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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

Received: 27 March 1998 / Accepted: 13 November 1998

Abstract We measured the horizontal and vertical movements of five adult yellowfin tuna (*Thunnus albacares*, estimated body mass 64 to 93 kg) near the main Hawaiian Islands, while simultaneously gathering data on oceanographic conditions and currents. Fish movements were recorded by means of ultrasonic depth-sensitive transmitters. Depth–temperature and depth–oxygen profiles were measured with vertical conductivity–temperature–depth (CTD) casts, and the current-velocity field was surveyed using an acoustic Doppler current profiler (ADCP). Large adult yellowfin tuna spent ≈ 60 to 80% of their time in or immediately below the relatively uniform-temperature surface-layer (i.e. above 100 m), a behavior pattern similar to that previously reported for juvenile yellowfin tuna, blue marlin (*Makaira nigricans*), and striped marlin (*Tetrapturus audax*) tracked in the same area. In all three species, maximum swimming depths appear to be limited by water temperatures 8 °C colder than the surface-layer

water temperature. Therefore, neither large body mass, nor the ability to maintain elevated swimming-muscle temperatures due to the presence of vascular counter-current heat exchangers in tunas, appears to permit greater vertical mobility or the ability to remain for extended periods below the thermocline. In those areas where the decrease in oxygen with depth is not limiting, the vertical movements of yellowfin tuna, blue marlin and striped marlin all appear to be restricted by the effects of water temperature on cardiac muscle function. Like juvenile yellowfin tuna, but unlike blue marlin and striped marlin, adult yellowfin tuna remained within 18.5 km of the coast and became associated with floating objects, including anchored fish-aggregating devices (FADs) and the tracking vessel. Like juvenile yellowfin tuna, large adult yellowfin repeatedly re-visit the same FAD, and appear able to navigate precisely between FADs that are up to 18 km apart. The median speed over ground ranged from 72 to 154 cm s⁻¹. Neither speed nor direction was strongly influenced by currents.

Communicated by M.H. Horn, Fullerton

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Introduction

Ultrasonic telemetry can be used to obtain precise and detailed data on the horizontal and vertical movements of pelagic fishes. It can thus define the physical environment used by these species, help clarify basic ecological relationships, and provide inferences on physiological abilities and tolerances (Carey 1983; Brill 1994). Extensive data sets on the horizontal and vertical movements of juvenile and small adult tunas (family Scombridae, tribe Thunnini) and large adult billfishes (family Istiophoridae and Xiphiidae) have been obtained using ultrasonic telemetry (Yuen 1970; Laurs et al. 1977; Carey and Olson 1982; Yonemori 1982; Carey 1990; Holland et al. 1990a, b; Holts and Bedford 1990; Cayré 1991; Block et al. 1992a, b, 1997; Brill et al. 1993). There are, however, comparatively few data on the short-term movements of large adult tunas (Carey and Lawson

1973), and there are no published telemetry data for large adult yellowfin tuna (*Thunnus albacares*).

Our main objective was to acquire telemetry data from large adult yellowfin tuna, and to do so in the same area and essentially under the same oceanographic conditions as data obtained from juvenile yellowfin tuna and bigeye tuna (*Thunnus obesus*), and blue (*Makaira nigricans*) and striped (*Tetrapturus audax*) marlins (Holland et al. 1990a, b; Block et al. 1992a, b, Brill et al. 1993). Our data, therefore, allow us to discern species-specific behaviors and the influence of body size on depth distribution. Our second objective was to acquire data relevant to fisheries management and population assessments issues including: mean and median rates of displacement (i.e. speed over ground), residence time of yellowfin tuna in nearshore areas of oceanic islands, and the effects of vertical thermal structure on vulnerability to specific fishing gears.

Neill et al. (1976) and Stevens and Neill (1978) were the first to hypothesize that the main selective advantage of tunas' vascular counter-current heat exchangers (described by Kishinouye 1923; Carey and Teal 1966; Carey 1973; Graham 1975) is that they slow rates of temperature change in deep red muscle following abrupt reductions in ambient temperature. In other words, vascular counter-current heat exchangers provide tunas an enhanced thermal inertia compared to other similarly sized fishes. Neill et al. (1976) and Stevens and Neill (1978) further argued that this effect allows tunas to maintain higher activity levels for longer periods when diving below the thermocline, and thus more effectively escape predators or exploit deep food-resources. Because larger individuals have an increased thermal inertia and slower rates of muscle-temperature change than smaller fish, a natural extension of this hypothesis is that large adult tunas should make more extensive vertical movements than juvenile fish. Thus, adult tunas should have the ability to spend more time below the thermocline and exploit food resources not available to juveniles. This assumes that muscle temperature is indeed the factor limiting vertical movements. Therefore, comparing the vertical movements of small yellowfin and bigeye tunas, large adult yellowfin tuna, and blue and striped marlins in the same area also allows us to test directly hypotheses on the advantages accorded tunas by their large thermal inertia.

Materials and methods

We employed two vessels, a 20 m commercial fishing boat ("Hana Like") and the 53 m National Oceanic and Atmospheric Administration (NOAA) research ship "Townsend Cromwell". The ultrasonic receiving systems aboard both vessels employed a Vemco (Halifax, Nova Scotia, Canada) Model VR 42 four-hydrophone array mounted beneath a weighted steel tow-body. The hydrophones were towed amidships ≈ 5 to 10 m beneath the surface. The four-channel receiver aboard the "Hana Like" was a Vemco Model VR28. (This system has been used previously to track *Thunnus albacares* in the eastern Pacific and is described in detail by Block et al. 1997.) Fish depth, encoded by the transmitter's pulse interval,

was decoded by the Vemco receiver aboard the "Hana Like" and recorded directly by an attached laptop computer. Aboard the "Townsend Cromwell", a Vemco four-channel receiver (Model CR40), frequency-counter, and laptop computer were employed to monitor and record depth data.

The fishes' aggregate time-at-depth and time-at-temperature distributions were calculated based on 10 m and 1°C bins, respectively, as described by Holland et al. (1990a, b). These data were subsequently expressed as a fraction of the total time each fish was followed, and the fractional data bins were averaged across all fish.

Fishing operations were centered off the western (leeward) coast of the Island of Hawaii (see Fig. 1), because in this area high volcanic mountains provide a lee of up to ≈ 18 km from the strong northeasterly trade winds. *Thunnus albacares* were captured by the crew of the "Hana Like" with standard commercial handline gear (described by Yuen 1979). Fish were identified to species, and body weights were estimated to the nearest kilogram independently by two experienced observers. Ultrasonic depth-sensitive transmitters (Vemco, Model V32) were attached to custom-made stainless steel darts with braided teflon-coated stainless steel cable. Using a standard fish tagging pole, the darts were pushed ≈ 8 to 10 cm into the dorsal musculature immediately lateral to the anterior edge of the first dorsal fin. Tuna were released by cutting the leader as close to the fish as practical. No attempt was made to retrieve the hook. Fish were usually tracked by the "Hana Like"; however, the "Townsend Cromwell" occasionally tracked in tandem.

Physical oceanography measurements were conducted aboard the "Townsend Cromwell", and consisted of continuous mapping of current velocity and sea-surface temperature, and a series of vertical conductivity-temperature-depth (CTD) casts. Measurements of the current-velocity field were made with a hull-mounted 150 kHz RD Instruments (San Diego, California, USA) acoustic Doppler current profiler (ADCP) system. The system was connected directly to the vessel's global positioning system (GPS) satellite receiver, and absolute current velocities over ground were calculated by removing the ship's speed vector (calculated from GPS data), pitch, and roll from the recorded current data. Current velocities were calculated by the ADCP from 5 min data-collection periods. Current velocity and direction profiles were subsequently time-averaged into 1 h bins and vertically averaged into two depth bins (20 to 75 m and 75 to 130 m). CTD casts were made at 86 stations using a Sea-Bird Electronics SBE 911Plus system (Sea Bird Electronics Inc., Bellevue, Washington, USA). The sampling design consisted of three repeated transects (7 to 9, 9 to 13 and 16 to 20 August 1995) of the study area from 19°00'N to 19°50'N and from near the 700 m isobath to 28 km offshore (see Fig. 1B). Hydrographic profiles were merged with data on the vertical movements of the fish based on the proximity of the fish to the CTD stations. The data from one profile were used if the fish was < 1.8 km from the nearest station; the averaged data from two or three closest profiles were used if the fish was further away.

Geographic positions were obtained aboard the "Hana Like" by means of a GPS satellite receiver. The tracking vessels' positions were assumed to be the same as those of the fish and were recorded manually approximately every 10 to 15 min. Speed over ground was calculated assuming that the fish moved in a straight line between successive geographical positions. The fishes' movements relative to anchored fish-aggregating devices (FADs) were also recorded [FADs are buoys designed specifically to aggregate pelagic fishes. The FADs deployed near the main Hawaiian Islands have been described by Brock (1985). Letters identifying individual FADs used herein are those assigned by the State of Hawaii.] Ultrasonic telemetry-receiving equipment accurately provides direction, but only subjective estimates of the range to the transmitter. As a result, the minute-to-minute movements of the fish could not be tracked exactly. Because FADs were anchored in water > 1000 m deep, their anchor lines allowed them to move with the currents over distances of several nautical miles. Therefore, it is possible to provide only subjective descriptions of fish movements relative to FADs.

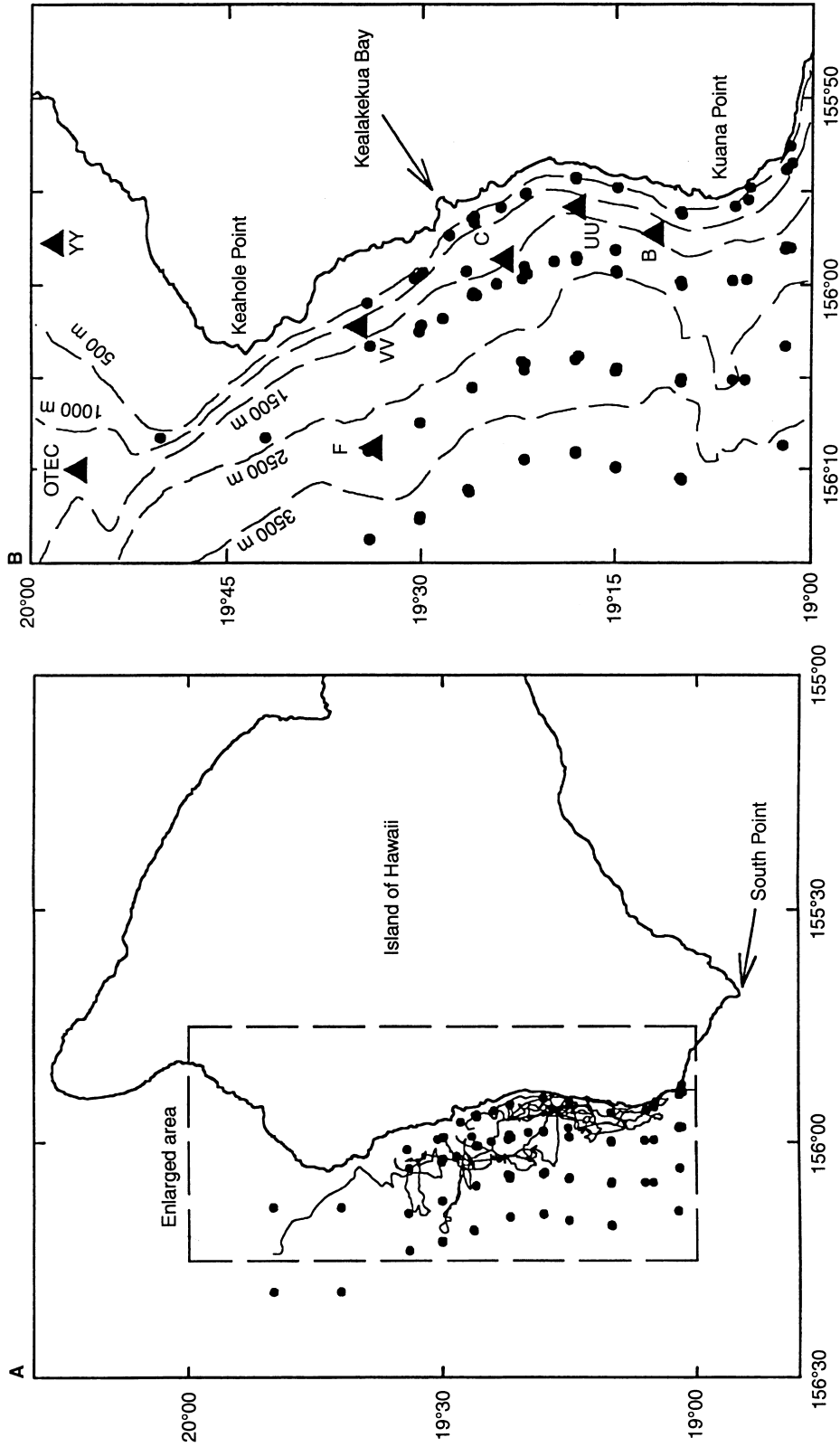


Fig. 1 Study area. **A** Positions of CTD stations (●), tracks of five adult *Thunnus albacares* tracked during our study, and area enlarged in Figs 2 and 10. **B** Bathymetry (dashed lines), positions of CTD stations (●), and approximate locations of FADs (fish-agggregating devices, ▲) off western (leeward) coast. Because FADs were anchored in water > 1000 m deep, their anchor lines allowed them to move with the currents over distances of several nautical miles. Letters identifying FADs (F, VV, C, UU, B, YY, OTEC) are those assigned by State of Hawaii. Scale is shown by longitude (1 min = 1.85 km = 1 nautical mile)

Results

The five *Thunnus albacares* tracked appeared to favor the area immediately south of Kealakekua Bay (Fig. 1). Contact with Fish Nos. 1 and 3 was lost after they entered an area of rough water not protected from the northeast trade winds near Kauna Point. It is possible that these two fish continued south, eventually to the windward side of the island. They also followed relatively straight courses; the straight-line distances between the start and end points were 85 and 70%, respectively, of the track (Table 1). The other three fish (Nos. 2, 4, 5) followed looping courses, which repeatedly traversed the same area; the straight line distances between the starting and ending points were only 21 to 35% of the total distances covered (Table 1).

Horizontal movements

Fish No. 1 was captured and released ≈ 5.5 km west of Kealakekua Bay (Fig. 2A) on 8 August 1995 at $\approx 05:30$ hrs (Hawaii Standard Time). For the duration of the 15 h track, the fish proceeded south, parallel to the shoreline. It came within ≈ 0.18 km of shore at its closest approach, moving into waters ~ 500 m deep. The bottom topography was extremely steep, so the depth could not be determined with certainty. The fish passed within 1.8 to 3.6 km of two FADs (UU and B; Fig. 2A), but did not appear to change course to approach either one. Contact was lost in deteriorating sea conditions near Kauna Point.

Fish No. 2 was captured and released ≈ 5.5 km northwest of Kealakekua Bay on 9 August 1995 at $\sim 09:20$ hrs, and tracked for 86 h (Fig. 2B). It proceeded offshore (west) for ≈ 5 h, then east and then southeast, eventually arriving at FAD-C. The fish then proceeded south, arriving at FAD-UU after dark. It maintained an irregular course over the next 36 h which took it within less than <1.8 km off the coast. The fish also re-visited FAD-UU several times and FAD-B briefly. These FADs are separated by ≈ 18 km. About 48 h after the start of the track, the fish moved due west, reaching 16 km from the coast, then north, then west (after sunset), eventually arriving at FAD-F. The fish returned to FAD-VV the following day, then moved north and northwest. Contact was lost about midnight, 15 km west of Keahole

Point, when the fish moved rapidly away from the tracking vessel.

Fish No. 3 was captured and released ≈ 8 nautical miles (15 km) south of Kealakekua Bay 14 August 1995 at $\sim 23:45$ hrs. For the 11 h duration of the track, it moved due south on a course parallel to Fish No. 1 (Fig. 2A). As Fish No. 3 approached FAD-B, a second transmitter was heard. This signal was probably from Fish No. 2, as the batteries in the transmitter carried by Fish No. 1 would have most likely have been depleted. Contact with the second transmitter was lost as Fish No. 3 continued south, a course it held for the remainder of the track. Contact with Fish No. 3 was lost due to deteriorating sea conditions near Kauna Point, close to where contact with Fish No. 1 was lost.

Fish No. 4 was captured and released ≈ 7.4 km west of Kealakekua Bay on 15 August 1995 at $\sim 16:40$ hrs. It was tracked for 46 h (Fig. 2C). It proceeded south for 21 h. The fish did not obviously alter its course to approach FAD-C, but did briefly approach FAD-UU. At dawn, 12 h after the track started, the fish become associated with the tracking boat. The fish remained in the immediate vicinity of the boat as the tracking boat drifted slowly south for the next 6 h, and continued even as the boat was purposefully driven north towards FAD-B. After dark, the fish broke its association, moved north, then looped south, re-visiting FAD-B. The fish continued south for 4 h, then looped north, then south. Contact was lost south of Kauna Point when the transmitter was shed.

Fish No. 5 was captured and released ≈ 18 km west of Kealakekua Bay on 19 August 1995 at $\sim 02:00$ hrs. It proceeded briefly southeast, then west for ≈ 6 h (Fig. 2A), then turned and retraced its course almost to the position where it had been captured. It turned and moved south from sunset through the night. By morning, the fish had become associated with a floating cargo net, which also had attracted schools of skipjack tuna (*Katsuwonus pelamis*), and remained with the floating object until tracking was terminated at noon.

Oceanographic conditions

The physical environment was well-stratified (Fig. 3) and stable, because the study area is mostly well shielded from the northeast trade winds. Sea surface (<5 m)

Table 1 *Thunnus albacares*. Estimated body mass, calculated fork length, dates tracked, duration of track, distance covered, and distance between start and end points for five yellowfin tuna

Fish No.	Estimated mass (kg)	Fork length (cm)	Dates of track (Aug.)	Duration (h)	Total distance covered (km)	Straight-line distance between start and end points (km)
1	88	164	8	15	52	44
2	64	148	9–12	86	279	72
3	77	157	14	11	44	31
4	93	167	15–17	46	148	51
5	64	148	19–20	36	87	18

equipped with ultrasonic depth-sensitive transmitters. Fork length was calculated from estimated body mass using regression equation of Nakamura and Uchiyama (1966)

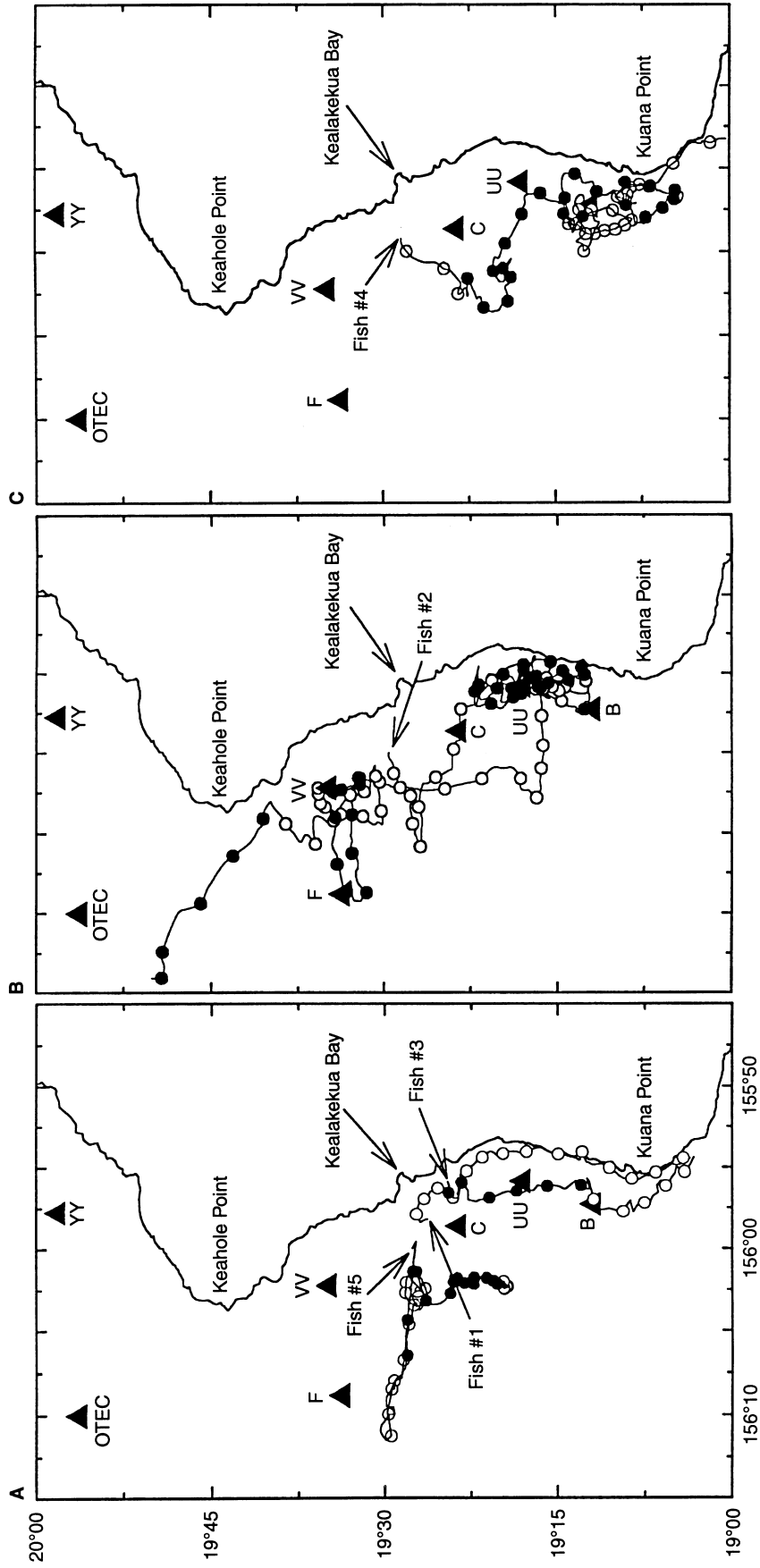


Fig. 2 *Thunnus albacares*. Horizontal movements of five adults tracked during our study (○ daytime hourly positions; ● nighttime hourly positions; nos. identifying fish show starting position of each track; ▲ approximate locations of FADs)

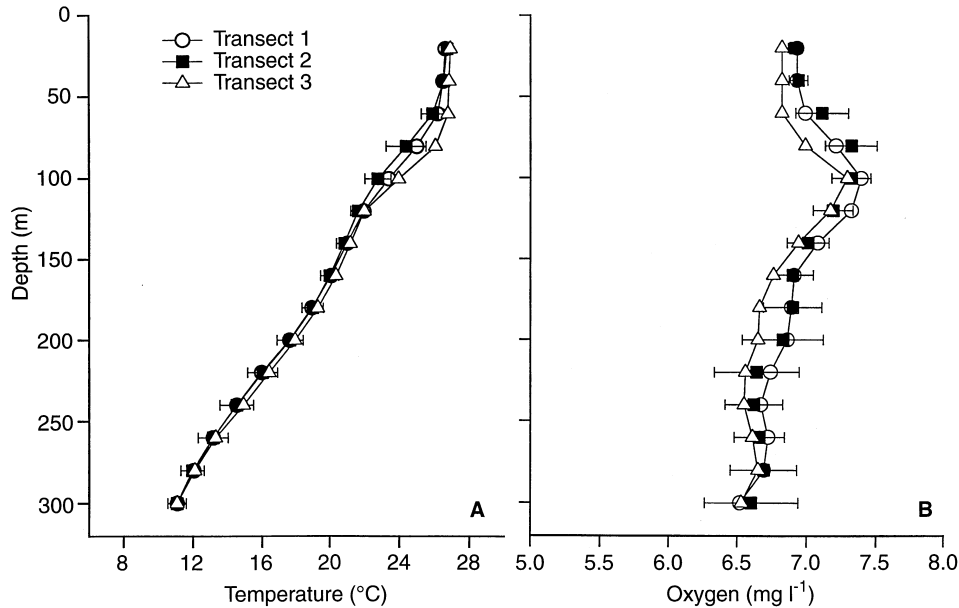


Fig. 3 Temperature and oxygen data from three repeated transects (conducted 7 to 9, 9 to 13, and 16 to 20 August 1995) in study area from 19°00'N to 19°50'N and from near 700 m isobath to 24 km offshore. Data are means for each transect; for clarity, error bars (± 1 SD) are shown only for Transect 2, but error bars were similar for the other two transects

temperatures were relatively uniform (26.3 to 27.9 °C), but were also over 1 °C warmer than the top of the thermocline (defined as a >1 °C change in water temperature over a distance of 8 m). Therefore, the region above the thermocline was not a true isothermal mixed layer and is hereafter referred to as the “surface layer”. The depth of the thermocline was ≈ 70 m near the coast and slightly shallower (≈ 60 m) about 25 to 30 km offshore. It had moderate horizontal variability but only minor temporal variability (Fig. 3A), and was deepest (>85 m) in the southern portion of the survey. This area had greater meteorological forcing because it was not as well shielded from northeasterly trade winds.

Vertical movements in relation to temperature and oxygen conditions

The five adult yellowfin tuna tracked spent most of their time within or immediately below the surface layer (Fig. 4). Approximately 80% of the time, fish were shallower than 100 m (Fig. 5A). They occasionally descended to water as cold as 18 °C (i.e. ≈ 8 °C below surface layer temperature), but spent $>90\%$ of their time in water above 22 °C (Fig. 6A). Mean (\pm SD) oxygen–depth data from all transects have been added to Fig. 5A. There were no biologically significant decreases in oxygen levels at the depths reached.

The nonparametric Kolmogorov–Smirnov test (Statgraphics 5.0, Manugistics, Rockville, Maryland, USA) revealed no significant differences between day

and night time-at-depth (Fig. 5B) or time-at-temperature (Fig. 6B) distributions that included data from all fish. This lack of a day–night difference is in part a result of the variability of vertical movements between fish. Fish Nos. 4 and Fish 5 tended to be shallower during the night than during the day (Fig. 7), although both remained in the surface layer (Fig. 4).

Horizontal displacement rates and their relationship to currents

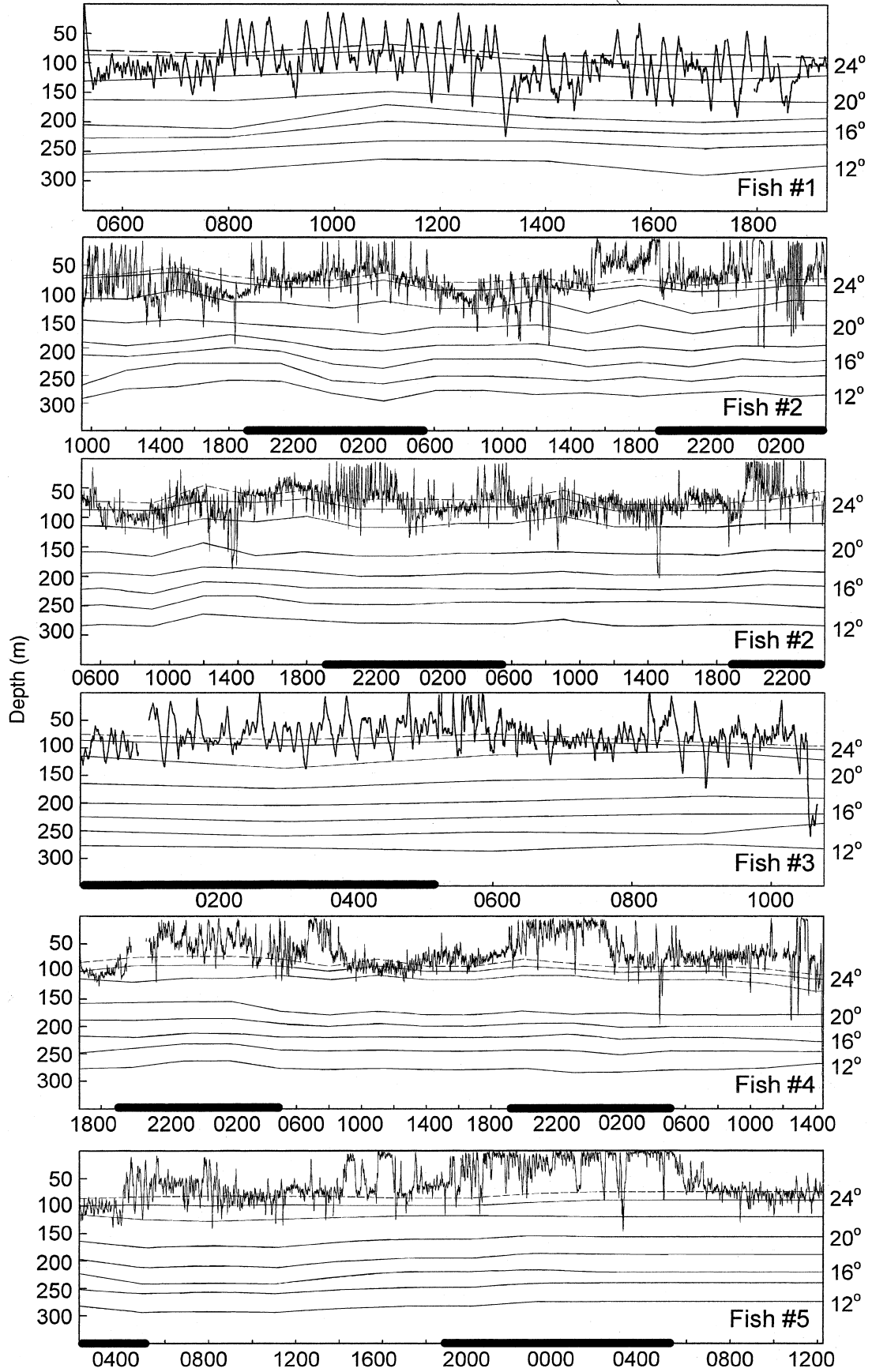
Most recorded speeds over ground (henceforth referred to as “speed”) were far less than the maximum recorded (Fig. 8). Approximately 90% of observed speeds were ≤ 200 cm s $^{-1}$ (Fig. 8A).

We compared the median speed data from our study with data similarly obtained for smaller individuals by other investigators (Fig. 9). Although the correlation of swimming speed and body length was not strong ($r^2 = 0.25$), the decrease in swimming speed with increasing body size predicted by Magnuson (1973), based on hydrostatic equilibrium speeds, did not occur. Rather, there appeared to be positive relationship between speed and body size. The equation describing the relationship is: median speed (cm/s) = $54 (\pm 20$ SD) + $0.42 (\pm 0.18$ SD) \times fork length (cm).

The ADCP data revealed that strong currents occurred primarily during the first half of the survey (7 to 13 August). North–northwest velocities in the 20 to 75 m depth layer of up to 75 cm s $^{-1}$ were recorded near both Keahole Point and ~ 25 to 30 km offshore (Fig. 10). During the same time period, currents in the

Fig. 4 *Thunnus albacares*. Vertical movements of five adults studied (Dashed line depth of surface layer; continuous lines 2 °C isotherms; black bars on abscissa nighttime) For clarity, depth record for Fish No. 2 is presented in two panels

Fig. 4



75 to 130 m depth layer had a similar direction but a maximum velocity of $<50 \text{ cm s}^{-1}$. With the exception of Keahole Point and South Point, current velocities in the 20 to 75 m depth layer within 9.2 km of the coast were reduced to $10\text{--}20 \text{ cm s}^{-1}$.

Current speed and direction had little obvious influence on the horizontal movements of adult yellowfin tuna, with the possible exception of the last 5 h of tracking Fish No. 3. During this period, its northwest course roughly paralleled current direction, and mean ($\pm \text{SEM}$) speed ($174 \pm 13 \text{ cm s}^{-1}$) exceeded that during the remainder of the track ($121 \pm 2.7 \text{ cm s}^{-1}$) ($p < 0.01$, Mann–Whitney rank sum test; SigmaStat. SPSS Inc., Chicago, Illinois, USA). These observations indicate that occasionally there can be an additive effect of water currents on fish speed.

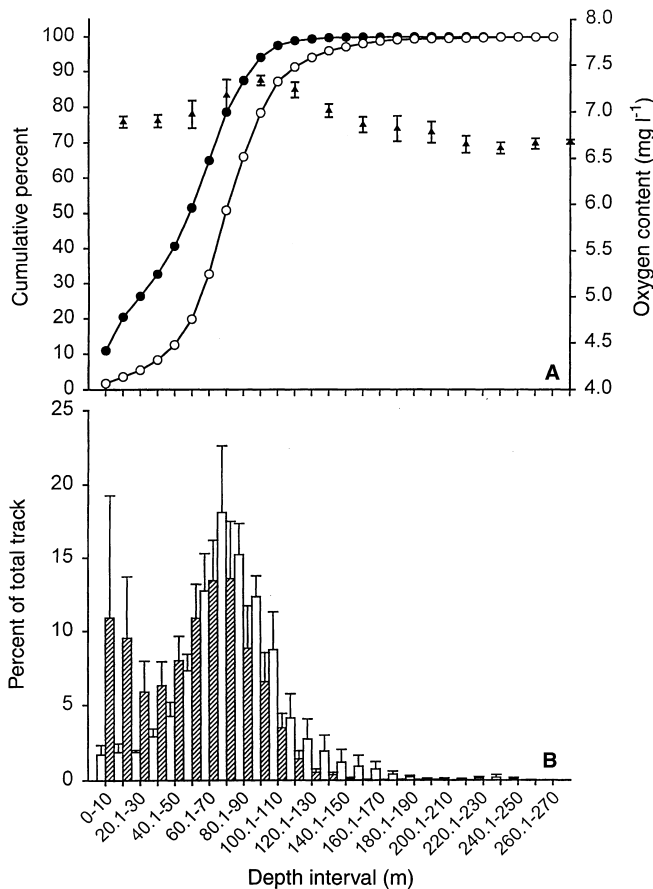


Fig. 5 *Thunnus albacares*. **A** Vertical distribution of five adults expressed as cumulative percent (\circ daytime; \bullet nighttime) and mean ($\pm \text{SD}$) oxygen–depth profile (\blacktriangle) for data collected during all 86 CTD casts; note that no biologically significant decrease in oxygen occurs near main Hawaiian Islands at depths reached by yellowfin tuna; a slight rise in oxygen levels occurs at approximately the bottom of the surface layer. **B** Vertical distribution expressed as percent time spent at specific depths (mean $\pm \text{SEM}$) (open bars daytime; hatched bars nighttime); by nonparametric Kolmogorov–Smirnov test (Statgraphics 5.0, Manugistics, Rockville, Maryland, USA), no significant differences were found between daytime and nighttime time-at-depth distributions that included data from all fish

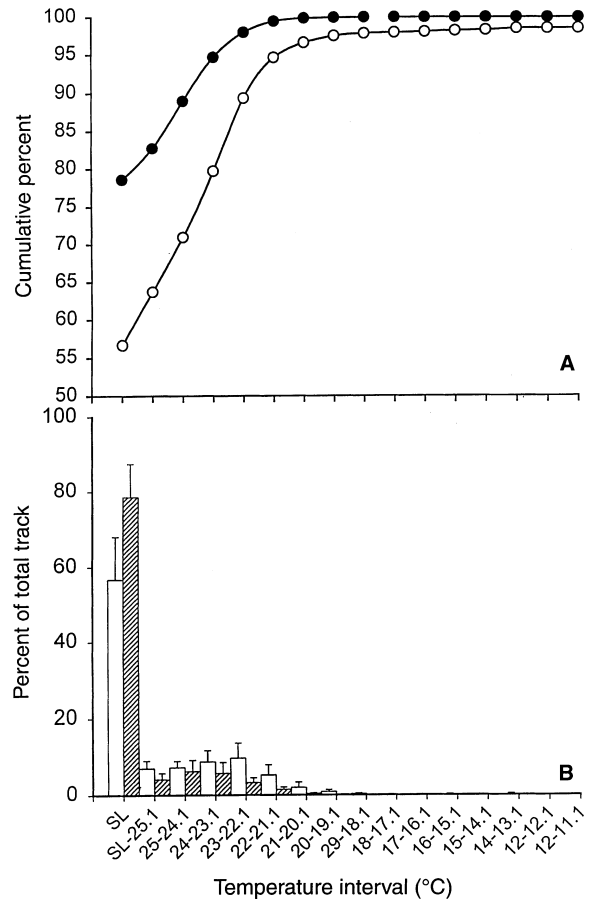


Fig. 6 *Thunnus albacares*. **A** Vertical distribution data of five adults expressed as cumulative percent (\circ daytime; \bullet nighttime); **B** vertical distribution expressed as percent time spent at specific temperature (mean $\pm \text{SEM}$) (open bars daytime; hatched bars nighttime)

Discussion and conclusions

Horizontal movements

Horizontal movements of five large adult yellowfin tuna, *Thunnus albacares* showed similarities to those of yellowfin and skipjack tunas tracked in the same area and in other regions of the Pacific. All clearly are capable of precise navigation between FADs that are $\approx 18.5 \text{ km}$ apart (Holland et al. 1990b; K. N. Holland and R. W. Brill unpublished observations). The mechanisms tunas use to navigate have not been conclusively proven; they most probably involve the demonstrated ability of these fishes to detect the earth's geomagnetic field (Walker 1984). Although large adult yellowfin tuna spent some time associated with FADs, none showed the precise 24 h rhythmicity of leaving and returning to FADs or features of the coastal topography demonstrated by smaller tunas (Yuen 1970; Holland et al. 1990b; Cayré 1991; Cillauren 1994). The reasons for these repetitive behaviors are unclear. Holland et al. (1990b) suggest that juvenile tunas leave the FADs at dusk to go on feeding excursions. However, analyses of gut contents

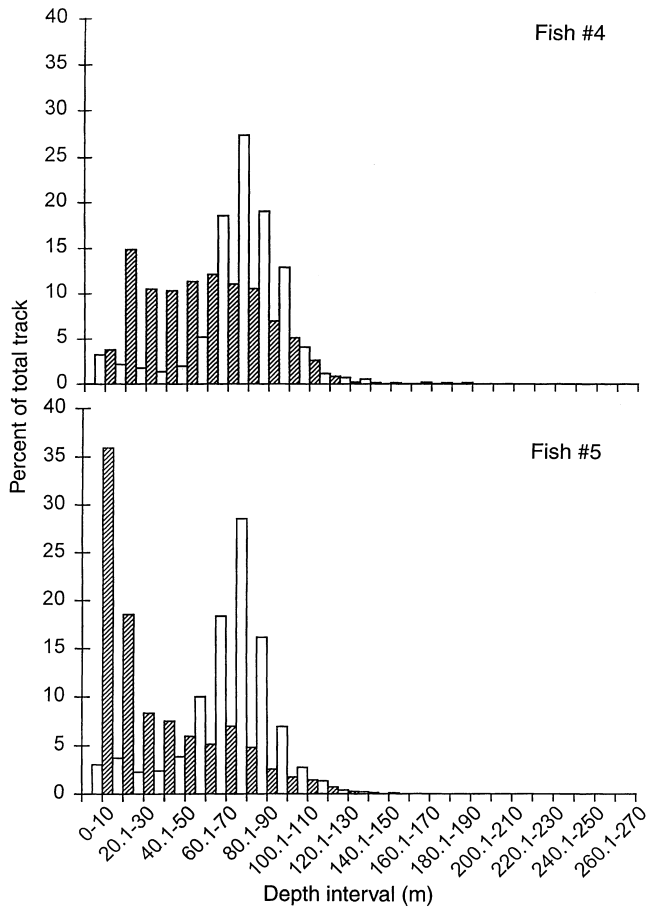


Fig. 7 *Thunnus albacares*. Vertical distribution of Fish Nos. 4 and 5 expressed as percent time spent at specific depths (open bars daytime; hatched bars nighttime)

suggest that, at night, yellowfin tuna feed infrequently if at all (Buckley and Miller 1994; Roger 1994a). Brock (1985) has shown that juvenile yellowfin tuna can deplete food resources around FADs and then begin feeding almost exclusively on oplophorid shrimps, a prey rarely found in the stomach of yellowfin tuna not associated with FADs. Lack of forage may be why the adult yellowfin tuna did not remain associated with FADs during our study. Fish No. 4 did remain associated with the tracking vessel for 6 h in the same way tunas and other pelagic fish have been reported to retain a tight association with floating objects (Hunter and Mitchell 1967) and fishing or sailing vessels (Fonteneau and Diouf 1994). Fish No. 5 remained tightly associated with a floating cargo net for at least 5 h before tracking was terminated. These durations exceed those that any large adult tuna remained associated with a FAD, and may indicate that yellowfin tuna treat anchored FADs and drifting objects differently, as first proposed by Holland et al. (1990b).

The horizontal movements of yellowfin tuna frequently covered the same area, were predominately parallel to the shoreline, and generally showed little or no obvious effect of currents. These movements contrast

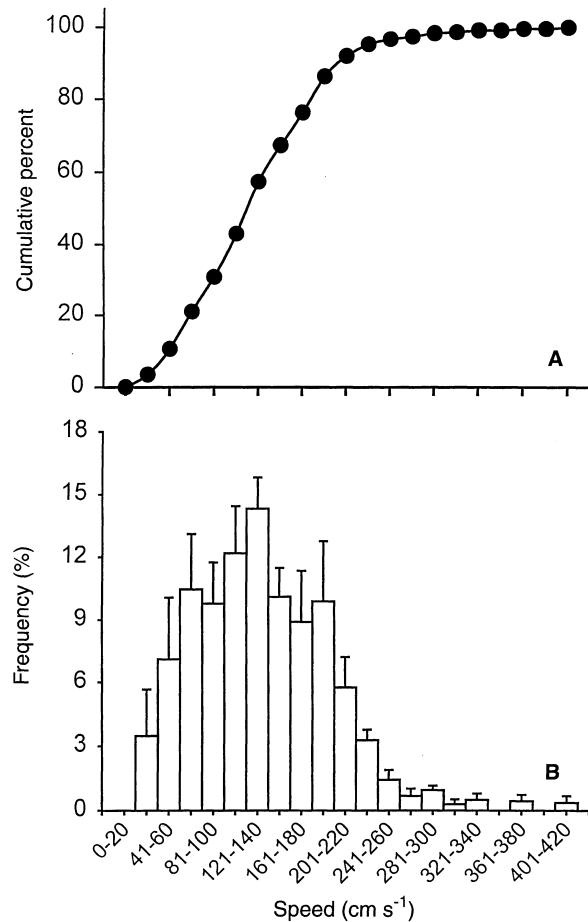


Fig. 8 *Thunnus albacares*. **A** Frequency of observed speeds over ground of five adults expressed as a cumulative total. **B** Frequency histogram (mean \pm SEM) of observed speeds; frequency of each speed interval was calculated as fraction of total number of observations for each fish, speed intervals were then averaged across fish

with those of blue and striped marlins tracked in the same area by Holland et al. (1990b), Block et al. (1992a,b), and Brill et al. (1993). These latter fishes tended to follow straight or slowly arcing courses, and usually moved almost directly offshore. The speed and direction of movement of marlins also often followed the eddy patterns (Fig. 10) that occur on the leeward side of the Island of Hawaii (Lobel and Robinson 1986; Qui et al. 1997). Sea-surface temperatures ranged only from 26.3 to 27.9 °C over the entire survey area. These data, plus the relatively uniform depth of the surface layer and relatively uniform depth-temperature, and depth-oxygen profiles (Fig. 3) indicate that there were no strong temperature fronts or sharp horizontal oceanographic features that adult yellowfin tuna would detect (Lauris et al. 1977, 1984; Fiedler and Bernard 1987). The fact that movements were predominantly north and south (i.e. parallel to the coast) rather than east and west (i.e. onshore and offshore) was not related to the physical oceanography, and remains to be explained.

The tight association of adult yellowfin tuna with the coastline during our 2 wk study could indicate a pro-

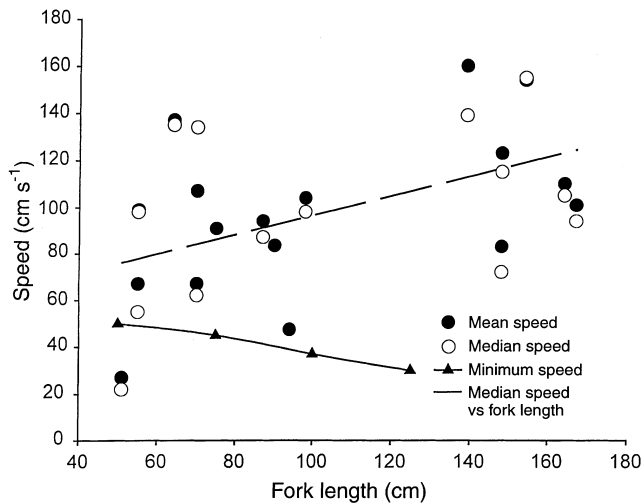


Fig. 9 *Thunnus albacares*. Mean and median speed over ground measured during ultrasonic telemetry studies. Incorporated are data for small (54 to 98 cm) fish from Carey and Olson (1982), Holland et al. (1990b) and Block et al. (1997). Regression line shows relationship of median speed and fork length [median speed (cm/s) = $54 (\pm 20) + 0.42 (\pm 0.18) \times \text{fork length (cm)}$, $r^2 = 0.25$] [▲ predicted minimum hydrostatic equilibrium swimming speed from Magnuson (1973)]

tracted residence time on the leeward sides of islands. Shomura (1959) has reported a greater apparent abundance, based on catch-per-unit-effort data, of yellowfin tuna on the leeward sides than on the windward sides of the main Hawaiian Islands. This phenomenon may result from relative forage abundance. The fast-swimming organisms (e.g. micronektonic fishes and squid) that compose the bulk of the yellowfin tuna's diet (King and Ikehara 1956; Buckley and Miller 1994) are not readily captured by micronekton nets, thus making it impossible to assess directly the abundance of the tuna prey-species (Sund et al. 1981; Clarke 1983). Planktonic organisms which support tuna prey are entrained by the eddies formed on the leeward sides of oceanic islands (Boehlert and Mundy 1993), so it is likely that tuna prey-organisms are also concentrated in these areas (Roger 1994b). Protracted residence of large adult yellowfin tuna in nearshore areas, which are readily exploited as fishing grounds by even small-boat troll and handline fishing methods, could have significant fishery-management implications, and needs further study.

Vertical movements and depth distribution

During our observation period, mean oxygen content remained $>6.5 \text{ mg l}^{-1}$ ($>80\%$ saturation at 15°C) to the maximum depths reached by the tracked fish ($\approx 270 \text{ m}$; Fig. 5). Although yellowfin tuna will make physiological adjustments to equivalent reductions in ambient oxygen at 25°C (Bushnell et al. 1990), such mild reductions are readily tolerated and do not impair oxygen delivery by the cardiorespiratory system (Bushnell and Brill 1991, 1992). Barkley et al. (1978), Sharp (1978), Sund et al. (1981)

Cayré (1991), and Cayré and Marsac (1993) describe areas within the Pacific and Indian Oceans where oxygen levels limit the vertical movements of yellowfin tuna. Near the main Hawaiian Islands, however, temperature rather than oxygen appears to be the limiting factor.

Ultrasonic telemetry and depth-of-capture data show that, near the main Hawaiian Islands, the depth distribution of yellowfin tuna, blue marlin, and striped marlin are essentially identical (Holland et al. 1990a, b; Block et al. 1992a, b; Boggs 1992; Brill et al. 1993). Taken together, these observations indicate that some common factor(s), other than ambient oxygen levels (Fig. 5A), may be limiting the vertical movements of these three species. As first noted by Brill et al. (1993) for striped marlin, and Hinton and Nakano (1996) for blue marlin, the determinant appears to be the change in temperature occurring between the surface layer and waters below the thermocline, rather than a specific water temperature per se. In Fig. 11, ultrasonic depth-telemetry data from yellowfin tuna in the eastern Pacific (taken from Block et al. 1997) are plotted with the data from large adult yellowfin tuna tracked near the main Hawaiian Islands. When temperature bins are expressed as degree intervals (Fig. 11A), the time-at-temperature distributions for yellowfin tuna in the eastern Pacific and near the main Hawaiian Islands are clearly different, because the warmest water available (i.e. the surface layer) in the eastern Pacific was only 19 to 20°C . When, however, the data are plotted with the temperature bins expressed as degree interval changes relative to surface-layer temperature (Fig. 11B), the time-at-temperature distribution for the two groups of yellowfin tuna become essentially identical. Although yellowfin tuna tracked in the eastern Pacific most probably have acclimated to the lower surface-layer temperatures, their vertical movements are still limited by the same relative reductions in water temperature that limit the vertical movements of yellowfin tuna tracked near Hawaii.

In contrast, the daytime depth distribution of juvenile (≈ 3 to 5 kg) bigeye tuna near the main Hawaiian Islands (determined using ultrasonic telemetry) is much deeper ($\approx 230 \text{ m}$) than that of yellowfin tuna or blue and striped marlins; their swimming depth appears to be set by the 15°C isotherm (Holland et al. 1990b). This is very similar to the vertical movement pattern of an adult ($\approx 70 \text{ kg}$) bigeye tuna recaptured near Hawaii that had carried an electronic data-recording tag for $\approx 3 \text{ mo}$ (C. Boggs, M. Musyl, R. Brill, NMFS-Honolulu Laboratory, unpublished observations). Recent ultrasonic tracking studies near Tahiti of large ($>25 \text{ kg}$) bigeye tuna show that they follow the daily vertical migrations of the small nektonic organisms (crustaceans, cephalopods, and fishes) of the deep sound-scattering layer (L. Dagorn, P. Bach, and E. Josse, Centre ORSTOM de Tahiti, personal communication), and thus appear to exploit prey not available to yellowfin tuna, skipjack tuna, and blue or striped marlins (Roger and Grandperrin 1976). It is also possible that small bigeye tuna use the deeper colder waters as a refuge from adult marlins

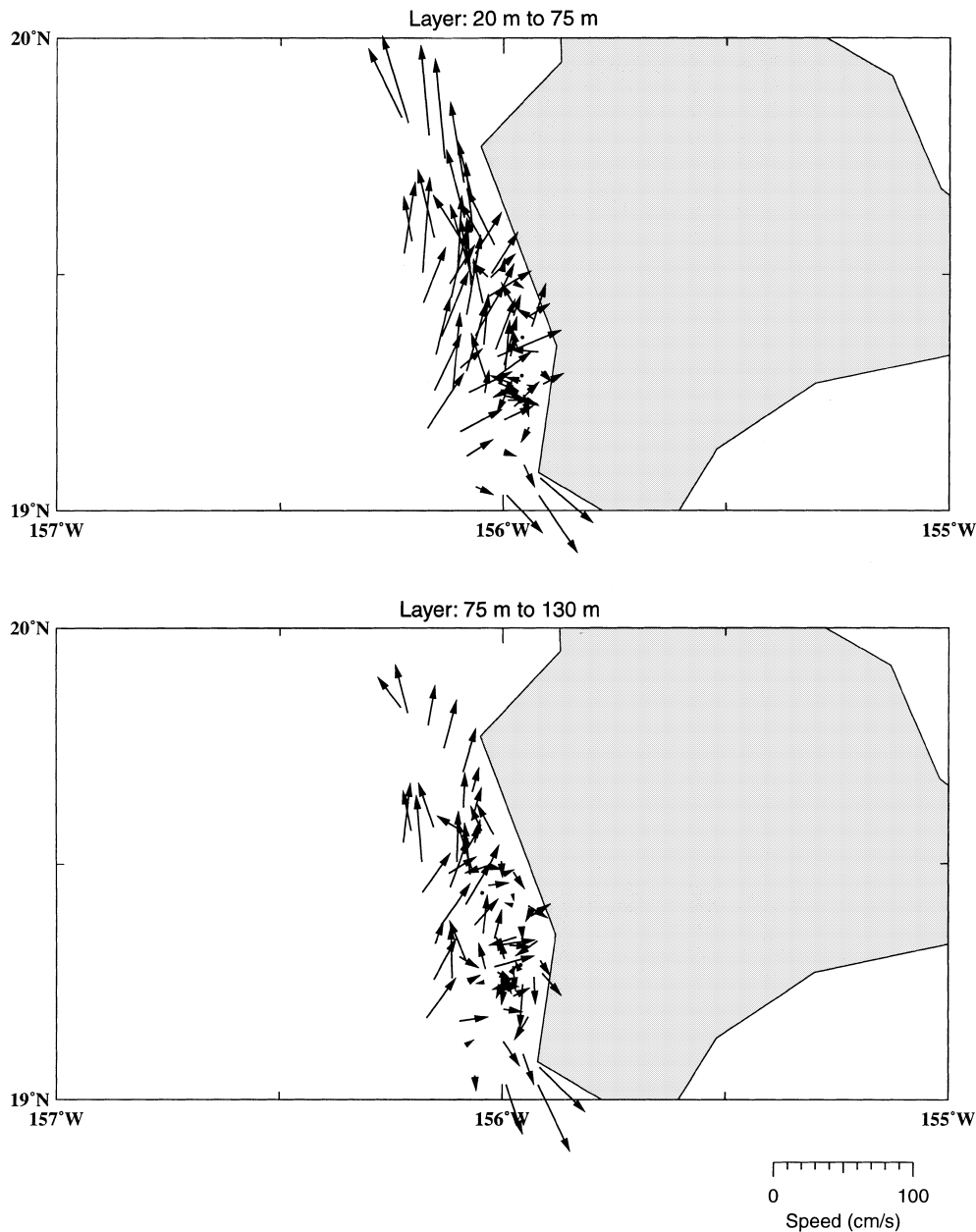


Fig. 10 Mean current speeds (proportional to lengths of arrows) and direction (indicated by *arrowheads*) measured by acoustic Doppler current profiler, recorded August 7 to 20 August 1995

which are predators of juvenile tunas (Brock 1984). The former explanation, however, seems more tenable, as both juvenile and adult bigeye tuna appear to have similar depth distributions.

Implications for physiological ecology of tunas and billfishes

Current hypotheses on the limiting effects of temperature on swimming activity, and selective advantages conferred by the presence of vascular counter-current heat exchangers, cannot explain how bigeye tuna are

apparently able to exploit deeper food resources than yellowfin tuna, blue marlin, or striped marlin. Neill and Stevens (1974), Neill et al. (1976), and Stevens and Neill (1978) suggested that the selective advantage provided tunas by the presence of vascular counter-current heat exchangers is that they slow rates of temperature change in deep red muscle following abrupt reductions in ambient temperature (Fig. 12). Specifically, Neill et al. (1976) estimated that the rate constant of a temperature change in deep red muscle for a 3 kg tuna is $0.027 \text{ C}^\circ \text{ min}^{-1} \text{ }^\circ\text{C}^{-1}$; whereas that of a 3 kg fish without vascular counter-current heat exchangers is $0.37 \text{ C}^\circ \text{ min}^{-1} \text{ }^\circ\text{C}^{-1}$. Based on equations presented in Neill et al. (1976), the rate constant of the temperature change in deep red muscle of a 77 kg yellowfin tuna (the mean size of the fish tracked during our study) should be approximately an order of magnitude less

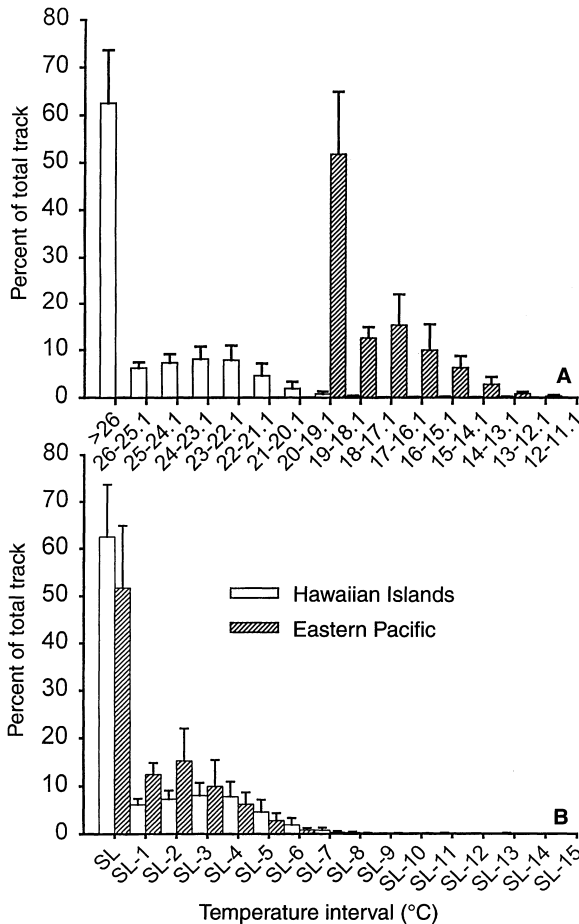


Fig. 11 *Thunnus albacares*. **A** Time-at-temperature for three fish (estimated body mass 8 to 16 kg) tracked in eastern Pacific by Block et al. (1997) (hatched bars) and five large adults (69 to 93 kg) tracked near main Hawaiian Islands (open bars); temperature expressed in degree intervals; the former, smaller, fish occupy colder temperatures because the surface-layer temperature (warmest water available) was ≈ 19 to 20°C in eastern Pacific, but $> 26^\circ\text{C}$ near main Hawaiian Islands. **B** Time-at-temperature, with temperature bins expressed as degree-interval changes relative to surface-layer (SL) temperature; note that time-at-temperature distributions for the two groups are now identical, indicating that (within reasonable limits) it is the change in water temperature rather than an absolute water temperature that limits vertical movements

($0.0063^\circ\text{C} \text{ min}^{-1} \text{ }^\circ\text{C}^{-1}$) than that of a 3 kg yellowfin tuna. This results in very slow rates of predicted temperature change in deep red muscle following abrupt changes in ambient temperature (Fig. 12). The ability to maintain muscle temperatures for longer periods should endow large adult fish with greater vertical mobility than juvenile fish. There are no data on rates of muscle-temperature change in marlin, but the effects of body size on the rates of muscle-temperature change are likely to be roughly similar.

Why then do large adult yellowfin tuna (or large blue and striped marlins) apparently not take advantage of greater thermal inertia to exploit the vertically migrating organisms of the deep sound-scattering layer, as bigeye tuna apparently do? Behavior patterns may be geneti-

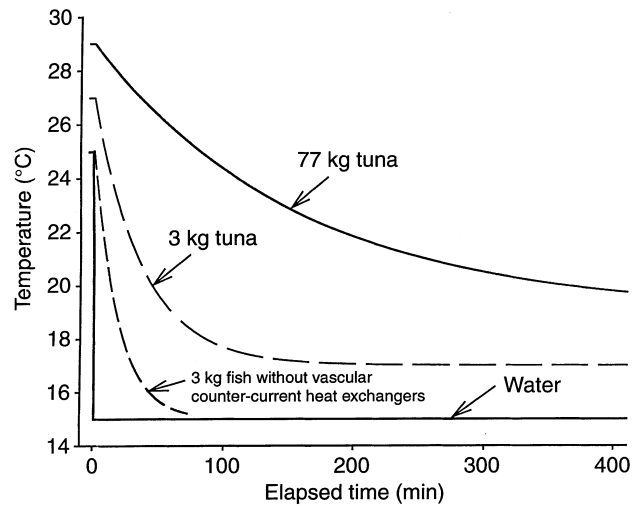


Fig. 12 Temperature change in deep red muscle following acute change in ambient temperature ($25 \rightarrow 15^\circ\text{C}$) in a 3 kg tuna, a 77 kg tuna (mean size of fish tracked during our study) and a 3 kg fish lacking vascular counter-current heat-exchangers. Rates of temperature change (0.0269 , 0.00634 and $0.0372^\circ\text{C} \text{ min}^{-1} \text{ }^\circ\text{C}^{-1}$, respectively) were calculated from equations developed by Neill et al. (1976). Based on observed muscle temperatures of swimming yellowfin tuna (Dizon and Brill 1979), sustained differences between water temperature and muscle temperature (i.e. steady-state excess muscle-temperatures) were assumed to be 2, 4, and 0°C for a 3 kg tuna, a 77 kg tuna and a 3 kg fish lacking vascular counter-current heat-exchangers, respectively. To simplify calculations, changes in temperature of deep red muscle were assumed to follow immediately changes in ambient temperature. In larger tunas, however, lag in the temperature change of deep red muscle will accentuate the differences shown (Brill et al. 1994)

cally fixed and species-specific. Species' differences in the anatomy of vascular counter-current heat exchangers in bigeye and yellowfin tunas (described in Godsfil and Bayers 1944), or in their physiological thermoregulatory abilities, could also explain the difference in behaviors. Available physiological evidence, however, indicates that yellowfin and bigeye tunas have roughly equivalent physiological thermoregulatory abilities (Dizon and Brill 1979; Holland et al. 1992; Brill et al. 1994; Dewar et al. 1994).

Most probably, a simple common physiological mechanism explains the similar depth distributions of yellowfin tuna, blue marlin, and striped marlin and the disparate depth distribution of bigeye tuna where oxygen is not limiting. We hypothesize that the common element is the effect on heart function of acute reductions in ambient temperature. In both tunas and marlins at all body sizes, the temperature of the heart will immediately reflect changes in ambient temperature because the heart is near the body surface and on the "downstream" side of tunas' vascular counter-current heat exchangers (Brill et al. 1994).

Unlike most teleosts, tunas depend more on increased heart rate than increased stroke volume when elevated levels of cardiac output are needed (Farrell 1991; Farrell et al. 1992; Korsmeyer et al. 1997a,b). Moreover, tunas increase their heart rate primarily by reducing the vagal tone (Keen et al. 1995). Laboratory

experiments on yellowfin tuna have shown that an acute reduction in ambient temperature (25° to 15 °C) results in an immediate decrease in heart rate ($Q_{10} = 2.37$; Korsmeyer et al. 1997a), a decrease which can not be counteracted with the injection of atropine (R. W. Brill, K. L. Cousins and T. E. Lowe unpublished observations). The lack of an effect of a vagolytic drug such as atropine under these circumstances indicates that yellowfin tuna (and by implication blue and striped marlins) have no ability to counteract the decreased heart rate and cardiac output. In other words, although possibly able to meet oxygen-delivery requirements at low swimming speeds, yellowfin tuna would not be able to meet the 3 to 5 fold increase in oxygen demand during elevated activity levels or recovery from exhaustive exercise (Brill and Bushnell 1991; Bushnell and Jones 1994; Korsmeyer et al. 1996, 1997b). It is still an open question how bigeye tuna [and possibly other tuna species such as albacore (*Thunnus alalunga*) and bluefin tuna (*T. thynnus*)] are apparently able to maintain cardiac function, and thus achieve their extensive vertical mobility and their ability to exploit food resources below the thermocline.

Acknowledgements This project was funded by Cooperative Agreements NA37RJ0199 and NA67RJ0154 from the National Oceanic and Atmospheric Administration with the Joint Institute for Marine and Atmospheric Research, University of Hawaii; and the National Marine Fisheries Service (Honolulu Laboratory, Southwest Fisheries Science Center). The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. The procedures employed in this study comply with all applicable laws of the United States. The participation of B. Block, E. Freund, and D. Marcinek was supported by Stanford University and National Science Foundation Grant #IBN9507499 to B. Block. The authors gratefully acknowledge the efforts of the captain and crew of the NOAA research vessel "Townsend Cromwell". We especially want to express our "aloha" and to say "mahalo nui loa" (thank you very much) to the Leslie family (Chuck, Alfred Sr., Wayne, Alfred Jr., and Kalani) of the fishing boat "Hana Like" (Hawaiian for "working together") for making us feel as welcome as family; keeping us well fed and entertained; reminding us of the importance, uniqueness, and beauty of the Hawaiian culture; and for showing us the true grandeur of "the loveliest islands afloat on any sea" (Mark Twain).

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