Abstract—The vertical and horizontal movements of southern bluefin tuna (SBT), *Thunnus maccoyii*, in the Great Australian Bight were investigated by ultrasonic telemetry. Between 1992 and 1994, sixteen tuna were tracked for up to 49 h with depth or combined temperature-depth transmitting tags. The average swimming speeds (measured over the ground) over entire tracks ranged from 0.5 to 1.4 m/s or 0.5 to 1.4 body lengths/s. The highest sustained swimming speed recorded was 2.5 m/s for 18 hours. Horizontal movements were often associated with topographical features such as lumps, reefs, islands and the shelf break. They spent long periods of time at the surface during the day (nearly 30%), which would facilitate abundance estimation by aerial survey. At night, they tended to remain just below the surface, but many remained in the upper 10 m throughout the night. SBT were often observed at the thermocline interface or at the surface while travelling. A characteristic feature of many tracks was sudden dives before dawn and after sunset during twilight, followed by a gradual return to their original depth. It is suggested that this is a behavior evolved to locate the scattering layer and its associated prey when SBT are in waters of sufficient depth. SBT maintained a difference between stomach and ambient temperature of up to 9°C.

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Vertical and horizontal movements of southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight observed with ultrasonic telemetry

Tim L. O. Davis
Clive A. Stanley
CSIRO Division of Marine Research
Castray Esplanade
Hobart, Tasmania, Australia 7000
E-mail address (for T. L. O. Davis): tl.davis@csiro.au

Southern bluefin tuna, *Thunnus maccoyii*, spawn in the northeast Indian Ocean south of the Sunda Islands from August to May (Farley and Davis, 1998). Young-of-the-year move down the west coast of Australia and first appear in the Great Australian Bight as 1-year olds. They aggregate in the Bight during the Austral summer, disperse to the east or west within latitudes of 30–40°S in autumn, and return to the Bight in spring. Juveniles between 1 and 4 years old return each summer to the Bight where they form extensive surface schools.

To provide a fishery-independent index of recruitment, line transect aerial surveys have been flown in the Bight each summer since 1990 to estimate the relative abundance of juveniles visible in the top 5 m (Chen et al.[1]). The largest source of variance in these estimates is thought to be environmental factors that influence both surfacing behavior and aerial detection. To investigate these problems, we used ultrasonic telemetry to provide the first information on surfacing behavior and short-term horizontal and vertical movement patterns that might influence sightings from the air. More comprehensive information on tuna surfacing for the whole of the three-month survey period is expected from an archival tagging program begun in 1992 (Gunn et al.[2]). Because these data are dependent upon the recapture of archival-tagged fish, this information will not be available for some time.

Because of Carey's pioneering work on Atlantic bluefin tuna (Carey and Lawson, 1973), ultrasonic telemetry has been used to study many tuna species, including Atlantic (Lutcavage et al., 2000) and Pacific bluefin tuna (Marcinek et al., 2001), yellowfin tuna (Carey and Olsen, 1982; Cayré and Chabanne, 1986; Yonemori, 1982; Holland et al., 1990a; Cayré, 1991; Cayré and Marsac, 1993; Block et al., 1997; Brill et al., 1999; Marsac et al.[3]), skipjack tuna (Yuen, 1970; Dizon et al., 1978; Levenez, 1982; Cayré and Chabanne, 1986; Cayré, 1991), bigeye tuna (Holland et al., 1990a, 1992; Holland and Sibert, 1994), and albacore (Laurs et al., 1977). A number of small (35–46 cm) southern bluefin tuna (SBT) have been tracked in the Indian Ocean off

[1] Chen, S., A. Cowling, and T. Polacheck. 1995. Data analysis of the aerial surveys (1991–1995) for juvenile southern bluefin tuna in the Great Australian Bight. 1995 Southern Bluefin Tuna Recruitment Monitoring Workshop Report RMWS/95/6, 57 p. CSIRO Marine Laboratories, Castray Esplanade, Hobart, Tasmania, Australia 7000.

[2] Gunn, J., T. Davis, T., Polacheck, A. Betlehem, and M. Sherlock. 1995. The application of archival tags to study SBT migration, behaviour and physiology. Progress Report—1994–95. Southern bluefin tuna recruitment monitoring and tagging program workshop, 7–10 August 1995, Hobart, Australia. Rep. RMWS/95/8, 17 p. CSIRO Marine Laboratories, Castray Esplanade, Hobart, Tasmania, Australia 7000.

[3] Marsac, F., P. Cayré, and F. Conand. 1995. Analysis of small scale movements of yellowfin tuna around FADs using sonic tagging. Expert Consultation on Indian Ocean tunas. 6th session. Colombo, Sri Lanka, 25–29 September 1995. Rep. TWS/95/2/10, 20 p. ORSTROM, Seychelles Fishing Authority, BP 570, Victoria, Mahé, Seychelles.

Western Australia (Fishery Agency of Japan[4,5]). All SBT in the current study were released and tracked in shelf waters, except for one fish that moved from the shelf into slope waters.

Methods

Tracking experiments on SBT were carried out in the Great Australian Bight over three years. In 1992, the tracking system was tested on a short cruise late in the fishing season and close to Port Lincoln. In 1993, the strategy was to obtain extended tracks of up to 48 hours to investigate day and night patterns in depth distribution and horizontal movement within the Great Australian Bight. In 1994, we planned short tracks to maximize the number of individual fish observed during daytime, so that their behavior could be linked to sightings by aerial survey carried out at the same time.

All SBT were caught by pole and line, except for tuna no. 7 (referred to simply as "tuna 7") which was caught on light game fishing tackle, and tuna 9, which swallowed the tag while free-swimming. The tuna were landed on a wet, plastic-covered, foam mat. The head was covered with a wet cloth, length of fish was measured, the tag attached or inserted, and the fish was released back into the school.

V16 (16 mm diameter) sonic tags (VEMCO, Halifax, Nova Scotia, Canada) of various frequencies (50–69 kHz), equipped with pressure sensors, were deployed on two fish in April 1992 and four fish in January and March 1993 (Table 1). Five of these tags were attached externally, behind the second dorsal fin of the tuna, by using the attachment technique described in Holland et al. (1985). The sixth was placed in the stomach with an oesophageal catheter.

V22 (22 mm diameter) tags transmitting on 40 kHz were used on ten tuna tracked in January and February 1994. These tags, which have stronger signals and lower transmission frequencies, have a much larger detection range than V16 tags. They also have the capacity for

Table 1

Release and tracking details of southern bluefin tuna tracked in the Great Australian Bight during the years 1992–94.

Tuna no.	Tag type	Date of release	Location	Length (cm)	Tag position	Duration of track (h)	Distance moved (km)	Mean speed m/s	Mean speed FL/s	Cause of termination
1	V16-P	29 Apr 1992	Cabbage Patch	90	external	12	34	0.79	0.87	weather
2	V16-P	30 Apr 1992	Cabbage Patch	90	external	18	48	0.74	0.83	poor signal
3	V16-P	27 Jan 1993	28 km W of Ward Island	94	external	49	175	0.99	1.06	voluntary
4	V16-P	30 Jan 1993	Ward Island	96	external	48	143	0.83	0.86	voluntary
5	V16-P	13 Mar 1993	Rocky Island	103	external	5	9	0.52	0.51	lost
6	V16-P	14 Mar 1993	Rocky Island	98	stomach	26	131	1.40	1.42	weather
7	V22-P	10 Jan 1994	7 km S of Cannan Reef	67	stomach	30	91	0.84	1.26	voluntary
8	V22-P	12 Jan 1994	7 km S of Cannan Reef	100	stomach	10	32	0.90	0.90	voluntary
9	V22-P	15 Jan 1994	Nuyts Reef	85	mouth	5	15	0.85	1.00	tag detached
10	V22-PT	16 Jan 1994	11 km SE of St Francis Island	92	stomach	13	40	0.85	0.93	tag regurgitated
11	V22-PT	17 Jan 1994	41 km W of Sceale Bay	114	stomach	13	46	0.98	0.86	tag regurgitated
12	V22-P	18 Jan 1994	41 km W of Sceale Bay	85	stomach	13	34	0.72	0.85	voluntary
13	V22-PT	19 Jan 1994	15 km W of Labatt Pt.	100	stomach	20	67	0.94	0.94	voluntary
14	V22-P	31 Jan 1994	41 km E of Sceale Bay	100	stomach	9	36	1.10	1.10	voluntary
15	V22-P	1 Feb 1994	7km S of Cannan Reef	102	stomach	1	2	0.64	0.63	fish lost
16	V22-P	2 Feb 1994	7km S of Cannan Reef	97	stomach	5	14	0.79	0.82	tag regurgitated

4 Fishery Agency of Japan. 1990. Report of 1988 research cruise of the R/V *Shoyo-Maru.* Distribution of juvenile southern bluefin tuna off west coast of Australia, December 1988–January 1989. Rep. Res. Dep., Fish. Agency Jpn. 63:1–125. Pelagic Fish Resource Division, 5-7-1 Orido, Shimizu, Shizuoka 424, Japan.

5 Fishery Agency of Japan. 1992. Report of 1989 research cruise of the R/V *Shoyo-Maru.* Distribution of juvenile southern bluefin tuna off west coast of Australia, September–December 1989. Rep. Res. Dep., Fish. Agency Jpn. 64:1–166. Pelagic Fish Resource Division, 5-7-1 Orido, Shimizu, Shizuoka 424, Japan.

dual channels enabling sequential transmission of pressure and temperature. Seven pressure tags and three pressure-temperature tags were deployed. All, except one, were inserted into the stomach. To retard regurgitation, two small hooks were tied to each tag with VICRYL dissolving sutures before being placed in the stomach. One tuna struck a tag with hooks during a calibration experiment, resulting in the tag attaching without the tuna leaving the water. This fish was tracked for five hours until the tag detached.

Standard tracking techniques were used (see Holland et al., 1985). The tracking equipment, including the remote-controlled hydrophone rotator, is described in Pepperell and Davis (1999). We attempted to track the fish at a distance of about 400 m, which we judged from signal strength, using distance and signal-strength calibrations carried out before tracking. The decoded data from single-channel tags were logged together with global positioning system (GPS) latitude and longitude, nominally at 1-second intervals, on a computer with VEMCO VSCAN/GPS software (Vemco, 1992). Temperature and depth data from dual-channel transmitters were logged at about 3-second intervals.

Conductivity-temperature-depth profiles were taken at the start and finish, and at convenient times during each track, with a digital data loggers international profiler. Additional information collected during each track included bottom depth, air temperature, wind speed, cloud cover (1–8 sectors covered), brightness (1–4), and presence of surface and subsurface schools of SBT. In 1994, we also recorded the depth distributions of SBT schools detected on the echosounder under the tracking vessel.

The tracking data were processed using a filtering program to delete spurious data, interpolate missing data, and generate data files at nominated time intervals. The program compared each depth with the seven previous data points (which were nominally recorded at 1-second and 3-second intervals for single- and dual-channel tags, respectively) and then deleted spurious records based on expected maximum and minimum depths and maximum depth-change rates. Similarly, a temperature filter deleted spurious values based on expected maximum and minimum temperatures and maximum temperature-change rates in data from the dual-channel transmitters. Complete vertical tracks were plotted against time with 20-second interval data. The position and sustained swimming speeds of tracked tuna were assumed to be the same as that of the tracking vessel. By using GPS data, speed was calculated over the ground from the straight-line distance travelled between points in 10 minutes. Vertical movements and horizontal movements in relation to the vessel were not considered. An attempt was made to match both the heading and speed of the tracked tuna so that the vessel reflected the movements of the fish.

Depth distribution of tuna was examined from 20-second interval data aggregated in 5-m depth bins stratified by day and night. The number of observations in each depth bin was then expressed as a proportion of the total number of observations in each day–night stratum. The speed distribution of tuna was examined from 10-minute interval data aggregated in 0.1 m/s bins stratified by day and night.

Results

The tracking system was developed for use on a variety of commercial vessels. In April–May 1992, five fish were released and two were tracked successfully (Table 1). Modifications were then made to the system and different transmission frequencies were selected to reduce interference. The improved system was used on two cruises in January and March 1993. Four fish were tracked for periods of up to 49 h (Table 1).

In 1994, tracking was carried out farther west because fish schools were not sighted farther east (Fig. 1), probably due to warm water remaining in the northwest section of the study area (Fig. 2). The whole period (8 January–3 February) was characterized by windy conditions that made catching and tracking fish difficult. Ten SBT were released with tags (Table 1). The longest track was 31 h, but some tracks were short because the fish regurgitated their tags. Other tracks were terminated voluntarily after sunset to maximize the number of daytime observations on different fish.

Tuna 1 was released SW of Liguana Island on 29 April 1992 at 0855 h (Figs. 1 and 2A). It headed WSW towards the shelf edge until tracking was terminated after 12 hours. Acoustic interference from the tracking vessel affected calculation of depth at certain vessel speeds, resulting in some gaps in the vertical data (Fig. 3A). During the day the fish spent most of its time at the surface, but frequently dived to near the bottom. Tuna schools spotted at the surface appeared to break up and then re-appear sometime later, more or less at the same rate that the tracked SBT moved in and out of the surface waters. The fish dived shortly after sunset and then returned to the mixed layer and oscillated around 30 m until tracking was terminated at 2108 h.

Tuna 2 was released SW of Liguana Island on 30 April 1992 at 1330 h (Fig. 1). The fish moved west throughout most of the track but slowed and changed direction many times from 0400 h. These direction changes occurred when the tuna reached cooler surface waters (Fig. 2A). It remained in the 17°C water, moving south along the boundary with the 16°C isotherm. Its vertical behavior can be seen in Figure 3B. Like tuna 1, this fish made a brief dive just after sunset.

Tuna 3 was released at The Lump, 28 km west of Ward Island on 27 January 1993 at 15:22 h and was tracked for 49 h (Figs. 1 and 2B). It moved into waters near the shelf edge, a movement matched by a conventionally tagged tuna that was released at 33°15′S, 133°49′E on 26 January 1993 and that was recovered five days later at 34°S, 132°17′E by a commercial fishing operation. The vertical behavior of tuna 3 is shown in Figure 4A. It spent considerable time near the surface in association with other tuna during the late afternoon on the first day. It seldom surfaced on the second day; neither did the other tuna. A commercial pole-and-line boat fishing in the same area

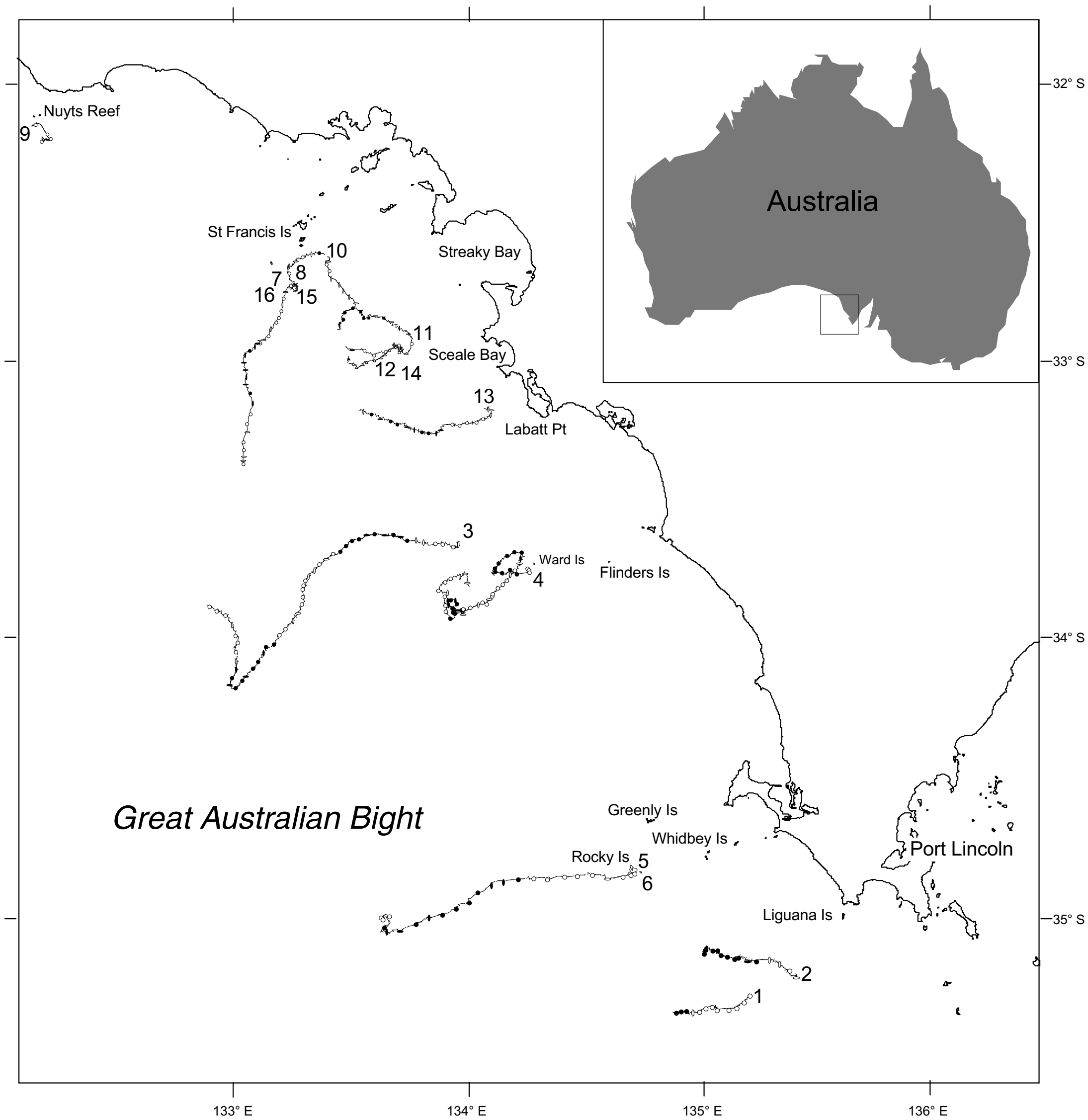

Figure 1

Geographic position of southern bluefin tuna tracks in the eastern Great Australian Bight. The number of each fish indicates the start of its track. Symbols along tracks represent hourly positions (open symbol=day, solid symbol=night).

on the second day could not chum fish to the surface; the fishermen had also observed many tuna at the surface the previous day.

Tuna 4 was released near Ward Island on 30 January at 16:40 h and was tracked for 48 hours. This fish remained within the general area of release until tracking was terminated (Figs. 1 and 2B). Vertical behavior is shown in Figure 4B. The fish was associated with surface schools until night on the first day. It was also associated with large numbers of tuna (observed on the echosounder) throughout the night. The surface activity of tuna schools was low throughout the next day. Tuna were observed on the echosounder at the same depth as the tracked tuna throughout the day and next night, but not in the same numbers as the day before.

Tuna 5 was released on 13 March 1993 at 11:50 h at Rocky Island (Fig. 1). It was tracked for about 4 hours before it was lost. At 1500 h the tracked fish, together with other tuna, followed a pole-and-line vessel that was chumming at the time and that had crossed our path. The fish was temporarily lost but was relocated an hour later, again following the chum line of the pole-and-line vessel.

Tuna 6 was released at Rocky Island on 14 March 1993 at 07:35 h and subsequently tracked for 26 h (Figs. 1 and 2C). At 08:15 h the tracked tuna was observed following the chum line of the pole-and-line vessel (Fig. 5B). It was associated with other tuna at or near the surface until about 11:00 h. At 12:00 h the fish moved rapidly offshore at about 2.5 m/s and was tracked to the shelf. On reaching the shelf break, it remained within a region of warmer

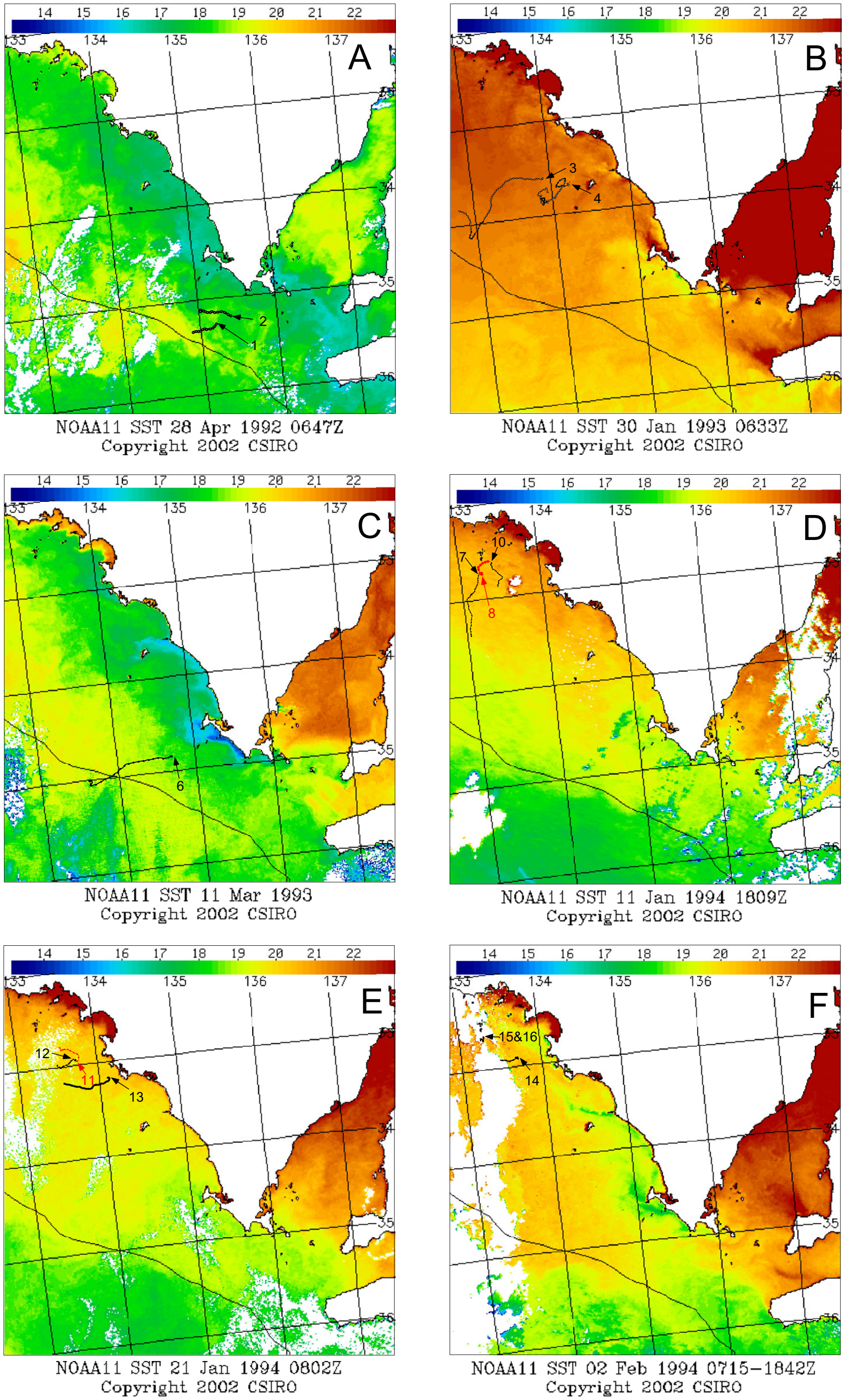

Figure 2

NOAA11 satellite sea-surface-temperature images of the study area during the periods of tracking with southern bluefin tuna tracks overlaid. (**A**) Tracks 1 and 2 on 29–30 April 1992. (**B**) Tracks 3 and 4 on 27–31 January 1993. (**C**) Track 6 on 14–15 March 1993. (**D**) Tracks 7, 8, and 10 on 10–16 January 1994. (**E**) Tracks 11–13 on 17–19 January 1994. (**F**) Tracks 14–16 on 31 January–2 February 1994.

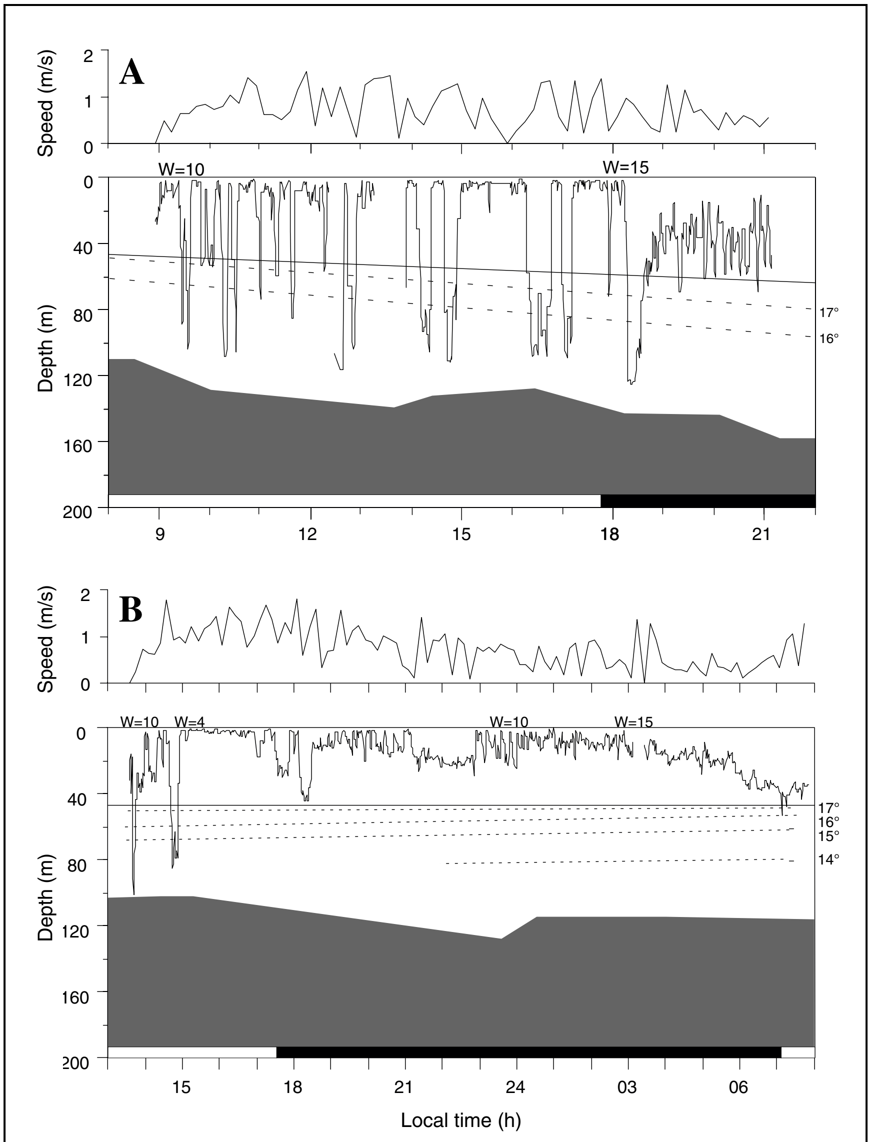

Figure 3

(**A**) Track of southern bluefin tuna 1 on 29 April 1992. (**B**) Track of southern bluefin tuna 2 on 30 April 1992. Speed over the ground (upper graph) and depth of the tuna (lower graph) are plotted against time. The sea bottom is indicated by shading, the solid line represents the bottom of the mixed layer and the dotted lines represent isotherms (°C). The black bar represents nighttime, the unshaded bar, daytime and W = wind speed in km/h.

surface water in association with a large subsurface school of tuna (Fig. 2C). While traveling to the shelf break, it remained near the bottom or just below the mixed layer. A deep sounding was made just after sunset and another just before dawn, the last reaching 180 m.

Tuna 7 was released at The Lumps 7 km south of Cannan Reef at 09:16 h on 10 January 1994 (Figs. 1 and 2D). This was the smallest fish tracked in this study. Unlike the others, it was caught on a trolled lure and landed after about a 5-minute struggle. Tracking was discontinued after 30 h due to bad weather. This fish was associated with large schools for the first five hours of tracking and again for three hours at first light the next day. It made postdusk and predawn dives (Fig. 6A).

Tuna 8 was released at The Lumps 7 km south of Cannan Reef at 10:58 h on 12 January 1994 (Figs. 1 and 2D). The fish was followed for 10 h until tracking was halted shortly after sunset. It remained in the upper 20 m for most of the track (Fig. 6B). At 12:50 h it followed the chum line of a pole-and-line vessel. From 14:00 to 16:00 h, it remained at the surface with a large school of tuna before slowing and sounding at a reef.

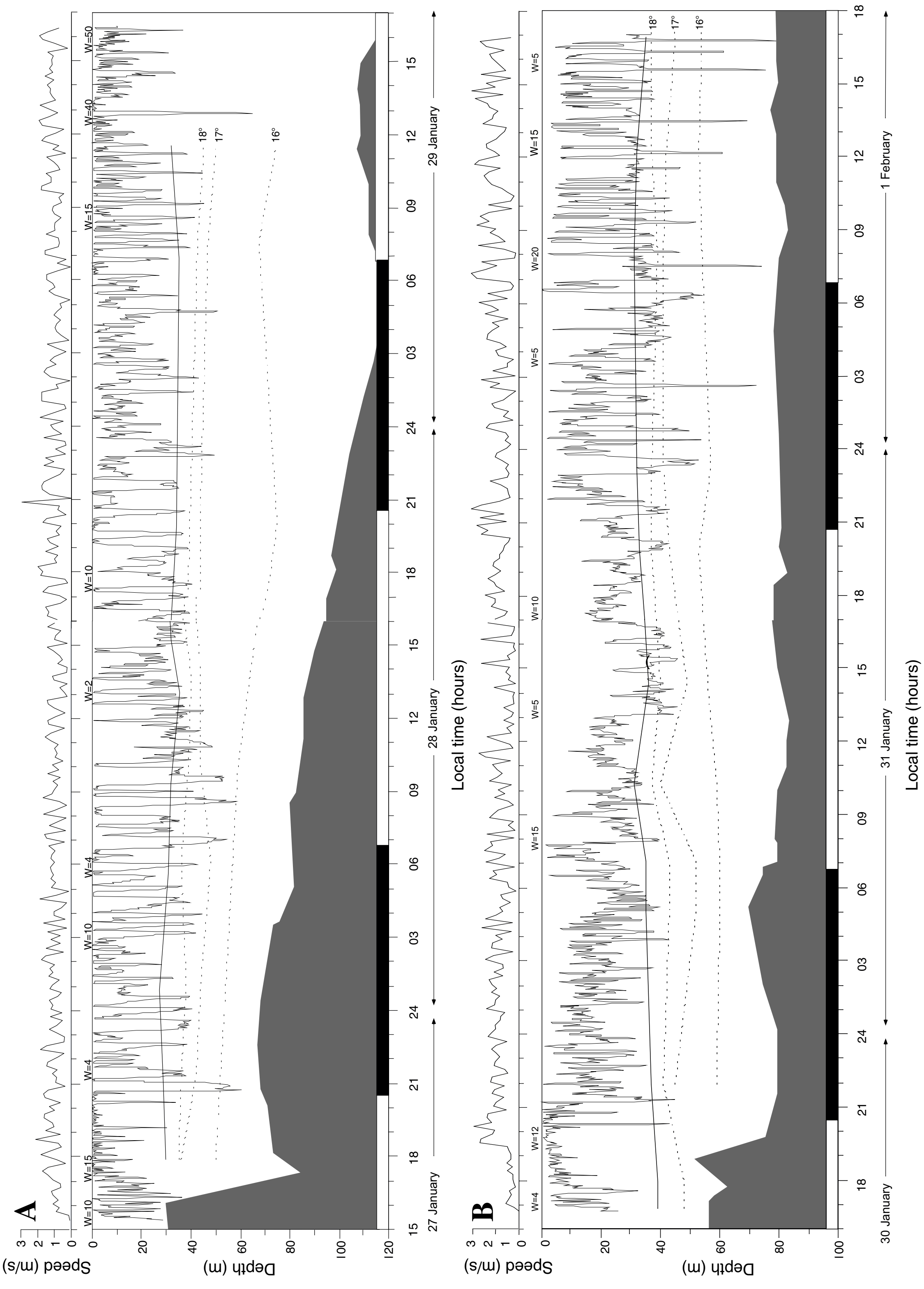

Figure 4

(**A**) Track of southern bluefin tuna 3 on 27–29 January 1993. (**B**) Track of southern bluefin tuna 4 on 30 January–February 1993. See Figure 3 for legend details.

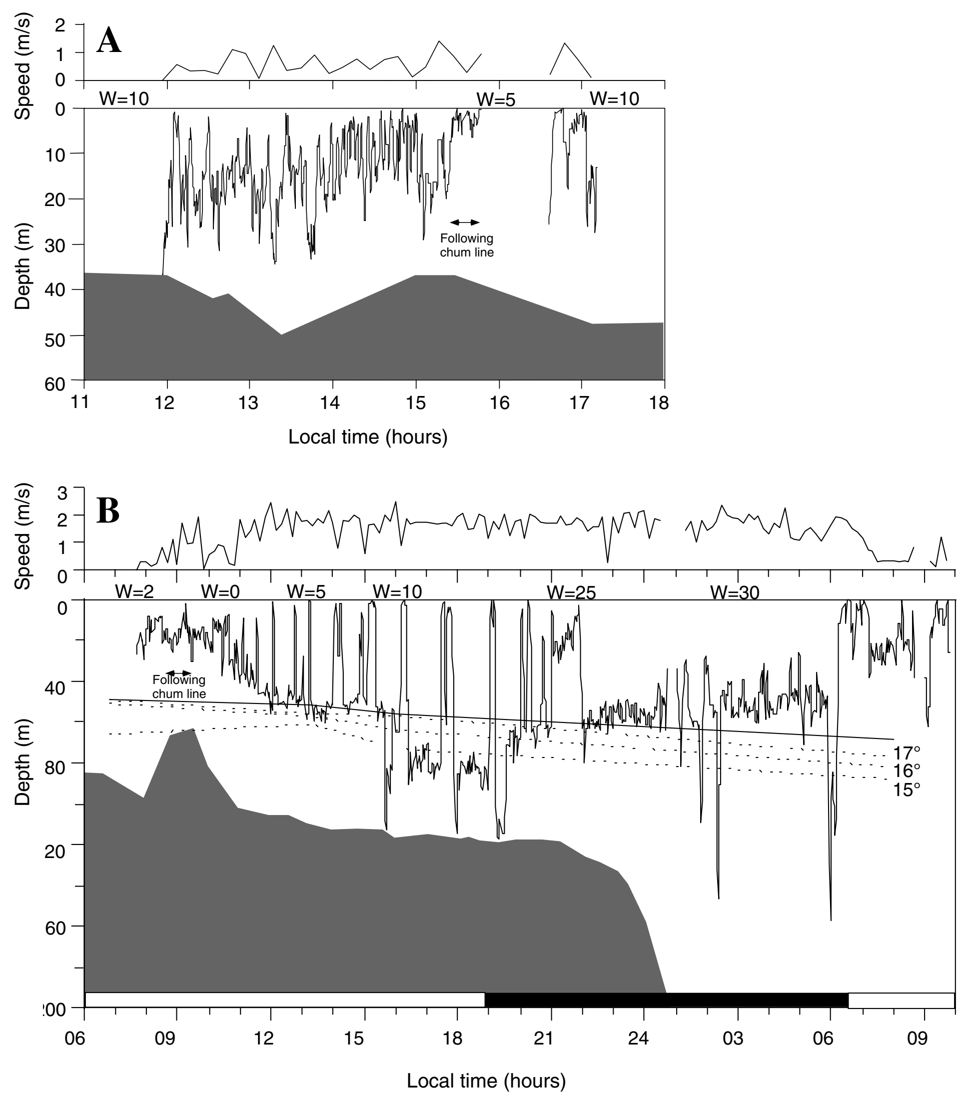

Figure 5

(**A**) Track of southern bluefin tuna 5 on 13 March 1993. (**B**) Track of southern bluefin tuna 6 on 14–15 March 1993. The period when the tuna followed the chum line is shown. See Figure 3 for legend details.

Tuna 9 struck at a tag during calibration experiments near Nuyts Reef at 09:05 on 15 January 1994 (Fig. 1). Consequently, it was tagged without leaving the water. The tag was either in the mouth or in the stomach. The tuna remained with tuna schools in the vicinity of tagging until 09:50 h and then moved away at considerable speed (2 m/s) for over an hour before sounding and slowing (Fig. 6C). It returned to the surface and remained there in association with a large surface school. The tag detached from the tuna at 1410 h.

Tuna 10 was released 11 km southeast of St Francis Island at 11:40 h on 16 January 1994. It was tracked for 13 h before it regurgitated the tag (Figs. 1 and 2D). The vertical movements of this fish differed from other tracks in that they were of relatively high amplitude (30+ m), traversed the water column, and were of moderate frequency (Fig. 7A). It spent little time at a particular depth, except for a short period at the bottom at the start of the track and again around 21:00 h. The fish was associated with tuna schools for most of the track. It made an extended dive just after sunset.

This was the first SBT to provide stomach-temperature data. The stomach temperature dropped rapidly initially, then increased to 25.4°C, which was about 6°C above water temperature. Temperature then decreased gradually for the rest of the track, but remained at least 4°C above ambient temperature.

Tuna 11 was released at The Lumps 41 km west of Sceale Bay at 13:57 h on 17 January 1994 with a temperature-pres-

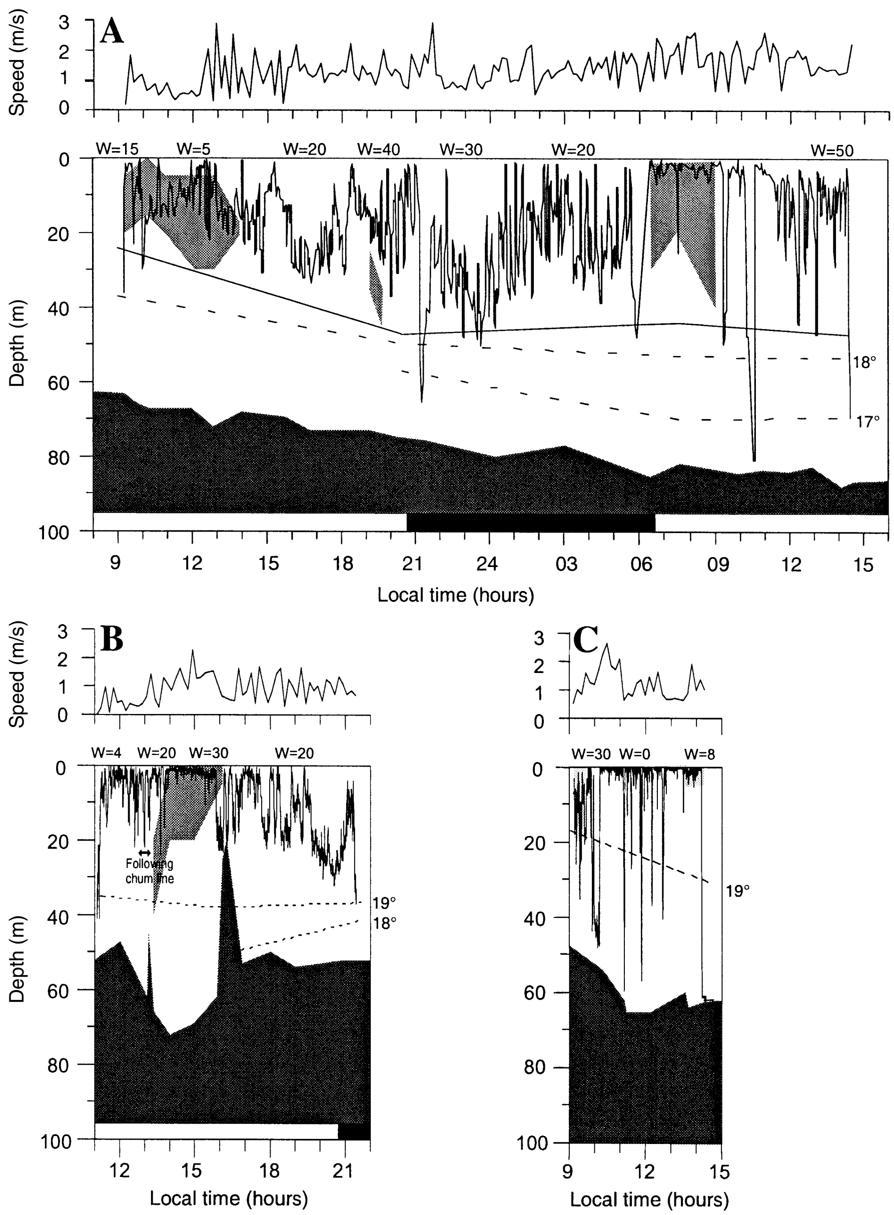

Figure 6

(**A**) Track of southern bluefin tuna 7 on 10–11 January 1994. (**B**) Track of southern bluefin tuna 8 on 12 January 1994. (**C**) Track of southern bluefin tuna 9 on 15 January 1994. Shading in the water column represents depth range of tuna schools detected by echosounder. See Figure 3 for other legend details.

sure tag in the stomach (Figs. 1 and 2E). This fish was associated with tuna schools for most of the track (Fig. 7B). Most vertical activity was oriented towards the surface, but periodic dives were made to or through the thermocline. At night the fish moved slightly deeper but continued to dive at regular intervals. It made an extended dive just after sunset.

The stomach temperature gradually increased through the night and by 01:00 h was at 28°C, which was 9°C above ambient temperature. At about 01:30 h there was a sudden drop in stomach temperature towards ambient temperature and then a gradual recovery that was most likely caused by the swallowing of prey or water (or both). The tag was regurgitated two hours later.

Tuna 12 was released at The Lumps 41 km west of Sceale Bay at 09:16 h on 18 January (Figs. 1 and 2E). It showed considerable vertical activity similar to tuna 10 and was associated with tuna schools throughout the track (Fig. 8A). It made an extended dive just after dusk.

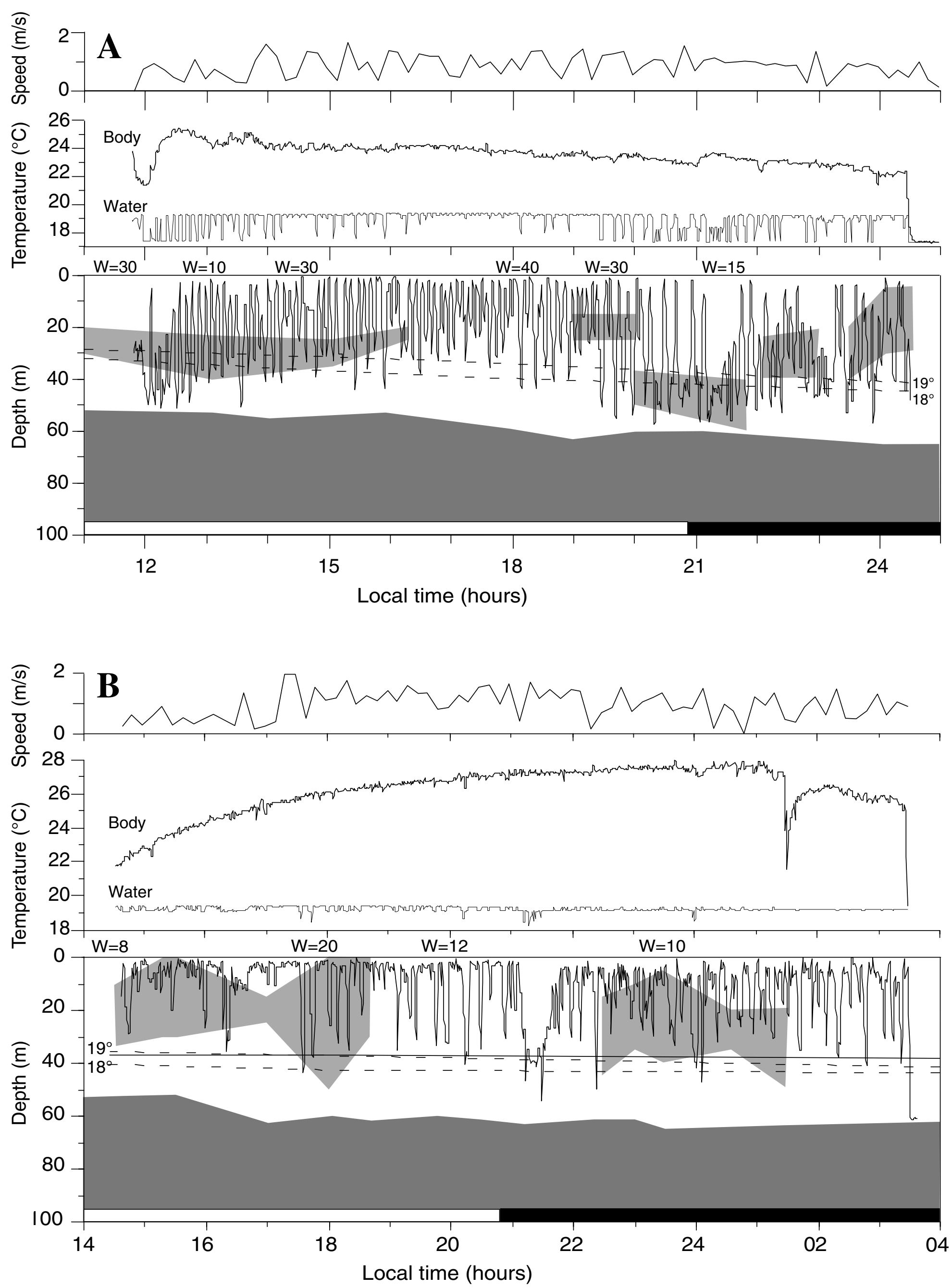

Figure 7

(**A**) Track southern bluefin tuna 10 on 16 January 1994. (**B**) Track of southern bluefin tuna 11 on 17–18 January 1994. See Figure 6 for legend details of upper and lower graphs. In the middle graph, stomach temperature and water temperature (interpolated from the depth of the fish and data logger temperature profiles) are plotted against time.

Tuna 13 was released 15 km west of Labatt Point at 1226 h on 19 January with a temperature-pressure tag in the stomach (Figs. 1 and 2E). This fish remained close to the surface during the day and deeper at the night, frequently staying just above the thermocline and sometimes diving through it. It made an extended dive after dusk and another just before dawn (Fig. 8B). It was associated with schools of tuna throughout the track. Although tuna schools did not appear on the echosounder during the afternoon, extensive bird activity and surface schools

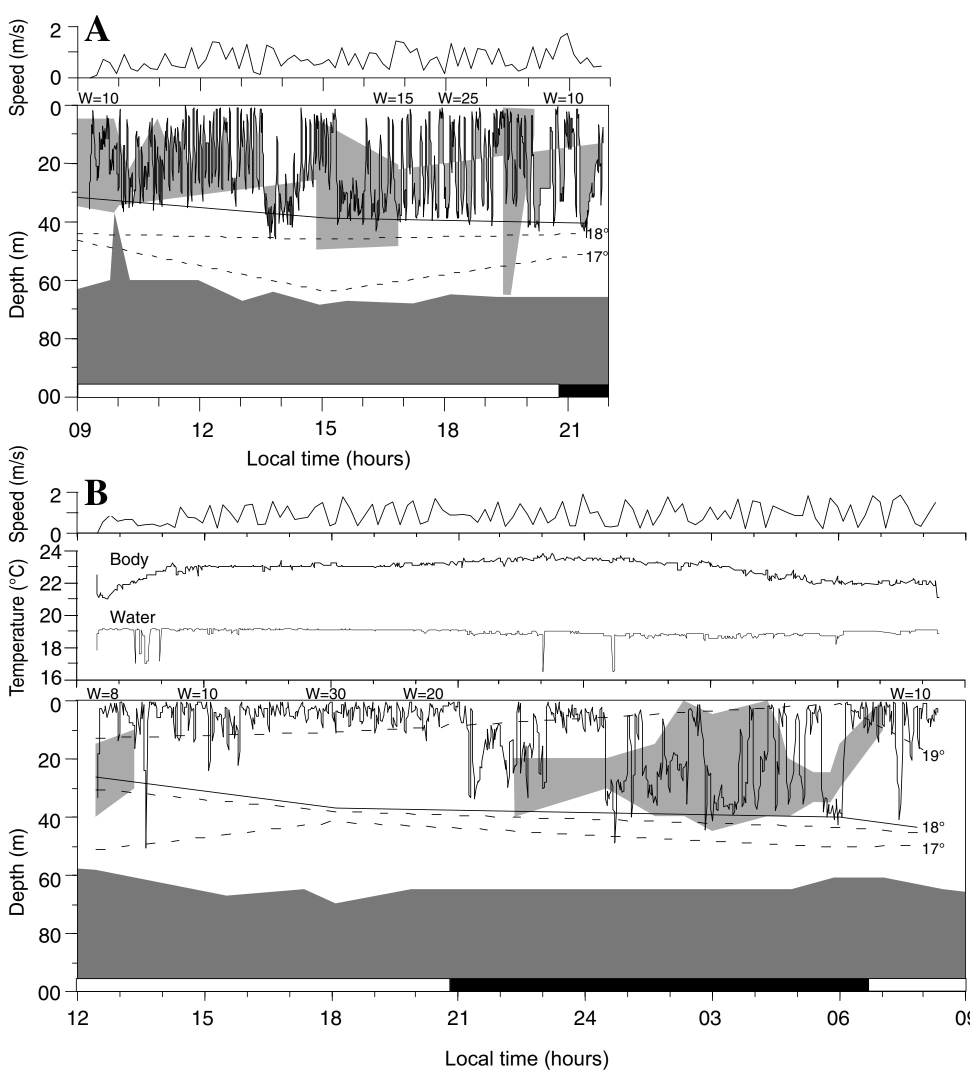

Figure 8

(**A**) Track of southern bluefin tuna 12 on 18 January 1994. (**B**) Track of southern bluefin tuna 13 on 19 January 1994. See Figure 7 for legend details.

of tuna were observed during the whole period that the tracked tuna was near the surface.

Stomach temperature showed a marked drop initially (presumably it swallowed water on its release) and then a gradual recovery. Temperature reached a peak of 23.8°C, about 4.5°C above ambient temperature, near midnight and then slowly declined throughout the remainder of the night.

Tuna 14 was released 41 km west of Sceale Bay at 12:26 h on 31 January 1994 (Figs. 1 and 2F). The tuna was lost for about 20 minutes early in the track (Fig. 9A). It had moved south before doubling back and returning to the reef where it had been tagged. At 16:40 h it then swam away with a school of tuna, remaining just above the thermocline and occasionally making excursions to the surface. It made an extended dive after dusk.

Tuna 15 was released at The Lumps 7 km south of Cannan Reef at 13:26 h on 1 February 1994 (Fig. 1). It joined a large school of tuna following the chum line of a pole-and-line vessel, but was lost one hour later.

Tuna 16 was released at The Lumps 7 km south of Cannan Reef at 09:30 h on 2 February 1994 (Figs. 1 and 2F). It was associated with schools initially, but they dispersed at about 1400 h (Fig. 9B). The tag was regurgitated at 15:20 h.

Time at depth

The proportion of time spent by tuna in 5-m interval depth strata was plotted by day and night for all tracks combined (Fig. 10). These data indicated that SBT are surface-oriented by day in the Great Australian Bight, spending a significant

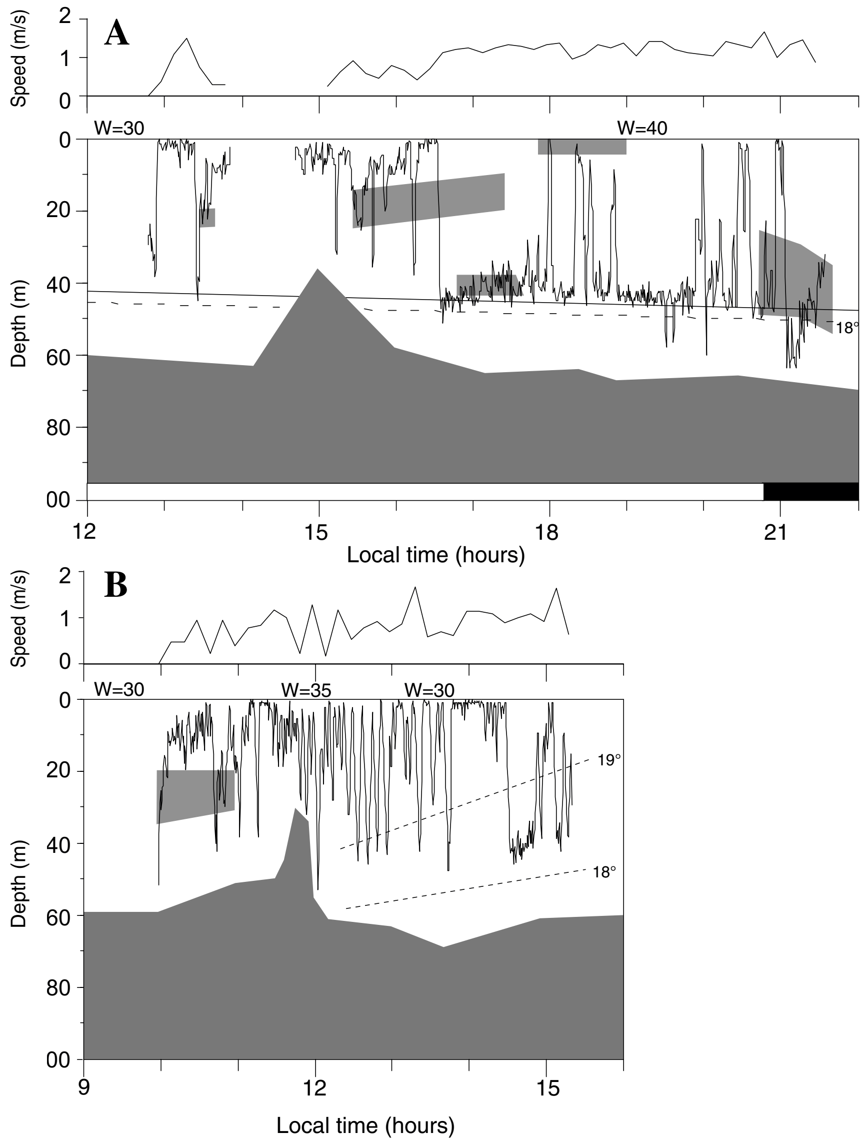

Figure 9

(**A**) Track of southern bluefin tuna 14 on 31 January 1994. (**B**) Track of southern bluefin tuna 16 on 1 February 1994. See Figure 6 for legend details.

proportion of their time (nearly 30%) in the upper 5 m. At night they tend to remain somewhat deeper, although they are present at the surface for part of the night. Tunas 4 and 12 were not surface-oriented during the day, but ranged evenly within the mixed layer. Both these fish were associated with large schools throughout the track and they exhibited rapid vertical oscillations, which we assumed spanned the vertical boundaries of the school. Tuna 6 also spent little time at the surface. It was associated with a small school of tuna and spent most of its time at or below the thermocline while travelling at 2.5 m/s towards the shelf edge. Tuna 14 also spent much of its time at the thermocline boundary while traveling during the day.

Swimming speed

The average swimming speeds of SBT over the entire tracks were in the range of 0.5–1.4 m/s or 0.5–1.4 body lengths/s. These speeds are based on the movements of the tracking vessel and therefore are considered conservative because they do not incorporate the horizontal or vertical meandering of the tracked fish or water currents. There were small differences in the mean speeds between day (0.90 m/s) and night (0.94 m/s) for all fish combined. The frequency distribution of these speeds differed markedly between day and night (Fig. 11). However, the number of observations during the day (n=1119) far exceeded those

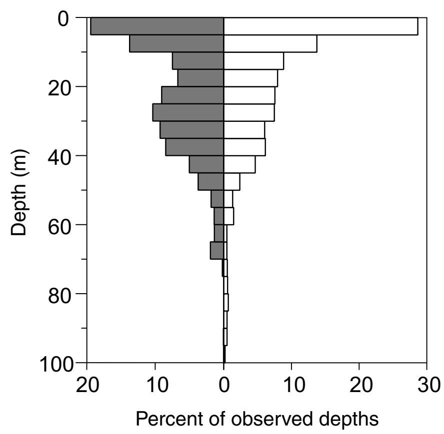

Figure 10

Distribution of observed depths (5-m intervals) by day (open bars) and night (shaded bars) for all tracked southern bluefin tuna.

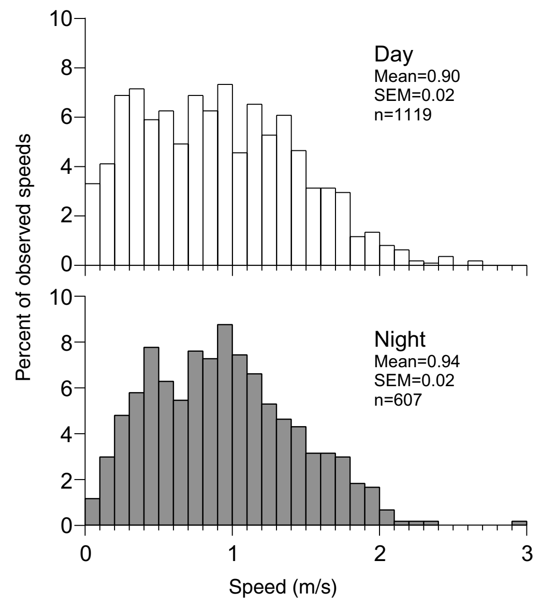

Figure 11

Distribution of observed speeds over the ground (0.1 m/s intervals) by day and night for all tracked southern bluefin tuna.

at night (n=607) and probably accounts for much of the difference in distributions.

Discussion

Horizontal movements

The average swimming speeds of SBT over entire tracks of 0.5–1.4 body lengths/s were similar to the range of mean speeds (0.6–1.0 body lengths/s) for Atlantic bluefin tuna (Lutcavage et al., 2000) and 1.02–1.34 body lengths/s for Pacific bluefin tuna (Marcinek et al., 2001). This is within the range of minimum speeds (0.5–2.0 body lengths/s) required to maintain hydrostatic equilibrium in scombrids (Magnuson and Weininger, 1978). A much higher sustained swimming speed of 2.5 m/s was recorded for tuna 6, which traveled at this speed for 18 hours, virtually in a straight line, from Rocky Island to the shelf break. The vertical movements of this fish were minimized by it orienting itself with the thermocline interface or the surface. And horizontal movements were not apparent. A speed of 2.5 m/s or 2.6 body lengths/s is probably a realistic sustained swimming speed for SBT. Although tunas are obviously capable of high bursts of speed, sustained swimming speeds seem to be very much lower. Yellowfin tuna have been tracked at speeds of 1.2–3.5 body lengths/s, and bigeye tuna at 1.4 body lengths/s (Holland et al., 1990a, Block et al., 1997). The sustained swimming speeds of Atlantic bluefin tuna, determined from sequential aerial photographs, were 0.8–1.6 body lengths/s (NOAA[6]). Brill (1996) considered that the specialized anatomy, physiology, and biochemistry of tuna evolved, not for high burst and sustained swimming speeds as proposed by Dickson (1995), but for rapid growth, digestion, and recovery from exhausting activity.

The horizontal movements and distribution of SBT suggest strong associations with regions of topographical variation or higher temperatures (or both). The SBT were in the warmer waters of the NW region of the study area in 1994, and the tracked fish also remained within areas of warmer water. In 1992 and 1993, all the tuna that traveled some distance swam to waters of similar or higher temperatures. Lutcavage et al. (2000) found that tracked North Atlantic bluefin tuna also traveled on the warm side of surface fronts and that offshore movements were generally associated with offshore warming of deep basins.

The temperatures measured during tracking sometimes did not match up with satellite sea-surface temperatures, owing to the inability of sea surface temperature (SST) algorithms to correct for the variability in atmospheric water vapour, cloud, and aerosols, etc. However, the relative temperature differences considered here appear to be robust. Within these temperature limitations, the tuna were initially located on lumps or near islands. Migration to new areas was often interrupted by brief stays at lumps on the way. The shelf break was clearly the destination of tuna 6. It was tracked near Rocky Island for three hours, before it left abruptly and moved in a straight line to

[6] NOAA (National Oceanic and Atmospheric Administration). 1975. A study of the applications of remote sensing techniques for detection and enumeration of giant bluefin tuna. Southeast Fish. Cent. contrib. no. 437 (MARMAP no. 108), 48 p. National Space Technology Laboratories, Bay Saint Louis, Mississippi 39520.

the shelf break, which it reached some 18 hours later. It remained in that area until tracking ended. These lump, reef, island and shelf-break associations matched the distribution of sightings by aerial survey (Cowling et al.[7]).

Surfacing behavior

Most SBT spend a large part of the day in the upper 10 m (Fig. 10) in the Bight in summer unless they travel to other areas. At night, they tend to move to deeper water, but some tracked tuna remained in the upper 10 m throughout most of the night. The relatively long time spent at the surface during the day in the Bight (nearly 30%) would facilitate sightings by aerial survey, and surfacing behavior would significantly influence aerial detection.

The surface behavior of southern bluefin tuna in the Bight contrasts with that of most other tunas studied. Yellowfin tuna near Hawaii have an average daytime depth of 71 m during tracks offshore and away from fish aggregating devices (FADs), with modes at 0–10 m and 50–60 m. When near FADs, they have an average daytime depth of 59 m. At night, yellowfin have modes at 0–10, 30–40, and 180–190 m (Holland et al., 1990a). Similar depth distributions for yellowfin tuna were observed in the western Pacific (Yonemori, 1982). In the eastern Pacific Ocean, at the northern extent of their range, yellowfin tuna remained at somewhat shallower depths during the day than in previous studies (Block et al., 1997), presumably because of the shallowness of the mixed layer which limited their depth distribution. In the western Indian Ocean, yellowfin tuna tracked both on and off FADs spent most of the day between 60 and 110 m (Cayré and Chabanne, 1986; Cayré, 1991; Marsac et al.[3]).

Tracked skipjack tuna spent little time at the surface during the day in waters off Hawaii (Yuen, 1970; Dizon et al., 1978), and Tahiti (Cayré and Chabanne, 1986), although they were surface oriented at night. In the western Indian Ocean, two skipjack tuna tracks were found at somewhat shallower depths but the modal depths were still between 10 and 20 meters (Cayré, 1991). Bigeye tuna tracked off Hawaii had a modal depth of 220 m during the day and 80 m at night (Holland et al., 1990a). Atlantic bluefin tuna appear to spend some time near the surface in inshore waters off the New England area (Carey and Lawson, 1973), although the modal depth of 0–15 m during the day (Lutcavage et al., 2000) is somewhat deeper than that for SBT in the Great Australian Bight. This nearsurface orientation of Atlantic bluefin tuna has prompted development of aerial surveys to assess the abundance and distribution of these tuna in these waters (Lutcavage and Kraus, 1997). The extensive surfacing behavior of SBT in the Bight does not appear to occur in the shelf waters of the Indian Ocean off Western Australia. Of the six SBT tracked in the west, only one spent significant time at the surface during the day (Fishery Agency of Japan[4,5]). However, this fish oscillated rapidly between 0 and 40 m rather than remaining near the surface. The different surfacing behavior of these SBT in the west may have been due to their much smaller size (35–48 cm compared to 67–114 cm), and that they were in a migratory mode moving southwards, assisted by the Leeuwin Current (Shingu, 1967; Maxwell and Cresswell, 1981), rather than in summer residency.

The conditions in which SBT come to the surface in the Great Australian Bight are quite varied. These tuna remain within the surface 5 m for extended periods during the day under a range of weather and sea conditions, although surfacing is more pronounced on warm days with little wind. A clear example of this type of movement was evident with tuna 9, which remained below the surface in a school of tuna for the first hour of the track, during which winds were documented at over 35 km/h. After the winds dropped, the tracked tuna surfaced and remained there, apart from occasional dives, for the rest of the track. Surface schools of tuna were observed as far as the eye could see during these calm conditions. In contrast, extensive surfacing can occur in adverse weather, as observed in fish 7 between 07:00 and 09:00 h during rough seas and winds >35 km/h. However, in these conditions, no surface fish could be seen from the vessel. Protocols for aerial surveys of SBT in the Bight restrict surveys to wind speeds of <18 km/h because of a marked decrease in school sightings at higher wind speeds (Cowling et al.[7]). The highest number of sightings per unit of effort occurred when aerial surveys were flown in conditions of low wind speeds and little cloud cover. The ultrasonic telemetry suggests that wind affects detection of schools from the air rather than their surfacing behavior.

One of the objectives of the aerial survey was to reduce uncertainty in aerial survey estimates of surface abundance by incorporating environmental and behavioral data into the aerial survey analyses. Although the results from ultrasonic tracking provided preliminary information on vertical distribution that might affect sighting by aerial survey, the intent of our study was to use the more extensive data that would be obtained from archival tags to model responses in surfacing behavior to environmental conditions through space and time. Aerial survey estimates of abundance could then be adjusted by incorporating the proportion of time that SBT would be visible during aerial surveys based on the environmental conditions that occurred at the time of survey flights.

A distinct surfacing behavior regarded as a characteristic of SBT in the Bight during summer is called "rippling" (Hynd and Robins, 1967). This behavior occurs under very calm, sunny conditions. Tuna laze at the surface for extended periods, often breaking this inactive phase by rolling from side to side. Unfortunately we did not have suitable weather conditions to observe this behavior. However, data from archival tags suggest that these fish derive significant heating benefits through both insolation and the transfer of heat from the warm surface waters (Gunn et al.[2]).

[7] Cowling, A., T. Polacheck, and C. Millar. 1996. Data analysis of the aerial surveys (1991–1996) for juvenile southern bluefin tuna in the Great Australian Bight. 1996 Southern bluefin tuna recruitment monitoring workshop report. Rep. RMWS/96/4, 87 p. CSIRO Marine Laboratories, Castray Esplanade, Hobart, Tasmania, Australia 7000.

Reference depths

Reference depths—the depths to which tuna return after regular excursions above or below them—are not well defined in SBT in the Bight. Bounce dives from the surface occur in tracks 1, 3, and 11, and brief excursions above and below the bottom of the mixed layer could be seen in parts of tracks 4, 6, and 14. None of these showed the movements characteristic of bigeye tuna, which use the 15–16° isotherm as a reference point and make regular excursions to the surface (Holland et al., 1990a). These excursions are thought to be a way of regaining optimum body temperature after foraging in cooler deep water (Holland et al., 1990a; Holland et al., 1992). Bluefin tuna have a more advanced vascular anatomy for physiological thermoregulation than bigeye tuna (Holland et al., 1992); therefore one would expect SBT to display less pronounced behavioral thermoregulation than bigeye tuna under the same thermal regime. Unfortunately, the temperature range of the shallow waters of the Bight was also not large enough to induce such a response.

The interface of the surface mixed layer and the thermocline is a reference point used by many tuna species. Yellowfin tuna often remain within this narrow depth band, especially when travelling in a straight line (Carey and Olsen, 1982; Holland et al., 1990a). Traveling fish have been observed to alternate abruptly between the thermocline interface and the surface, which might assist in straight-line orientation (Holland et al., 1990a). Tracks 6 and 14 provide the clearest examples of use of the thermocline interface during sustained straight-line migration. Tuna 6 remained at a depth of about 20 m while staying in the area. However, once it started swimming toward the shelf break, it maintained a relatively constant depth within or just above the thermocline. While this behavior is apparently a characteristic of yellowfin tuna travelling alone (Carey and Olsen, 1982), our tracks were for SBT travelling in schools. Tunas 7 and 8 remained at the surface during fastest straight-line swimming, suggesting that both depth zones might be used during straight-line swimming. Although it appears that the thermocline interface provides some advantage to sustained straight-line movement, it is not clear whether the advantage is in orientation: possibly this temperature range balances heat build-up from sustained swimming.

In contrast to returning to a reference depth, some tracked fish oscillated rapidly within a depth band. This behavior was observed in parts of tracks 4, 7, 10, and 12. This "frenzied" activity might be ascribed to disturbed behavior caused by the tagging or tracking (or both). However, this behavior might reflect individuals traversing the vertical boundaries of the school (Carey and Olsen, 1982). When this behavior was observed in our study, the tracked fish appeared to be part of a school. However, there were many times when the fish was in a school but rapid vertical oscillations were not apparent. Possibly the schools did not extend over sufficient depth range to make this behavior obvious.

Predawn and postdusk dives

A feature of many of the tracks of SBT was the deep dive made just before dawn as the sky began to lighten, and just after sunset before all light was gone. In these dives, the tuna descended rapidly, stayed a short time at the bottom of the dive, and then usually rose gradually to its original depth. These signature dives were observed in tracks 1, 3, 4, 6, 7, 11, 12, 13, and 14 and possibly occurred in other cases obscured by repeated dives over the twilight period. Archival tag data showed clear signature dives in the Bight and more varied behavior off the shelf (Gunn et al.[2]). They also showed that in the central Indian Ocean, SBT dive at dawn, remain at great depth throughout the day feeding on squid, and return to the surface at night. The dawn dives we tracked might correspond to the first part of this movement, but the shelf waters of the Bight are too shallow to have a significant scattering layer, and therefore usually do not allow for the detection of prey. Perhaps this dive at dawn is a fixed behavior that has evolved to locate the scattering layer when SBT are in waters of sufficient depth.

If tuna rely largely on sight to locate prey, twilight would be the first opportunity (dawn), and last opportunity (dusk), in which to find the scattering layer as it rises during the night and descends during the day. Dawn and dusk dives have been observed in eastern spotted dolphin in the eastern tropical Pacific Ocean (Holland[8]). During the day, these dolphin remained in the shallow mixed layer (10–15 m). However, at late dusk they dived to depths of about 65 m. These were followed by further dives, each one a little shallower than the last, until diving was again largely confined to the mixed layer. Just before dawn the pattern was reversed. A line drawn along the bottom of the dives from dusk to dawn would describe a bell shape. The dolphins' behavior was thought to be in response to the vertical movement of the scattering layer. Dawn and dusk dives have since been noted in Atlantic bluefin tuna tracked in shelf waters off New England (Lutcavage et al., 2000) and are apparent in tracks of Pacific bluefin tuna in the eastern Pacific (Marcinek et al., 2001). Block et al. (1997) reported predawn dives in yellowfin tuna tracked in the California Bight. Their vertical track plots suggested that postdusk dives may also occur. Similar vertical behavior has been apparent in the track of one skipjack (Cayré and Chabanne, 1986) and one yellowfin tuna (Carey and Olsen, 1982). However, the absence of similar dives in other studies suggests that the timing of the dives was coincidental.

Stomach temperature

Muscle and stomach temperatures of Atlantic bluefin tuna were monitored in several tracking experiments (Carey and Lawson, 1973; Carey et al., 1984). Both were shown

[8] Holland, K. N. 1996. Personal commun. University of Hawaii, PO Box 1346, Coconut Island, Kaneohe, Hawaii 96744.

to be well above ambient water temperature. Stomach temperature increased after feeding, which was attributed to the hydrolytic processes of digestion and an increase in metabolic rate. Possibly raised stomach temperature speeds digestion and enables a higher feeding frequency when food is abundant. The capacity to maintain higher stomach temperature is enhanced by thermal isolation through heat exchangers, the gas bladder, and the fatty body wall (Carey et al., 1984). Therefore, stomach temperature would reflect activities associated with feeding and digestion, rather than temperature changes occurring in the body. SBT, while very much smaller than the giant bluefin tuna tracked by Carey, also showed a marked differential between stomach and ambient temperatures. The largest differential of 9°C (track 11) was found in the largest SBT tracked, which may be relevant. Because temperature increased steadily during the track, it was probably due to digestion of a meal. All pole-and-line–caught SBT tracked during these experiments were initially chummed with pilchards and could have eaten pilchards just before tracking. In some instances, tunas regurgitated pilchards while the tag was placed in their stomachs. A caecal temperature differential reaching 10°C has also been observed in a 103-cm SBT after being fed in cage experiments (Gunn et al.[9]). The smaller temperature differential observed in the other two tracked tuna (tuna 10 and 13) may have been a consequence of their having less food in their stomach to digest, or their smaller size.

Tuna 11 showed the characteristic changes in stomach temperature associated with the swallowing of prey or water or both. Two swallowing events occurred, a minute apart, resulting in a drop in stomach temperature to ambient temperature. Stomach temperature recovered rapidly, but not quite to the level before swallowing. Carey et al. (1984) managed to have Atlantic bluefin tuna retain tags in their stomachs for up to 13 days by feeding them to ensure that their stomachs never remained empty. Several hours before regurgitation of the tag, a series of cold pulses were observed in stomach temperature, presumably from swallowing water which lowered the stomach temperature briefly. If these cold pulses persisted, the tag would be spat out a few hours later. If the tuna was fed, the tag was usually retained. If regurgitation to purge indigestible items from the stomach normally occurs after digestion is complete and the stomach is relatively empty, as suggested by Carey et al. (1984), then it is likely that the swallowing events observed in tuna 11 involved little or no food. Because a very marked drop in stomach temperature was observed in tuna 11, a large amount of water must have been swallowed.

[9] Gunn, J., T. Polacheck, T. Davis, M. Sherlock, and A. Betlehem. 1994. The development and use of archival tags for studying the migration, behaviour and physiology of southern bluefin tuna, with an assessment of the potential for transfer of the technology to groundfish research. Proc. ICES mini-symposium on migration, St. Johns, Newfoundland. ICES C.M. Mini:2.1, 23 p. International Council for the Exploration of the Sea, Palægade 2-4, DK-1261 Copenhagen K, Denmark.

The effects of chumming on tuna behavior

Observations on tracked tuna being caught up in chumming by commercial pole-and-line fishing have provided us with insights into these operations. Tunas 5, 6, 8, and 15 were associated with chum lines for part of their tracks. They all followed the chum line at a depth of about 20 m for 15–30 minutes, and some came to the surface for brief periods. The tuna schools extended to at least 200 m behind the vessel that was chumming. Pole-and-line operators usually steam forward at about 2 m/s, chumming with live and, sometimes, frozen pilchards. They progress from tuna school to tuna school hoping to combine schools. Most tuna appear to be below the surface and well behind the boat. Fish progress to the front of the school and come to the surface to take chum, replacing tuna that were there before them. Based on our tracking, it appears that tuna after spending a short time at the surface, break away from the chum line in groups or in schools.

Effects of tagging and tracking on tuna behavior

There is a concern that capture, tagging, and tracking procedures change the behavior of the fish being observed. A number of criteria are used to support the view that the fish behave normally: they remain within a school (Yuen, 1970; Cayré, 1991; Cayré and Marsac, 1993); show similarity in vertical and horizontal movements across tracks (Holland et al., 1990a; Cayré, 1991) or through experimental procedures such as evaluating swimming performance when tags are attached externally (Arnold and Holford, 1979; Blaylock, 1990) or observing food consumption when tags are placed in the stomach (Lucas and Johnstone, 1990).

There is however, evidence that SBT do react adversely to being tagged. Hampton (1986) found that lower than expected numbers of SBT tagged with dart tags were recaptured in the first 5 days after release. Also, recaptured fish were in significantly poorer condition than untagged fish—the effect being greatest in those at liberty for 5–20 days (Hampton, 1986) and 13–24 days (Hearn, 1986). Presumably, the adverse effects were related to reduced feeding.

Fish generally undergo a phase of recovery from the trauma of capture and tagging. The resumption of "typical" behavior is often taken as a sign that the fish is behaving normally (Holts and Bedford, 1990). In our study, five tuna initially dived to the bottom, five dived below the depth distribution of the tuna school, and six returned immediately to the school. All returned to schools, which were usually near the surface, within 20 minutes. Most significantly, four tracked tuna actually joined the chum lines of commercial pole-and-line vessels shortly after tagging. However, it could not be determined whether these four tuna were feeding because they did not have temperature-pressure tags in their stomach.

Stress associated with capture and tagging is more obvious in larger fish: blue and striped marlin remain at depth for many hours before returning to normal depths

(Holland et al., 1990b; Holts and Bedford, 1990; Block et al., 1992a). Black marlin dive after release but usually return to normal depths soon after (Pepperell and Davis, 1999). High, sustained, swimming speeds for up to the first six hours of blue marlin tracks were attributed to increased ram ventilation to reduce anaerobic debt (Block et al., 1992b). Undoubtedly there is trauma associated with capture and tagging, but pole-and-line capture is fast, and SBT are not as tired as they would be if caught on a rod and line. In most of the SBT tracks, swimming speed was much slower in the half hour after release than for the remainder of the track. Possibly this slow swimming relates to a recovery phase. However, it more likely reflects the nature of pole-and-line fishing and the association of the chummed school with the boat. After catching and releasing the fish, chumming is stopped. However, the school usually remains with the boat for a short period. The strong schooling behavior of SBT appears to quickly override trauma-induced behavior, such as remaining at depth, that might keep tagged fish away from the school.

Association of the tracked fish with schools is probably the most encouraging sign to the field worker that the tuna is behaving normally, or at least that its movements are representative of the school as a whole. This association was marked in our study. However, on the occasions when the tracked fish appeared to be alone, it was not clear whether this isolation was due to the normal breakup and dispersal of the schools aggregated by the chumming operation or to the tagging and tracking procedure. We were concerned that "herding" (the vessel following the fish influencing the direction of its movements) over a period of time might separate a fish from its school. However, it is also not clear whether it is possible to detect if the tracked fish is solitary or with a school. Depending on the skill and knowledge of the observer, schools can usually be detected in good weather if there is surface or subsurface activity. At night or in rough seas, the usual way of detecting schools is by echo-sounder, but this works only if the school is under the tracking vessel. The school must therefore be large and extend well behind the tracked fish (which is nominally tracked at a distance of 400 m). Often "solitary" tracked tuna displayed the repeated and predictable behaviors seen in other SBT tracks and generally accepted as criteria of "normal" behavior, the most striking of which are the predawn and postdusk dives.

Three methods of tag attachment were used in our study—five tags were attached externally behind the second dorsal fin, ten were placed internally in the stomach, and one tag was accidentally struck by a free-swimming tuna and was attached by the force of the strike. The effects of attaching tags are not currently quantifiable because of the diversity of tuna behaviors. However, the tracks of SBT with stomach tags were more dynamic than the tracks of tuna with tags attached externally. Tunas with stomach tags seemed more responsive to their environment: their behavior included fast, sustained swimming, large translocations, and these tuna were frequently observed with other tuna attracted by chumming operations. Externally attached tags presumably created physical disturbances, such as drag, turbulence, and attachment wounds to which the tuna had to adjust. These are more likely to cause short-term disturbance in behavior than swallowed tags. However, stomach tags had unpredictable, and often short, retention times, which counteracted their advantages.

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