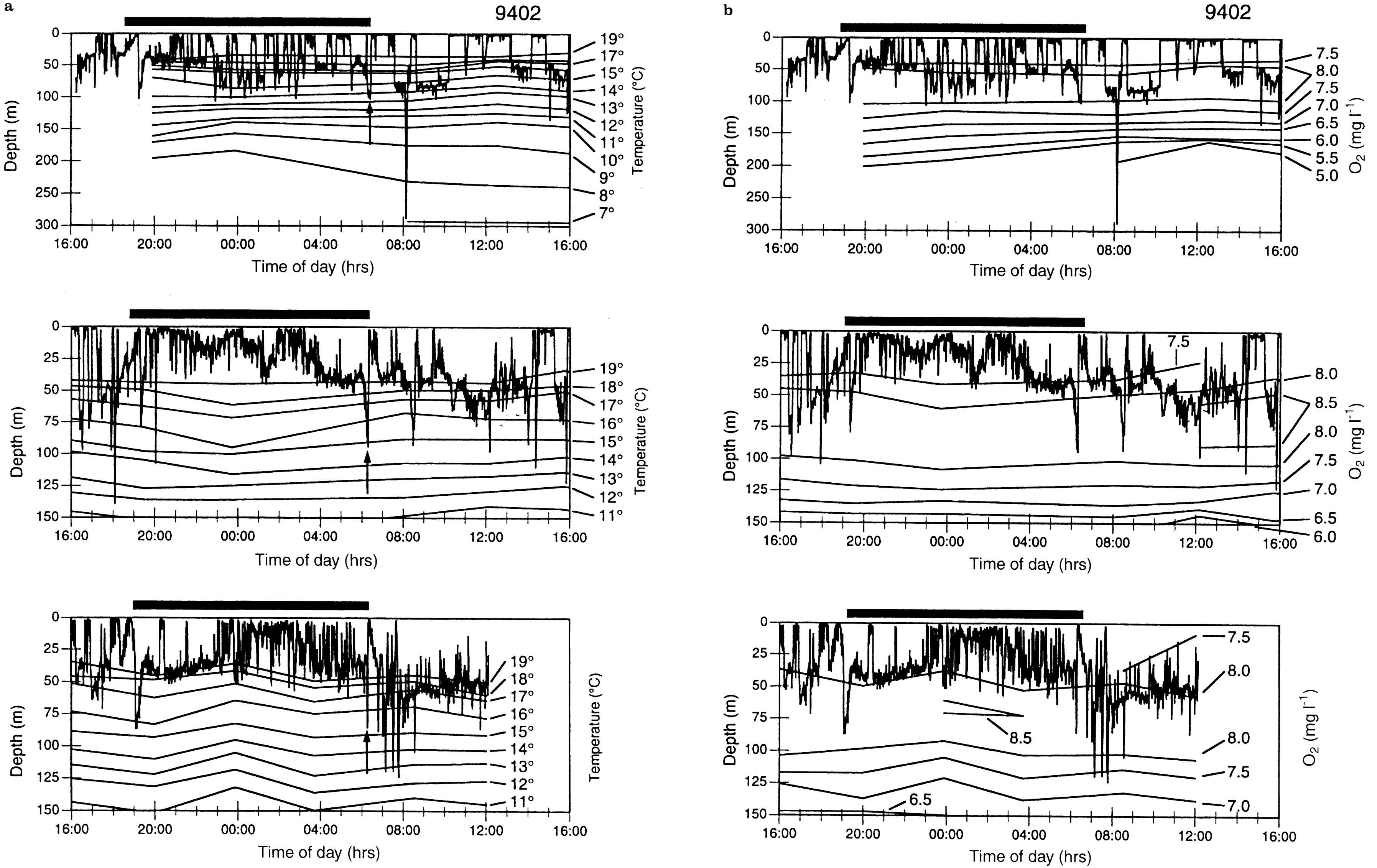

Fig. 3 *Thunnus albacares*. **a** Depth movements over time of Yellowfin Tuna #9402; **b** depth movements of 9402 as a function of oxygen concentration (this fish spent prolonged periods during first day of track in oxygen-rich zones). Further details as in legend to Fig. 2.

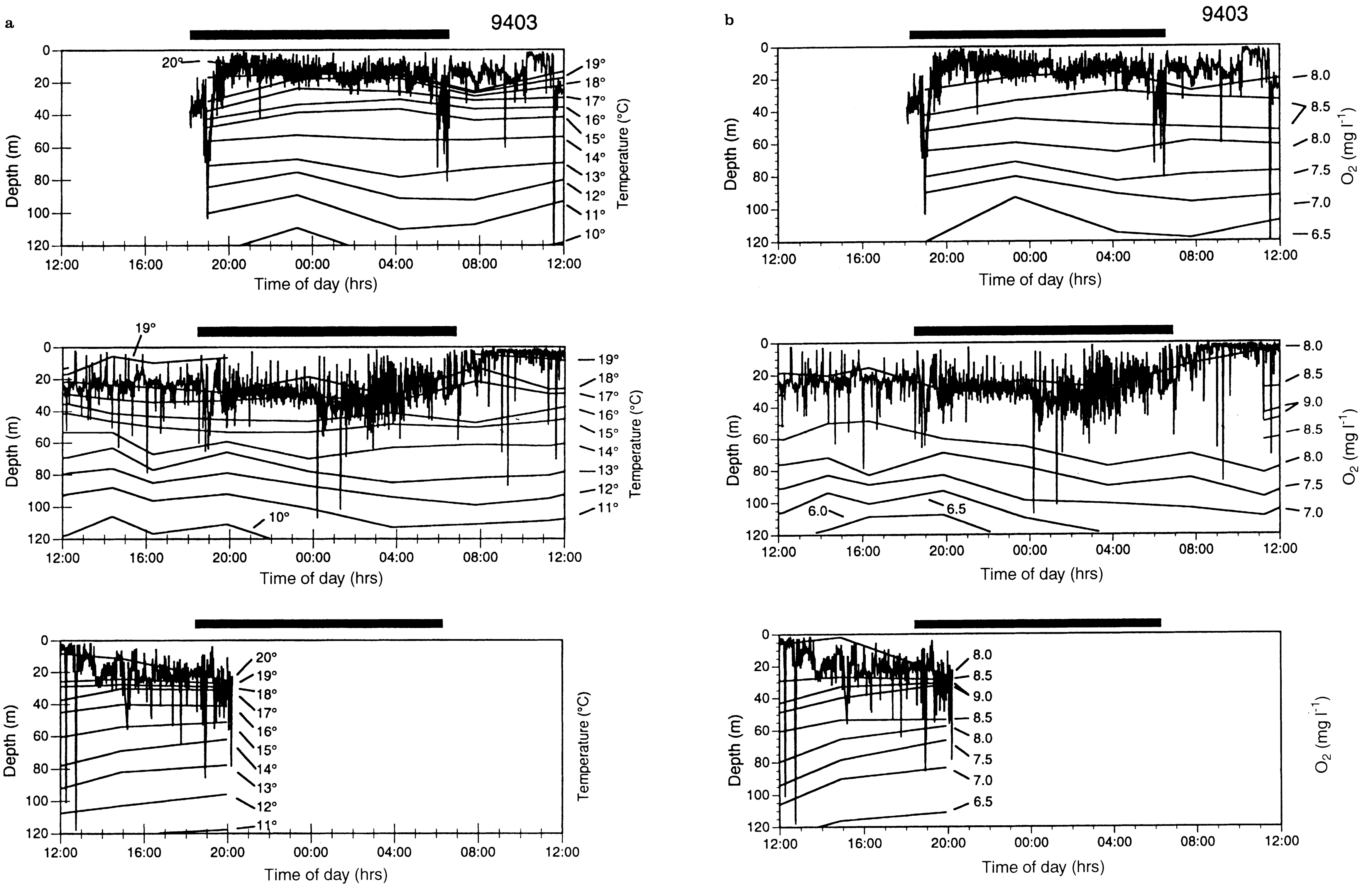

Fig. 4 *Thunnus albacares*. **a** Depth over time of Yellowfin Tuna #9403; **b** depth distribution in relationship to oxygen concentration for 9403. Further details as in legend to Fig. 2.

0.91 m s^{-1} (1.766 knots) for Tuna 9403 (Table 2). Upon scaling for differences in estimated body length (BL), average speeds of 0.51, 0.93 and 1.21 BL s^{-1} were obtained for Tunas 9401, 9402 and 9403, respectively. A peak sustained swimming speed (i.e. maintained for at least 1 h) was estimated for Tuna 9403 as 3.5 BL s^{-1}. It must be noted that these calculations assume the fish to be moving in a straight line at constant depth and thus represent underestimations of the true swimming speed.

Frequently, we observed a repetitive pattern of a descent followed by an ascent (up and down) which was maintained for long periods of time (Fig. 10). Rates of ascent and descent were calculated assuming a constant distance between the fish and boat, and are presented in Fig. 11. The following limitations were imposed prior to use of the data in the calculation of rate of change of depth: (1) only straight-line changes in depth with no apparent pauses at a particular depth during the ascent or descent were used; (2) the first and last data point along each straight line, representing the "turn-around" or initial/final depth were not used; (3) for ascents, points within 5 m of the surface were not used since the approach to the surface would necessitate a behavioral change in ascent rate; and (4) only changes in depth of more than 30 m were used, in order to ensure a reasonable number of data points over which the rate of depth change could be calculated. The mean ascent rate was 0.46 ± 0.02 m s^{-1} (~0.9 knots) and was significantly greater than mean descent rate of 0.34 ± 0.02 m s^{-1} (~0.65 knots) (Mann–Whitney rank sum test, $p < 0.001$). Furthermore, the distribution of descent rates was extremely left-skewed, with >65% of all dives being at speeds of <0.3 m s^{-1} (Fig. 11).

Discussion

Niche breadth

Previous studies (Carey and Olson 1982; Holland et al. 1990) have demonstrated that *Thunnus albacares* in tropical waters have a marked preference from the surface mixed layer down to the top of the thermocline, encountering temperatures between 19 and 26 °C. In the southern California Bight (warm temperate waters) in October of 1994, we found that yellowfin tuna also have a strong preference for the surface mixed layer while moving through northern latitudes. Movements of these small tuna appeared to be limited by the thermocline. The three tunas tracked (Fig. 6) spent the majority of the time in waters of 17.5 to 20.5 °C, the warmest waters available in the California Bight in the fall of 1994. Such temperatures are well below the 26 to 29 °C surface-water temperatures common for this species at lower latitudes in the southern part of their range distribution.

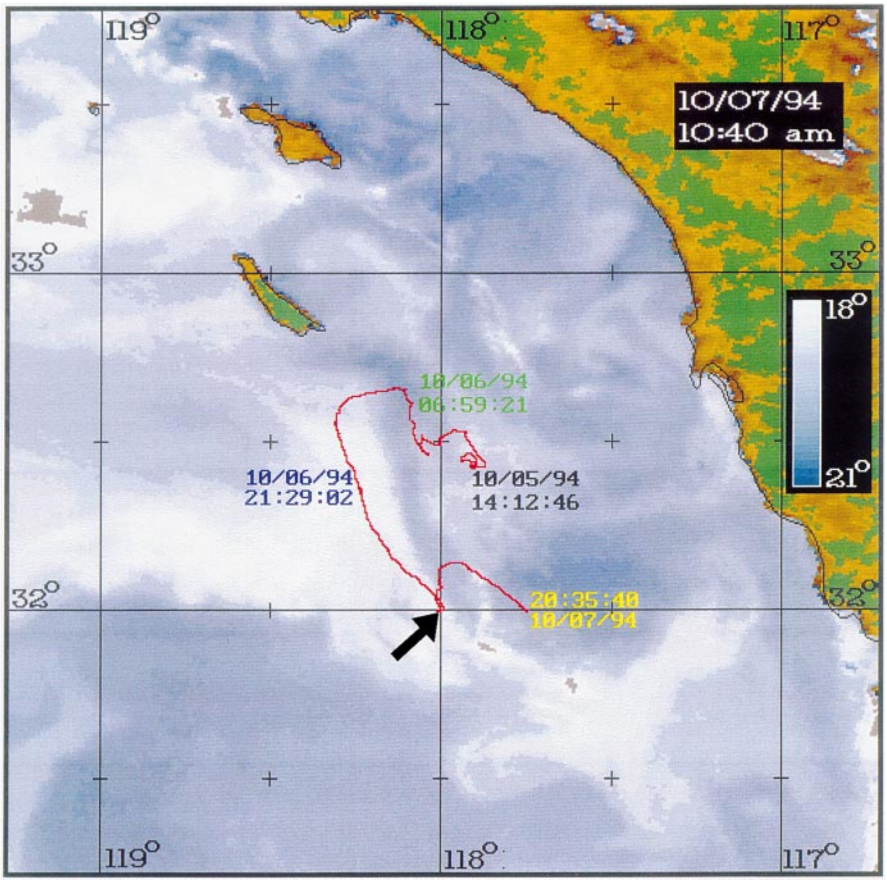

Fig. 5 *Thunnus albacares*. Sea-surface satellite temperature-image with track of Tuna 9403 superimposed (*arrow* indicates 180° turn as fish approaches edge of front and heads into warmer waters)

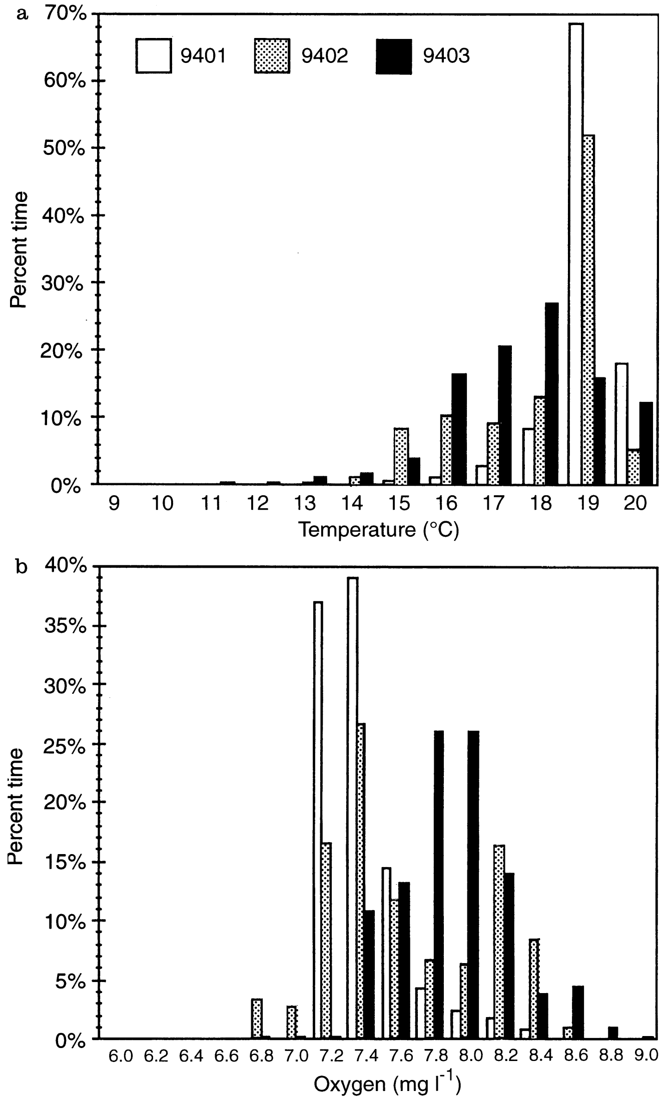

Fig. 6 *Thunnus albacares.* Temperature preferences as percent time spent in each temperature interval (**a**) and oxygen preferences (**b**) of Individuals 9401, 9402, 9403 in California Bight area. Temperature intervals from 16.0 to 16.9 °C, 17.0 to 17.9 °C, etc.; oxygen values are actual concentrations measured

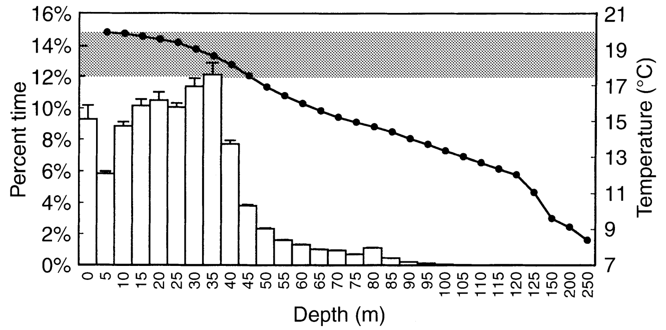

Fig. 7 *Thunnus albacares.* Percent occupancy of temperature intervals as a function of depth (*data points joined by line* indicate mean water temperatures at each depth; *shaded area* encompasses > 90% of total time and highlights preference of species for water temperatures > 17.5 °C; depth intervals = 0 to 4.999 m; 5 to 9.999 m; 10 to 14.999 m, etc.)

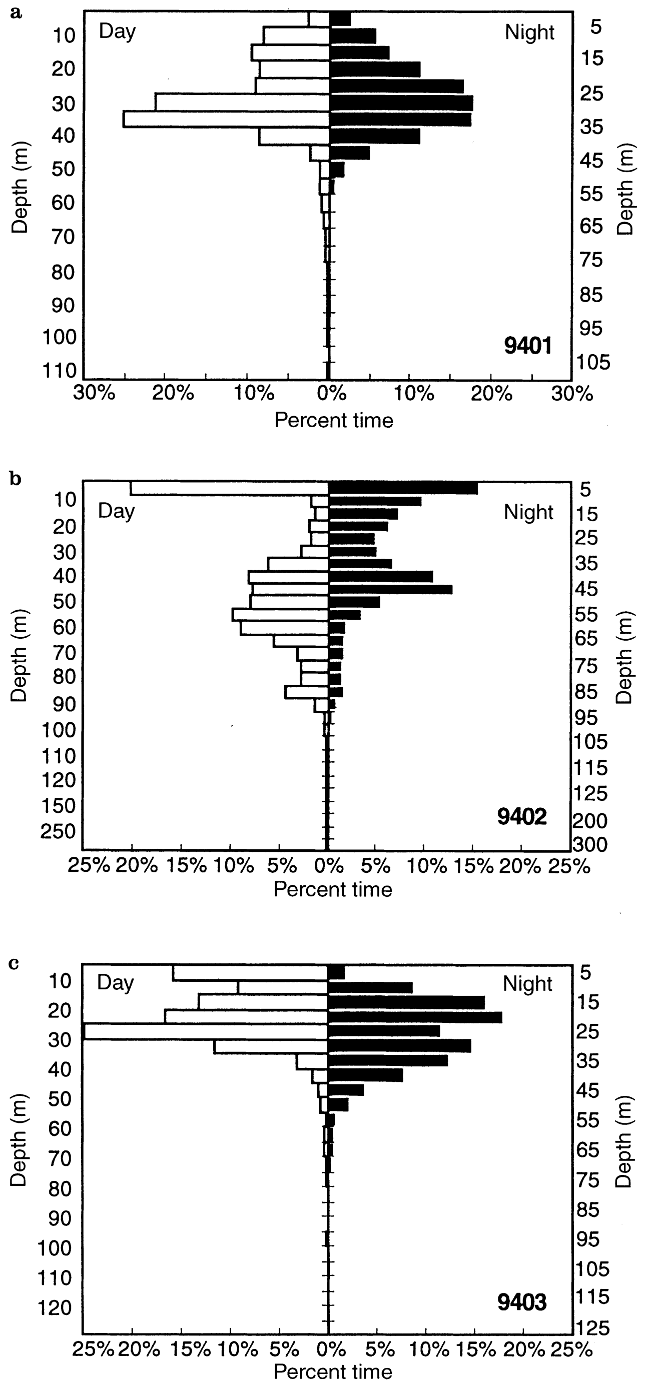

Fig. 8 *Thunnus albacares.* Summary of diurnal occurrence as a function of depth. There were no significant differences between depth preferences during day or night. Depth intervals = 0 to 5 m, 5.1 to 10 m, 10.1 to 15 m, with interval denoted by last depth of the increment (*Percent time* refers to time during day or night fish spent at each depth interval)

Previous studies (Carey and Olson 1982; Holland et al. 1990) reported frequent movements of the yellowfin tuna between the surface mixed layer and the top of the thermocline in waters that ranged from 20 to 27 °C. Thus, when swimming in northern latitudes, the shallowness of the mixed layer largely defines the spatial distribution of yellowfin tuna within the water column. The smallest tuna tracked, #9403, provided the most notable example of this behavior. As the tuna traveled to the cold side of a water mass, the fish was confronted with thermocline depths as shallow as 15 m, which limited its vertical diving pattern (Fig. 4a). Although yellowfin tuna made dives into the cooler waters beneath the thermocline, the duration was usually short (1 to 2 min). Infrequently, all three yellowfin tuna made rapid dives to impressive depths and temperature extremes. One 300 m dive by #9402 took the fish into waters as cool as 7 °C in a matter of minutes. Such dives may in fact be a behavioral response (predator or ship avoidance) rather than a preferred type of movement. Our results thus demonstrate that the vertical distribution of yellowfin tuna in the northern (and coolest) portion of its latitudinal range is largely limited to a narrow 2.5 C° thermal corridor and there is no evidence of niche expansion associated with the presence of endothermic strategies (Block et al. 1993) in this member of the *Thunnus* clade. Regional catch records suggest that the other two members of the warm water group, *T. atlanticus* and *T. tongol* may, like the yellowfin tuna, face similar thermal constraints. Tracking studies on the other tropical and warm-temperate species are necessary to determine if a narrow thermal niche is a common feature of the *Neothunnus*.

Tag-and-release studies of yellowfin tuna in the Eastern Tropical Pacific, and results from molecular genetics (Ward et al. 1994) suggest that yellowfin tuna remain in the eastern Pacific throughout most of their life cycle. Both tag and release as well as catch-effort data (Sund et al. 1981) from fisheries indicate that in general eastern tropical yellowfin tuna move north in the summer and fall and return to the tropics in the winter months. In this study we have shown that as the yellowfin tuna move north they spend most of their time above the thermocline. Thus, while they may be taking

Table 2 *Thunnus albacares*. Swimming speeds. These were calculated from straight-line distances between hourly Global Positioning System locations and are thus mimimal estimates. SEMs are given in parentheses

Tuna No.	Speed (knots)			Speed (m s^{-1})		
	mean	max	min	mean	max	min
9401	0.924 (0.054)	1.858	0.150	0.475 (0.028)	0.955	0.077
9402	1.623 (0.070)	2.726	0.156	0.834 (0.036)	1.401	0.080
9403	1.766 (0.092)	5.061	0.345	0.908 (0.047)	2.602	0.177

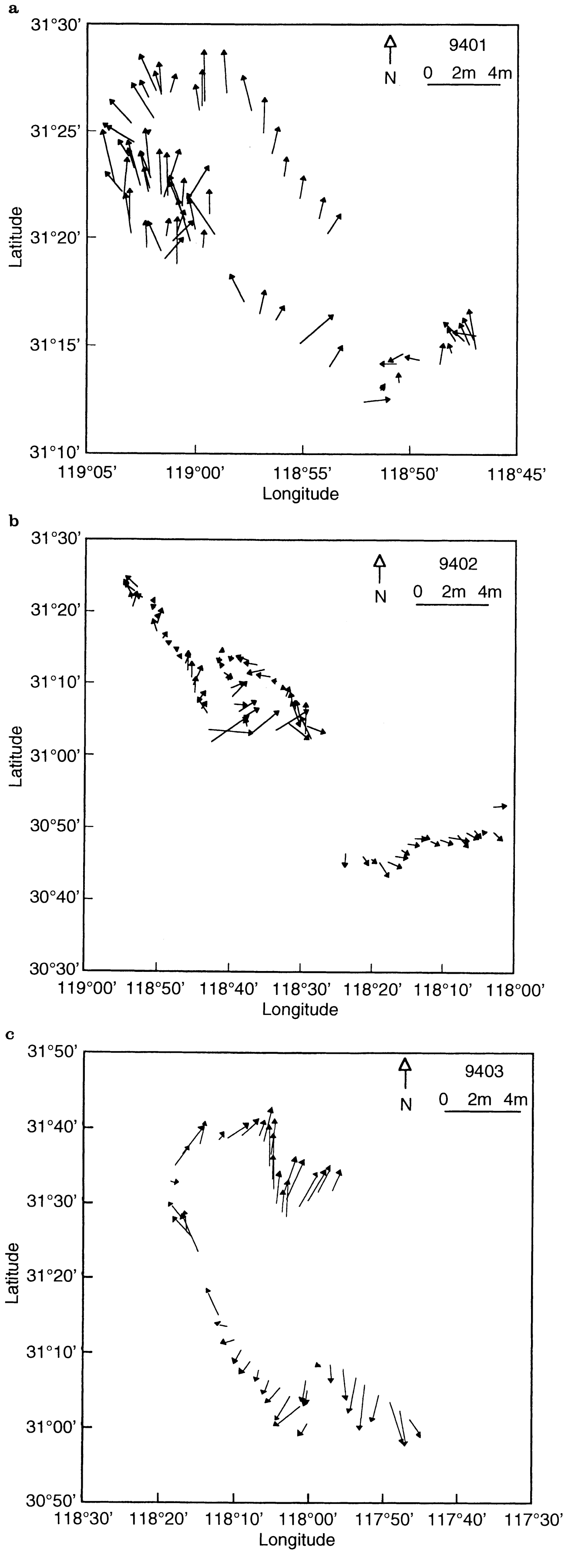

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Fig. 9 *Thunnus albacares*. Acoustic Doppler current profiles corresponding to tracks of Tunas 9401, 9402 and 9403, illustrating current pattern measured along each track

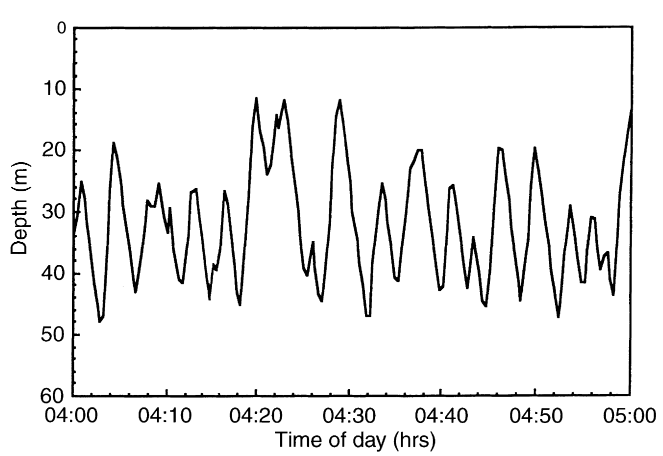

Fig. 10 *Thunnus albacares*. One-hour recordings of Tuna #9402 showing regular up-and-down movement or oscillatory swimming pattern. Downward descents are thought to be glides, while upward ascents are powered with thrusts of the tail

advantage of the higher prey abundance in northern latitudes, they are doing so by occupying the warm surface-waters.

The preference of the yellowfin and other tropical tunas for warmer waters throughout their range would accentuate the already high metabolic rates evident in the yellowfin tuna (Brill 1987). The high metabolic rate of this species coupled with the prolonged life-history stages in warmer waters most likely underlies the capacity for fast growth rates and high fecundity of yellowfin (Brill 1996; Schaefer 1996). The inability of the small yellowfin tuna to utilize a greater extent of the epipelagic zone in northern latitudes latitudes suggests that it may not be using the heat-conservation strategies characteristic of *Thunnus* for expanding its thermal range into cooler regimes. It is possible that the frequent dives into cooler waters may be accompanied by short periods of reduced whole-body conductance and physiological thermoregulation. However, the limited duration of the dives evident in the current tracks would suggest that the yellowfin tunas are not employing the thermoregulating strategies swordfish (Carey 1990), blue sharks (Carey and Scharold 1990), and bigeye tuna (Holland et al. 1992) to increase foraging time beneath the thermocline. It is possible that larger yellowfin (100 to 160 kg) with a greater thermal inertia could employ such strategies. However, recent studies of 100 kg tunas in warmer waters have provided little evidence of vertical movements that were distinct from those of smaller (5 kg) tunas followed in the same tropical waters (Brill et al. 1996). Thus, yellowfin tuna appear to reside in the top of the water column and use its reduced endothermic and heat-conservation strategies to elevate tissue temperatures a few degrees above the already warm ambient-water temperatures.

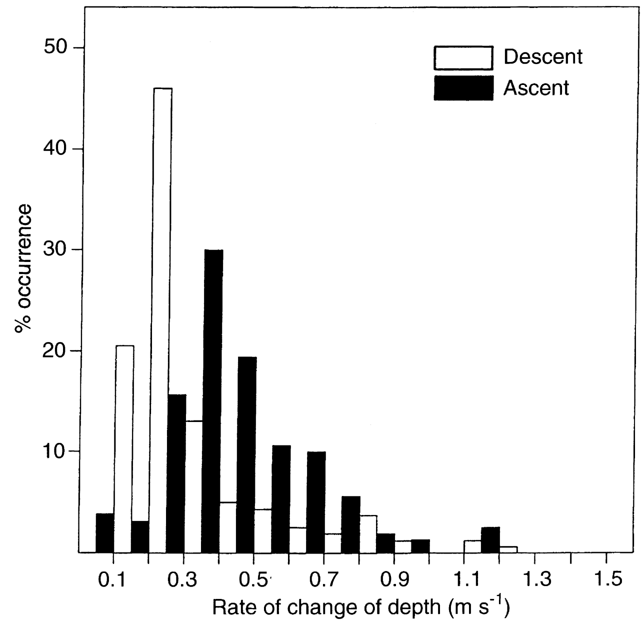

Fig. 11 *Thunnus albacares*. Rates of ascent and descent. Data have been pooled for all three tracks and calculated as straight-line changes in depth. Criteria used in calculation of these rates is included in "Results." Rates were determined from 161 ascents and 160 descents; Ascent/descent rates were grouped into intervals of 0.1 m s^{-1} [*0.1* = 0 to 0.1; *0.2* (not labeled) = 0.1001 to 0.2; *0.3* = 0.2001 to 0.3, etc.], and frequency of occurrence was plotted

Systematics and the thermal niche-expansion hypothesis

Morphologists have divided the genus between those species that inhabit cold-temperate or deeper waters and those that occupy warmer environs. *Thunnus albacares* is grouped with the *Neothunnus*, which are considered by morphologists to be more primitive than the bluefin group (Collette 1978). Tunas that inhabit cooler temperate or deeper waters (northern and southern bluefin, albacore and bigeye tuna) are united by a series of vascular characters (striations of the liver, lateral heat-exchangers only, and cranial retia) that would be advantageous for invasion of colder habitats. From a morphological perspective, this group of tunas is thought to represent the advanced condition for endothermic characters (Gibbs and Collette 1967; Collette 1978). The entire *Thunnus* clade is hypothesized to have radiated from a pantropical distribution to a more temperate and subpolar niche (Collette 1978; Sharp and Pirages 1978). The yellowfin tuna thus would be considered a primitive member of the *Thunnus* clade, with less sophisticated abilities for heat conservation (reduced lateral retia, lack of cranial and visceral retia), and perhaps because of this morphological reduction it is restricted to warm-water niches. Taken in this light, the telemetry data reported here might reflect this putative primitive condition of the yellowfin tuna in the genus.

Recent phylogenetic studies of tunas using molecular data from several genes suggest an alternative hypothesis for the evolution of the *Thunnus* radiation and the endothermic condition (Block et al. 1993; Chow and Kishino 1995; Finnerty and Block 1995). The mitochondrial DNA data is inconsistent with the placement of the yellowfin as a primitive member of the clade. In sharp contrast to morphological taxonomies, molecular genetic phylogenetic analyses suggest that the cold-water tunas such as the albacore and the bigeye are earlier offshoots of the *Thunnus* radiation than yellowfin (Sharp and Pirages 1978; Block et al. 1993; Ward et al. 1994; Chow and Kishino 1995; Finnerty and Block 1995). These data indicate that the albacore *T. alalunga* is the most primitive of the extant *Thunnus*, and suggest that the yellowfin tuna is most recent. If correct, these data imply that the most recent common ancestor of *Thunnus* may have lived in a cooler ocean environment than that which exists today, and that radiation into the more warm-temperate and tropical oceans was a more recent event. Importantly, this implies that the endothermic condition evolved in cold seas. Examination of the endothermic specializations of the genus *Thunnus* in the light of the molecular phylogenies indicates that the physiological and morphological attributes of the cold-water tunas (high standard metabolic rate, heat-retention mechanisms, internal localization of red muscle) were the basal attributes of the clade. This interpretation would suggest that yellowfin tuna as well as the other *Neothunnus* have only recently moved into the warm-temperate and tropical warm-water niche. This phylogenetic interpretation suggests that the inability of yellowfin to generate a large thermal excess and its reduced capacity for heat conservation (in red muscle, the head and digestive tract) may represent a secondary adaptation or a reduction of endothermic traits coincident with the movement of the *Thunnus* lineage back into warm-temperate and tropical waters. The telemetry data indicate that the species behaviorally remains most of the time in the warmest waters available throughout its range and tissue temperatures would only have to be raised a few degrees to achieve the same internal tissue temperatures as cold-water *Thunnus* species. The morphological specializations for endothermy of the *Neothunnus*, as represented by the yellowfin, may represent a life-history strategy that emphasizes warm water (hence little need for heat conservation), fast growth rates, and remarkably high fecundity (Brill 1996; Schaefer 1996).

Swimming speeds

One long-held tenet for the advantage of tuna endothermy is that warming of the locomotory muscles permits the attainment of elevated sustained and burst-swimming speeds, thus aiding in the search for prey in a patchy oceanic environment and predator avoidance. Tests of this relationship are complicated by the diffculties in obtaining measurements of sustained or burst-swimming speed measurements from free-swimming tunas. Direct measurements of swimming speeds of tunas with ultrasonic speedometer transmitters (Block et al. 1992a) have not yet been made. However, accurate positioning via GPS of the ship provides a reasonable means to assess the swimming speed of the yellowfin tuna being tracked. The data on estimated swimming speed over ground in this study were improved from previous ultrasonic tracking experiments by having continuous GPS data that updated the position of the tracking vessel every few seconds. The capacity to monitor the distance from the tuna quite accurately with the new tracking system also provided a better means of maintaining a fixed distance (0.3 to 0.4 nm) between the tracking vessel and the tuna. The acoustic Doppler current data permitted assessment of the influence of currents on movements. Mean swimming speeds (Table 2) in this study ranged from 0.48 to 0.91 m s^{-1} (0.924 to 1.766 knots), with sustainable speeds of >5 knots being evident for Tunas #9402 and #9403. Sustainable swimming speeds of 0.5 to 1.0 BL s^{-1} were routinely observed, but higher speeds (up to 3.5 BL s^{-1}) were maintained by #9403, the smallest tuna in the study, for >1 h. Currents during the track of #9402 were negligible, whereas periods of the #9403 track were associated with significant currents that may have aided the fish. The speeds observed in this study are consistent with those estimated by Carey and Olson (1982), and similar to speeds of larger yellowfin recently tracked in Hawaiian waters with the same acoustic tracking system (Brill et al. 1996). Telemetry studies on large blue marlin (Block et al. 1992b), which lack central or lateral heat-exchangers, indicated sustained speeds similar to the slower speeds observed for the yellowfin tunas, but higher continuous speeds were not witnessed. The higher sustained capabilities of these small tunas may in fact corroborate the hypothesis that warmer muscles result in higher sustained swimming speeds (Altringham and Block 1996). Models of aerobic swimming performance based on cardiovascular specializations of tunas have predicted that the high aerobic scope of tunas may be a specialization that permits higher rates of continuous swimming (Bushnell and Brill 1991; Korsmeyer et al. 1996).

The ability to track fish using a larger oceanographic vessel permitted simultaneous oxygen measurements and examination of its influence on vertical movements. Given the increased oxygen demands of tunas, it has been suggested that low oxygen in the eastern tropical Pacific might limit the tunas' distribution (Sund 1981; Brill 1994). The correlation of periods of sustained movement and the positioning of Tuna #9402 in the region of the water column with maximum oxygen concentrations was striking. The fluorometry data from CTD casts indicated that the oxygen increase was associated with an increase of phytoplankton. This photosynthetic oxygen-maximum region may thus create a microenvironment that the tuna can seek out during periods of sustained cruising. Importantly, this behavior only occurred during the most stressful first day of the track and could therefore be associated with increased oxygen demands required for recovery from the tag-and-release process.

Tunas in this study periodically moved in an oscillatory fashion (Fig. 10), consistent with a previously observed dive-and-glide pattern recorded for this species and bigeye tuna (Weihs 1973; Carey and Olson 1982; Holland et al. 1990). Analysis of ascent and descent speeds indicated that the tuna in this study descended at a consistent rate between 0.2 and 0.3 m s^{-1}. The rate of ascent was much more variable. Mean ascent rates were significantly higher than descent rates, as expected if tailbeats are limited to the ascent phase. Although no direct measurements are available and all calculations have a large number of underlying assumptions, it is tempting to suggest that the descent rate represents the glide phase. The estimated angle of descent during this phase of the locomotory cycle ranged from 24 to 33°, and was higher than previous estimates (Carey and Olson 1982; Holland et al. 1990). This dive–glide behavior suggested from the acoustic data is also consistent with new observations on similar-sized tunas in the Outer Bay Exhibit of the Monterey Bay Aquarium. Yellowfin tuna are frequently observed gliding downward in the 12 m tank without using the tail for propulsion. Pectoral fins are always extended during the lift-based glide phase. Tailbeats are restricted to a subsequent ascent phase. This type of swimming behavior is thought to be more energetically efficient (Weihs 1973), reducing locomotory effort at slow swimming speeds.

In conclusion, over 35 d of acoustic tracking of yellowfin tuna ranging in size from $\simeq$4 kg to 110 kg have now been obtained (Carey and Olson 1982; Holland et al. 1990; Brill et al. 1996; present study), and strong patterns of the environmental preferences for this species have emerged. The species is consistently found above the thermocline in the surface mixed layer. Yellowfin tunas dive beneath the thermocline, but only for short periods. Interestingly, the yellowfin rarely spend time at the immediate surface (0 to 3 m depth), and instead are usually at least 10 to 20 m below the surface in current tracks. This is in contrast to the behavior of similar-sized bluefin tuna and blue marlin that do appear to swim at the immediate surface of the water column (Holland et al. 1990; Block et al. 1992a; T. Itoh, archival-tag data, personal communication). However, yellowfin are similar to blue marlin and striped marlin tracked in Hawaiian waters in that they prefer to be above the thermocline. The tunas tracked in this study showed striking behavior patterns just prior to sunrise in that they rapidly ascended to the surface during the sunrise event. This behavior has recently been recorded in archival-tagged bluefin tuna and its timing coincides exactly with changes in the isolume (T. Itoh personal communication). The significance of the movement remains unclear and may be associated with predatory behavior.

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