

Spike dives of juvenile southern bluefin tuna (*Thunnus maccoyii*): a navigational role?

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Abstract Tunas make sharp descents and ascents around dawn and dusk called spike dives. We examine spike dives of 21 southern bluefin tuna (*Thunnus maccoyii*) implanted with archival tags in the Great Australian Bight. Using a new way to categorize this behavior, we show that spike dives are similar among all the fish in the study. The dive profiles are mirror images at dawn and dusk and are precisely timed with respect to sunrise and sunset. We analyze the possible reasons for spike dives, considering the timing of spike dives, the characteristic dive profile, and

the tuna's magnetic habitat. In addition, we present anatomical evidence for elaboration of the pineal organ, which is light mediated and has been implicated in navigation in other vertebrates. The new evidence presented here leads us to suspect that spike dives represent a survey related to navigation.

Keywords Migration · Pineal gland · Compass · Magnetic navigation · Polarized light · Archival tags

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Introduction

Archival tag data from tuna often show distinctly shaped ascents and descents at dawn and dusk known as spike dives. Precise light data at these times are helpful in estimating the fish's latitude and longitude, and so changes in light intensity caused by spike diving is often considered a nuisance (Welch and Eveson 1999; Teo et al. 2004). Spike diving is mentioned (rarely) in the scientific literature but is common among large pelagic predatory fish such as tuna (Gunn and Block 2001). Explanations that have been proposed for spike diving by tuna include (1) locating the base of the mixed layer, (2) surveying prey fields, (3) performing a geomagnetic survey for navigation, and (4) undertaking a general environmental survey of the water column (Gunn and Block 2001).

In this study, we provide a description of spike dives, examine the behavior in the context of the sensory capabilities and physical environment of tuna, and consider a number of alternative explanations for spike dives. We use depth data from archival tags deployed on juvenile southern bluefin tuna (SBT, *Thunnus maccoyii*) to provide a more rigorous characterization of spike dives in place of what has been, until now, anecdotal reporting about the

timing and frequency of this behavior. The tuna used in this study were tagged and recovered in the Great Australian Bight. Presentation of spatial movements derived from the light data has been partly published elsewhere (Bestley et al. 2008). All the tuna in this study were migratory and performed long range movements during the time they were tagged. The round trip journeys, which were not explicable by ocean current advection, ranged between 5,000 and 16,000 km. These annual cyclical journeys are thought to be motivated by the feeding ecology of juvenile SBT (Bestley et al. 2008).

Our analysis shows that spike dives are a distinct and habitual behavior for juvenile SBT with a precise association with dawn and dusk. The shape and timing in relationship to the physical environment led us to suggest a number of new hypotheses about the navigational system of juvenile tuna that we hope will lead to productive avenues for future research. Navigational ability is critical to the life cycle of various tuna species (Bakun and Broad 2003). Tuna undertake migrations over thousands of kilometers (Sharp and Dizon 1978; Gunn and Block 2001) and can return to locations with fidelity of less than 10 km (Klimley and Holloway 1999; Ohta and Kakuma 2005). Adult SBT travel over 8,000 km from Southern Ocean feeding grounds to return to their only known spawning ground south of Indonesia (Davis and Farley 2001; Patterson et al. 2008). As a consequence, sensory mechanisms and behavioral strategies that increase the accuracy of long-distance movements should be strongly favored by natural selection. Both the characteristic shape of spike dives and their precise timing with respect to unique patterns and changes of light near sunrise and sunset lead us to ask if the explanation for this behavior lies in navigation. Tuna have well-developed eyes. Tuna also have a pineal window, which allows sunlight to illuminate part of the surface of the brain through a hole in their skull. In all species of tuna, the pineal apparatus penetrates the skull through an oval window between the eyes (Sharp and Dizon 1978). Cells on the outer surface of the pineal gland are similar to retinal photoreceptors (Murphy 1971). The pineal instrument, which is remarkably elaborated in tuna (and for which there is no other explanation of function), is related to navigation in other vertebrates (Deutschlander et al. 1999). Since both sensory organs are light mediated, we discuss both the pineal and the eyes with respect to a behavioral explanation of spike dives.

Since spike diving may not be related to navigation but to some other purpose such as hunting, we also investigate this possible explanation. Organisms that form the deep scattering layer (DSL) undergo diurnal vertical migration around dawn and dusk (Burd & Lee 1951), as do the larger animals that feed on the DSL and may be target prey items for tuna (Dagorn et al. 2000; Onsrud et al. 2004; Schaefer

and Fuller 2003). The DSL and its diurnal vertical migration is a worldwide phenomenon, and observations during a solar eclipse have shown that the vertical movement is light mediated (Kampa 1974). The DSL ranges in depth during the day from 100 to 500 m and moves toward the surface during the night. We consider whether tracking the movement of the DSL might provide an alternative explanation for the characteristic pattern of spike diving in juvenile SBT.

Materials and methods

We used data from 20 archival tags (type MK7, Wildlife Computers, Redmond, USA, <http://www.wildlifecomputers.com>) that recorded light, external temperature, depth, and internal temperature every 4 min. All tags were surgically implanted into SBT in the Great Australian Bight (GAB) between 1998 and 2002 and were recovered as part of the juvenile SBT monitoring program (Davis 2002). The fish were at liberty for between 135 and 494 days and ranged in size from 71 to 110 cm [length to caudal fork (LCF) at release]. Fish grow up to 30 cm in length per year at this age (Laslett et al. 2002); however, size was only known at the time of release for the majority of fish. Therefore release size was used, without correction, in the analysis. We estimated dawn and dusk from the tag's raw light trace, when the light intensity was at 50% of the difference between maximum and minimum light level recorded during each 24-h period. The tunas' positions, calculated using the archival tag light trace, ranged from the southern Indian Ocean to the Tasman Sea with an accuracy of about 1° latitude or longitude (Bestley et al. 2008). Analysis was conducted using programs written in Matlab (<http://www.mathworks.com>).

One additional tag (type MK9, Wildlife Computers, Redmond, USA, <http://www.wildlifecomputers.com>) sampled at an interval of 20 s. This tag was deployed December 19th 2005 (32.67° S, 133.17° W) in a juvenile SBT (LCF, 96 cm) released in the GAB, which was at liberty for 65 days. This tag was used to test if sampling frequency of 4 min for the set of 20 tags accurately described the vertical components of spike dives. We tested this by sub-sampling the 20 s tag in all (12) variations of 4 min intervals and comparing the results to each other and to the full 20 s dataset.

Initial exploration of dive characteristics—definition of a spike dive

Spike dives were initially defined as the deepest point in the depth record within a 16-min period around the times of dawn and dusk (defined from the 50% light threshold explained above). The 16-min interval was approximately the minimum duration of the characteristically shaped dive

profile. For initial exploration, we extracted all the depth records for two arbitrarily chosen fish (Table 1, fish 55 and 56, over 394 and 305 days at liberty) for the period around dawn/dusk, then aligned and averaged these for all days at liberty in order to compare mean spike dive profiles.

Timing of spike dives and sun elevation

For each daily estimated geographic location derived from the light data, we determined the elevation of the sun from the NASA sun elevation model (http://ecco2.jpl.nasa.gov/data1/matlab/air_sea/sunrise.m) at the time of the spike and calculated the time of the spike in relation to the time of sunset and sunrise for the estimated position.

Hypotheses and statistical tests

The hypotheses tested with respect to the 20 tags, which sampled depth at 4-min intervals were as follows:

- H1: Dawn spike ascent rates are indistinguishable from ascent or descent rates at other times selected randomly for each fish.
- H2: Dusk spike descent rates are indistinguishable from ascent or descent rates at other times selected randomly for each fish.
- H3: Dawn spike ascent rates are indistinguishable from inverted dusk spike descent rates for each fish.

Dives were not classified as “spike” or “no spike,” and thus, all dawns and dusks were treated similarly for all fish. Data from dawns and dusks were not included if the calculated day length was illogical or other corruption of the data was suspected (i.e. during times when tuna were caught and transported in cages and thus unable to move naturally).

We used two sample Student's *t* tests to test the hypotheses that one group of dive statistics was indistinguishable from another. The use of *t* tests is appropriate given the intention to demonstrate, in a robust way, broad simple relationships about spike dives and their similarities without obfuscation by complex statistical treatment (Murtaugh 2007). Hypotheses were rejected at a confidence level of 95% ($\alpha=0.05$). For comparison with dives not made around dawn and dusk, we used randomly selected times during the day and treated them in a similar way to times that had been identified as dawn or dusk by the 50% light

Table 1 Hypotheses tests based on the frequency distribution of ascent or descent rates of spike dives for 20 southern bluefin tuna (*Thunnus maccoyii*) that were tagged in the Great Australian Bight with archival tags

| Fish number | Date Released | Release latitude °S. | Release longitude °E | Days at liberty | Length LCF (cm) | H1 | H2 | H3 | Mean dawn spike ascent rate (m/4min) | Mean dusk spike descent rate (m/4min) |
|-------------|---------------|----------------------|----------------------|-----------------|-----------------|----|----|----|--------------------------------------|---------------------------------------|
| 55 | 3-Jan-98 | 32.18 | 132.6 | 394 | 97 | R | R | R | 78.28 | -94.57 |
| 56 | 26-Jan-98 | 33.11 | 132 | 305 | 90 | R | R | NR | 75.67 | -84.39 |
| 57 | 26-Jan-98 | 33.28 | 131.43 | 388 | 98 | R | R | R | 62.57 | -81.17 |
| 58 | 17-Feb-00 | 33.57 | 132.15 | 241 | 99 | R | R | NR | 72.27 | -72.20 |
| 59 | 26-Jan-98 | 33.28 | 131.43 | 225 | 100 | R | R | R | 73.21 | -89.49 |
| 60 | 3-Jan-98 | 32.8 | 132.6 | 446 | 98 | R | R | R | 56.45 | -68.55 |
| 61 | 1-Mar-99 | 33.3 | 131.48 | 232 | 110 | R | R | NR | 79.39 | -76.94 |
| 62 | 17-Feb-00 | 33.57 | 132.15 | 299 | 99 | R | R | R | 63.33 | -76.67 |
| 63 | 17-Feb-00 | 33.57 | 132.15 | 286 | 104 | R | R | NR | 67.56 | -68.45 |
| 64 | 26-Jan-98 | 33.28 | 131.43 | 208 | 98 | R | R | NR | 64.65 | -68.47 |
| 65 | 3-Jan-98 | 32.8 | 132.6 | 330 | 93 | R | R | NR | 73.20 | -70.07 |
| 66 | 3-Jan-98 | 32.8 | 132.6 | 336 | 96 | R | R | NR | 66.83 | -78.21 |
| 70 | 14-Feb-01 | 34.08 | 123.45 | 334 | 72 | R | R | NR | 51.97 | -56.61 |
| 71 | 14-Feb-01 | 34.08 | 132.45 | 418 | 71 | R | R | NR | 37.30 | -39.81 |
| 72 | 17-Feb-00 | 33.57 | 132.15 | 369 | 99 | R | R | NR | 64.42 | -60.59 |
| 73 | 17-Feb-00 | 33.57 | 132.15 | 406 | 106 | R | R | NR | 65.88 | -73.42 |
| 75 | 1-Mar-99 | 33.3 | 131.48 | 135 | 102 | R | R | NR | 80.58 | -78.89 |
| 76 | 26-Jan-98 | 33.12 | 132 | 494 | 97 | R | R | NR | 63.69 | -73.61 |
| 78 | 21-Feb-02 | 32.63 | 132.62 | 330 | 87 | R | R | NR | 48.48 | -48.19 |
| 79 | 19-Feb-02 | 33.62 | 132.32 | 275 | 105 | R | R | NR | 72.24 | -68.50 |

Hypotheses tests: H1—dawn spike ascent rates are indistinguishable from other times selected randomly; H2—dusk spike descent rates are indistinguishable from other times selected randomly; H3—dawn spike ascents are indistinguishable from inverted dusk spike descents for this fish
R rejected at $\alpha=0.05$, NR not rejected

threshold described above; that is, we identified the maximum rate of ascent or descent within a 16-min interval around a randomly selected time.

Maximum ascent and descent rates may be related to maximum sustained swimming speed. Generally, as the fish is swimming in a three-dimensional space, we are unable to infer swimming speed from only depth and time data; however, the maximum rate may indicate a critical swimming speed. We made a comparison of dawn and dusk spike dive ascent or descent rates between each unique pair of fish (20 fish=190 unique fish–fish comparisons for dawn and dusk) to determine if maximum ascent or descent rate was correlated with fish size. We calculated a ratio of rejected hypotheses to non-rejected hypotheses for each set of *t* tests for a given size-difference interval and determined correlation by linear regression analysis.

Visualization of the pineal apparatus

We made a magnetic resonance imaging (MRI) scan of the head of an albacore tuna (*Thunnus alalunga* LCF 100 cm)

to visualize the pineal apparatus using a human medical scanner. This similar species was used instead of SBT, as a good quality SBT specimen was not available when access to the MRI equipment was permitted. The head had been frozen immediately after death and was thawed to room temperature for the scan.

Results

Spike dive characteristics

Spike dives are evident in archival tag depth time series (Fig. 1). The characteristic components include a near-surface visit immediately preceding or following the steep side of the dive. There is considerable variability in the depth of spike dives recorded in these data (50–605 m), but the characteristic shape remains consistent and lasted from 15 min to 1 h. Figure 1b shows a day with spike dives of up to 400 m in depth, more than double the depth of any other activity during the day, while Fig. 1c shows the converse,

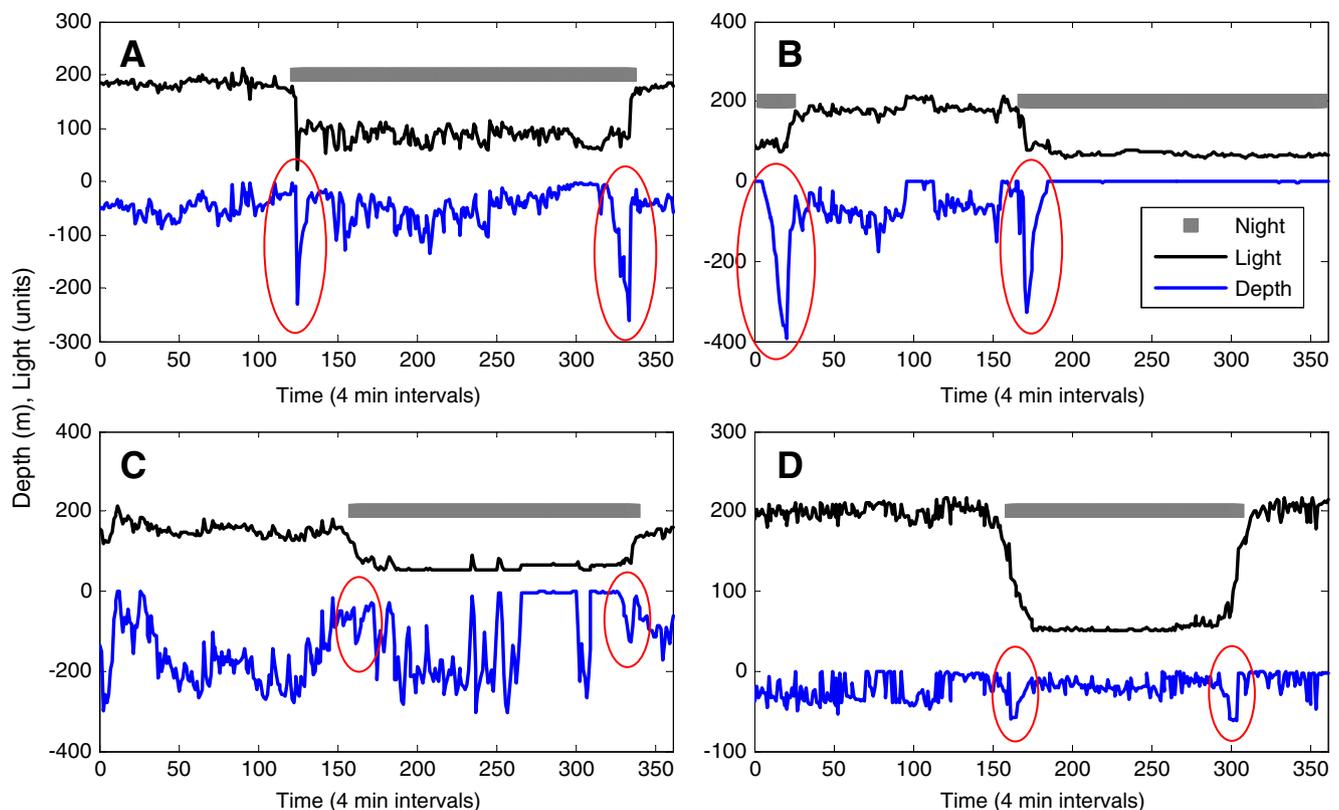


Fig. 1 Spike dives (circled). **a** Depth and light for southern bluefin tuna (*Thunnus maccoyii*) number 57 on 7 July 1998 in the Great Australian Bight (approximate position—33° S, 133° W). The tuna was fitted with an archival tag, which sampled every 4 min and had been at liberty for 163 days. Typical spike dives occur when the light decreases at dusk and increases at dawn. **b** Very prominent spike

dives, fish number 79, 138 days at liberty (6 July 2002). **c** Characteristic shape spike dives among activity at greater depth in both day and night, fish number 58, 202 days at liberty (5 August 2000). **d** Spikes apparently truncated by sea floor at 70 m with tips 16 min wide, fish number 55, after 21 days at liberty (23 January 1998)

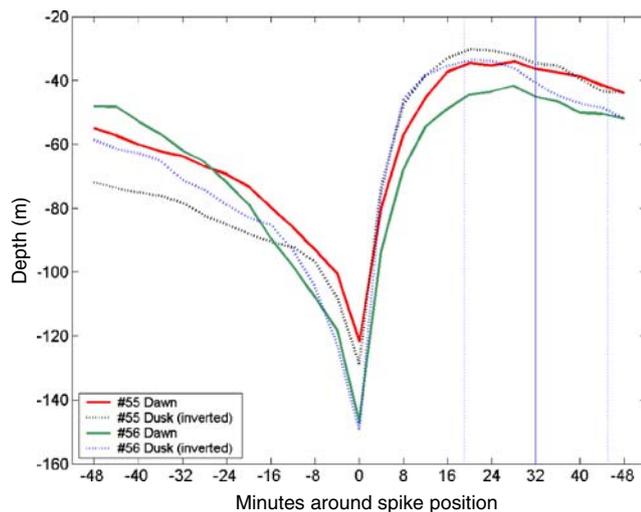


Fig. 2 Qualitative comparison of mean spike dives between dawn and dusk and between fish. Mean depth around all spike dives for southern bluefin tuna numbers 55 and 56, over 394 and 305 days. Spike position calculated as deepest point within 16 min of the time of 50% light from archival tag data. The mirror image of the dusk profile is shown for direct comparison and is similar in shape to the dawn profile. The mean position (± 1 standard deviation) of sunrise or sunset relative to all spikes is shown as blue vertical lines

spike dives, which are characteristic in shape but much less prominent than other activity during the day and night. Sometimes, the spikes appear truncated (Fig. 1d), and it appears that depth truncation is due to the sea floor (because there are no other dives deeper than the base of the truncated spikes in the 24-h period); however, the remainder of the characteristic spike dive profile is retained.

Exploratory analysis of the two arbitrarily selected tags shows that mean dawn spike dives are mirror images of the mean dusk spike dives (Fig. 2). The depth of the mean spikes and their characteristic shape are similar between the two fish. This analysis shows that maximum rate of ascent or descent around dawn and dusk is a good indicator of both the magnitude of spike dive and the characteristic sequence of spike dive components and was used throughout the remaining analysis as a single datum to characterize and identify a spike dive.

Spike dive characteristics inferred from coarse temporal scale tags

The total number of dives identified from 6,451 total days was 5,072 at dawn (76.3% of days) and 5,495 at dusk (85.2%), for a total of 10,567 dives (Table 1). The maximum dawn ascent rate was 386 m in 4 min (96.5 m min^{-1}), and the maximum dusk spike dive descent was 605 m in 4 min (151 m min^{-1}). Maximum dusk descent rate was greater than maximum dawn ascent rate in 18 out of 20 fish. The two groups of maxima dawn to dusk

were significantly different from each other (paired t test; $t_{38}=4.28$, $p<0.001$).

Spike dive characteristics inferred from fine temporal scale tag

Spike dives for an archival tag recording depth at 20-s intervals were extracted using the same method as for the 4-min tags. Maximum dawn spike dive ascent rate was 84 m in 20-s interval (4.38 body lengths per second, 252 m min^{-1}), and the maximum dusk descent rate was 66.5 m in 20 s (3.46 body lengths per second, 199.5 m min^{-1}). The mean of the dawn spike ascent rates was $90 \text{ m min}^{-1} \pm 145 \text{ m min}^{-1}$ (mean ± 1 SD), and the mean of dusk descent rates was $112.5 \pm 100 \text{ m min}^{-1}$. Mean dawn and dusk dives were mirror images of each other (Fig. 3) and are different from dives at points chosen randomly and treated in the same way as those at dawn and dusk (Fig. 4). Re-sampling the 20 s tag to replicate a 4-min tag (12 point re-sampling) showed that the mean difference in determining the maximum depth using 12 re-samples was $11.7\% \pm 9.5\%$ (mean ± 1 SD), $n=130$ spike dives, and the mean difference in determination of maximum ascent or descent rate in one measurement interval using 12 re-samples was $5.58\% \pm 3.7\%$ (mean ± 1 SD), $n=130$ spike dives. Thus, the components of spike dives were sampled relatively accurately with a 4-min sampling interval, and so, the larger 4-min tag data set is suitable for describing the behaviors in the subsequent sections. The mean speed of ascent or descent is more accurately determined with the 20-s tag;

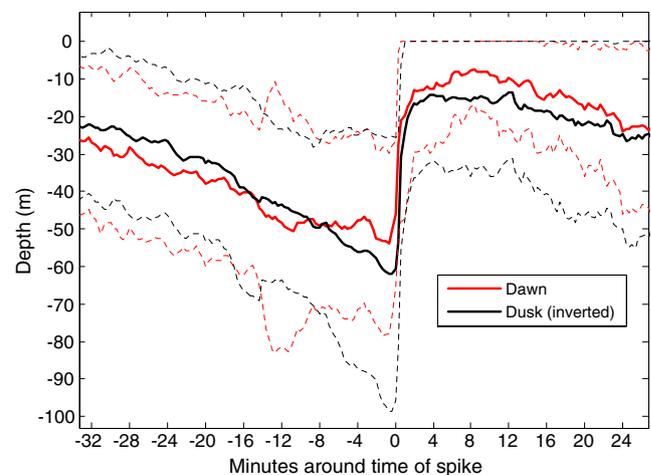


Fig. 3 Mean and one standard deviation of depth around spike dives for southern bluefin tuna number 1,046 for 65 days at liberty with a 20-s sampling tag. The dusk profile has been inverted laterally for comparison with dawn. The graph shows that the mean dawn dives are a mirror image of the mean dusk and of a similar depth and gradient. Treatments of points randomly chosen for dusk and dawn show no spike profiles

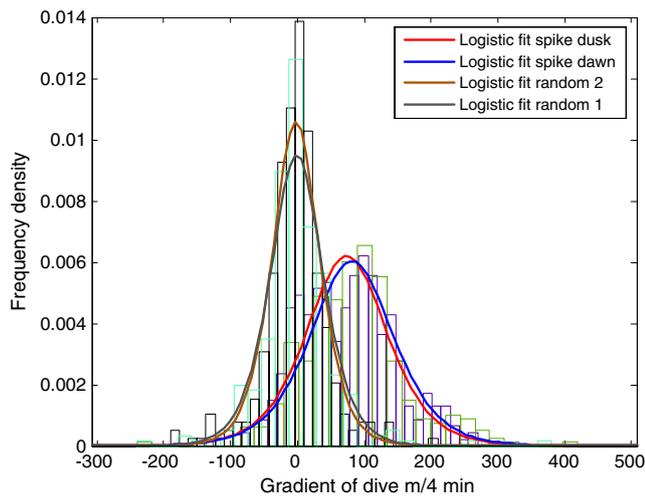


Fig. 4 Frequency density function of distribution of ascent and descent rates of spike dives and dives treated in the same way using a random time rather than dawn and dusk. Fish number 56, over 305 days. Dawn dives have been inverted to be sign similar to the dusk dives. The distributions show best fit (using maximum log likelihood) to the logistic probability density function (solid lines). Dusk and dawn spike ascent and descent rates are indistinguishable from the mirror image of the other

however, the relative ascent and descent rates within one measurement interval are well sampled by the 4-min tag.

Frequency distribution of dive gradients

Frequency density plots of maximum rate of ascent or descent during dawn and inverted dusk spike dives and that of dives within a 16-min interval around randomly chosen times, for one fish over 305 days, shows similarity between spike dives and differentiation between spike dives and dives at randomly selected times (Fig. 4). In both cases, the frequency distributions are better fitted with a logistic probability distribution function (PDF) rather than a normal PDF as determined by least log likelihood (dfittool.m, <http://www.mathworks.com>). This indicates that the groups of gradients are more tightly constrained around one or more values than if they were normally randomly distributed. Nevertheless, the distributions were not significantly different from normally distributed (Jarque-Bera test, jbstest.m <http://www.mathworks.com>); therefore, it is acceptable to compare distributions using a *t* test. This pattern of

frequency distributions was similar for all fish in the study justifying the use of two sample *t* tests for statistical comparison of spike dive data.

Timing of spike dives and sun elevation

Spike dives are offset by about 30 min on the dark side of sunrise or sunset, which corresponds to a sun elevation of about -6° at both times of the day (Table 2); that is, the highest rate of ascent (immediately following the deepest point of the spike dive) of dawn spike dives occurs approximately 30 minutes before sunrise, and the highest rate of descent (immediately before reaching the deepest point of the spike dive) of the dusk dive occurs approximately 30 min after sunset. A plot of relative frequency of depth data less than 20 m (Fig. 5) demonstrates that there is a maximum between the main depth change and the calculated position of sunrise or sunset; this suggests that the fish were more often closer to the surface during this period than at other times during the characteristic spike dive pattern.

Hypothesis tests and correlation to length

The distributions of both dawn and dusk dives were significantly different from those of dives chosen at random times (Table 1). In 15 of 20 cases (75%), the dusk dives were indistinguishable from the mirror image dawn dives for the same fish (Table 1).

The differences in mean ascent or descent rate for dawn dives and dusk dives were positively and significantly correlated to the differences in fish size using linear regression (dusk, $R^2=0.36$, $p=0.005$; dawn, $R^2=0.53$, $p<0.001$; Fig. 6). Descent rates are slightly higher than the ascent rates, but the difference is not statistically significant (paired *t* test, $t_{38}=1.45$, $p=0.15$). The more similar the fish are in length, the more similar are their maximum rates of ascent or descent (Fig. 7), indicating that the speed of ascent/descent may be constrained by fish size.

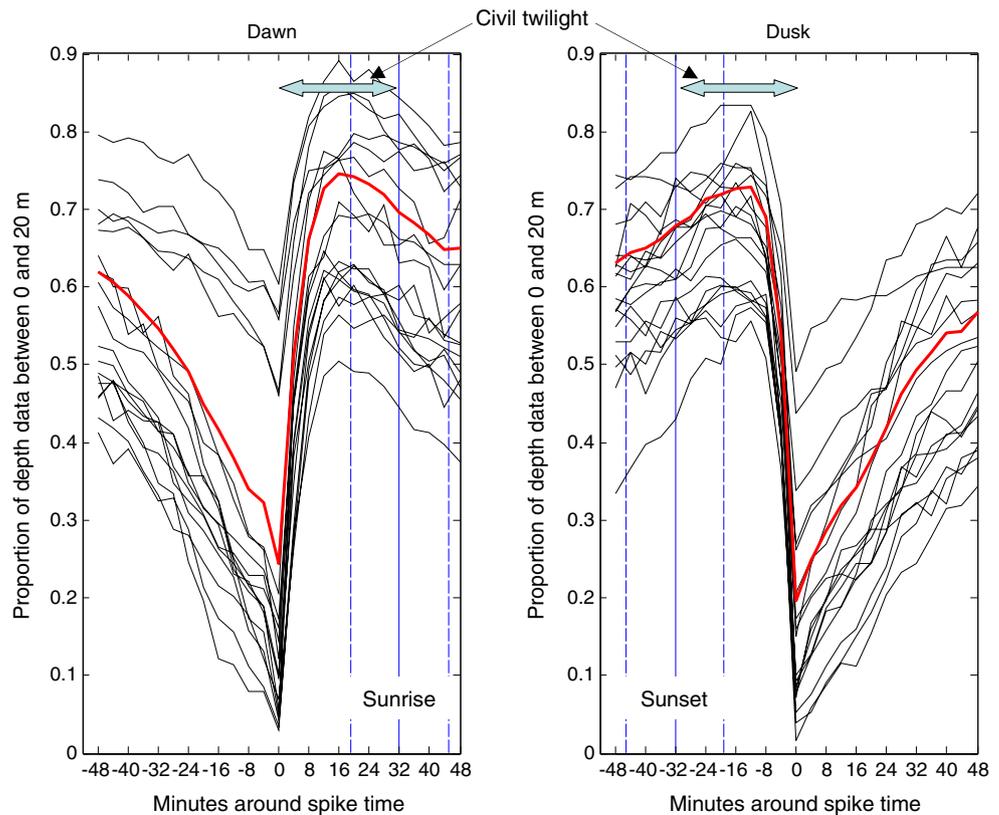
MRI scan and physiological examination

The MRI scan shows the whole pineal apparatus in situ (Fig. 8). Physiological examination of the tuna (*Thunnus*

Table 2 Difference in time between the spike dive (mid-interval of steepest gradient) and the time of sunrise or sunset for the estimated location (offset) and estimated elevation of sun at same point

| | Mean sun elevation at spike (deg) | SD sun elevation at spike (deg) | <i>N</i> for elevation | Mean offset (min) | SD offset (min) | <i>N</i> for offset |
|----------|-----------------------------------|---------------------------------|------------------------|-------------------|-----------------|---------------------|
| Sunrises | -5.9 | 2.5 | 4,763 | 30.9 | 12.6 | 4,773 |
| Sunsets | -6.2 | 2.5 | 4,589 | 32.3 | 13.2 | 4,849 |
| All | -6.1 | 2.5 | 9,352 | 31.6 | 13 | 9,622 |

Fig. 5 Proportion of depth data less than 20 m below the surface around the times of spike dive position for southern bluefin tuna (*Thunnus macoyii*) in study. The mean values are shown as *thicker red line*, and the mean estimated position of sunrise and sunset for all the fish in relation to spike dive is shown as *vertical blue lines* (with dashed lines at 1 SD). The similarity of the mean patterns of all fish between dawn and dusk is evident as is the maximum in frequency of shallow data around the period between the spike (sun elevation about -6°) and point of 0° sun elevation (sunrise and sunset). This period is called civil twilight and is uniquely suitable for sensing geographic compass direction using the patterns of polarization of sunlight near the surface of the ocean



albacares LCF 1 m) head used in the MRI scan confirmed the presence of a cartilaginous tube connecting the semi-spherical pineal gland anterior to the brain to a translucent window in the skin on the surface of the head. Dissection of

20 SBT heads in the field to expose the pineal apparatus showed that light passes through the structure (Willis, personal observation), whereas detectable levels do not pass through the surrounding bone, muscle, and other tissue (Murphy 1971). The cartilaginous tube that carries light

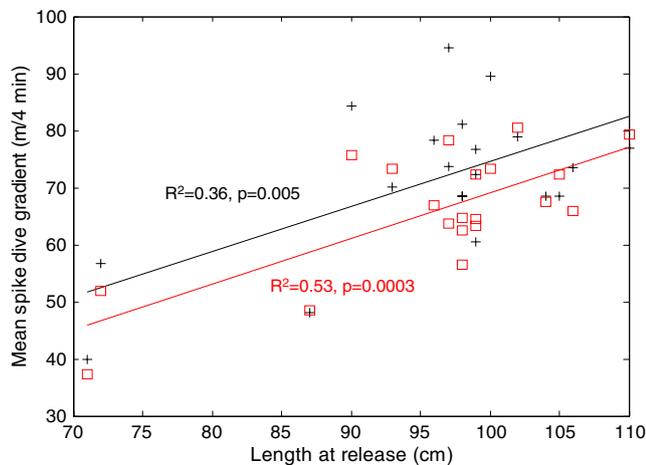


Fig. 6 Mean spike dive rates of ascent and descent plotted against LCF at release for 20 southern bluefin tuna released in the Great Australian Bight between 1998 and 2002. Each point represents the mean and thus weight of roughly 300 data (Table 1). *Black symbols* represent dusk spike dives (descent), *red symbols* represent dawn (ascent). The graph shows that the mean rates of ascent and descent of both the spike types are similarly positively correlated to the length of the fish at release and suggests that downward speed is greater than upward speed, although the difference is not statistically significant

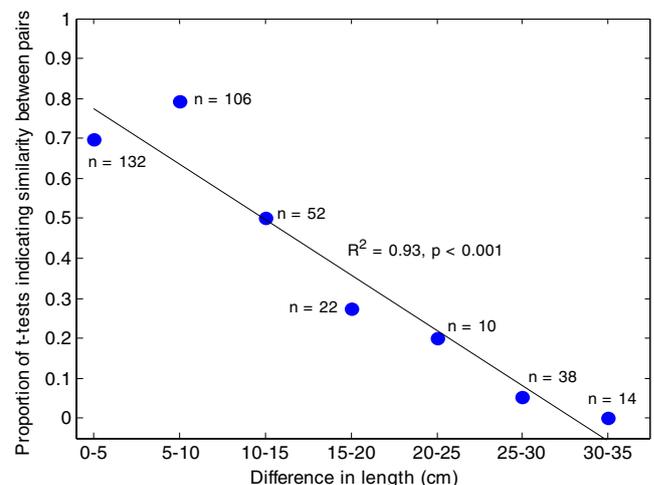


Fig. 7 Proportion of tests suggesting that spike dive ascent and descent rates are similar between pairs of fish plotted against the difference in length between the pair. Thus, fish that are more similar in length are more likely to have indistinguishable spike ascent or descent rates. Twenty fish morning and evening=380 unique cross-correlations

used to acquire light-independent navigational information. Together, these cues could then provide the basis for map information and/or be used to calibrate multiple compasses, both of which are critical for long-distance migrants. We do not have a complete answer to present here; rather, we discuss the behavior in relation to the various environmental cues that are available to the tuna around the time and depths of these dives, in the hope that new hypotheses may be developed that can be tested in the field.

Distinct sensory modalities for deep and shallow part of spike dive

The time of the shallowest portion of the spike dives coincides with civil twilight, which is the time of day best suited for the detection of celestial polarization patterns by marine animals (Novalés Flamarique and Hawryshyn 1997; Waterman 2006). At sunrise and sunset both the band of maximum polarization (BMP) and the e-vector of polarization are vertically aligned on the horizon, and the spectral composition of the light has a relatively high proportion of frequencies in the ultraviolet (UV) (Cronin and Shashar 2001 and see Fig. 7b in Novalés Flamarique and Hawryshyn 1997). In the ocean, the intensity of polarization decreases rapidly in the first few meters of water (Waterman 2006). Consequently, polarized light patterns can only be detected just under the surface (Waterman 2006). Sensitivity to polarized light has not been studied in tuna but has been demonstrated in many groups of fish, where it is mediated by photoreceptors in the retina (Hawryshyn et al. 1990). The size and complexity of the pineal apparatus revealed by the MRI scan may also suggest a role in a light-dependent sensory process, since it (like the retina) receives light, including polarized light. In view of its role in navigation in other vertebrates (Deutschlander et al. 1999; Rivas 1953; Adler 1976), the behavior of the tuna during the shallow portion of spike dives at precisely first and last light could therefore also be related to the operation of the pineal.

Polarized light patterns at dawn and dusk have been shown to be important for the calibration between multiple compass systems, for example, in migratory birds (Muheim et al. 2006). Averaging the intersection of the BMP with the horizon at sunrise and sunset provides an estimate of geographic (rotational) north that is independent of latitude and time of year (Muheim et al. 2006). As a result of the consistent higher frequency of movement close to the surface during civil twilight (Fig. 5), we suggest that tuna, may use polarized light cues in a similar way to birds to obtain true geographic reference information and calibrate one or more other compasses (magnetic or otherwise).

The rapid ascent that precedes the shallow portion of the dive at sunrise and the rapid descent that follows the shallow portion of the dive at sunset could provide tuna

with a direct vertical profile of one or more environmental variables. Alternatively, these rapid depth changes could reflect the close association of times that are best suited for obtaining one type of sensory information at depth (e.g., map information) and another type of sensory information at the surface (e.g., polarized light-based compass or compass calibration information). Both the pineal organ and ethmoid magnetoreceptors, which have been implicated in the magnetic map and compass behavior of other vertebrates, are relatively highly developed in tuna (Fig. 7 and see Wiltshcko and Wiltshcko 2005; Rivas 1953; Walker et al. 1984; Deutschlander et al. 1999). Yellowfin tuna (*T. albacares*) are capable of responding to magnetic stimuli (Walker 1984), but we have no information about the use of magnetic cues during compass orientation or true navigation. Nevertheless, considering the highly developed tuna magnetoreceptors and other examples of aquatic vertebrates using the magnetic field for navigation (Quinn 1980; Kalmijn 1982; Walker 1984; Phillips et al. 2002; Freake et al. 2006), we wonder whether the deeper elements of spike diving may be related to magnetic navigation.

The geomagnetic field in marine environments

The magnetic field in marine environments differs from that in terrestrial environments in three ways: (1) Ocean swells, tides, waves and currents produce localized changes in the magnetic field (Lilley et al. 2001, 2004); (2) normal fluctuations of the Earth's magnetic field, called the quiet daily variation, are present but can be amplified by the coastal effect (Lilley et al. 2001); (3) sea floor magnetic anomalies cause intensity variations of around 100 nT and are often predictably horizontally aligned, and their wide-scale gridded pattern has been suggested also as a potential aid to navigation (Walker et al. 2002).

Sea floor anomalies are spatial anomalies often associated with sea mounts, islands, continental shelf edge, and other bathymetric features, which are of great importance to juvenile SBT feeding ecology and movement behavior (Willis and Hobday 2007). Vertical movements may provide the tuna with useful information about the type and direction of these features. The other main sources of temporal and spatial magnetic anomalies unique to marine environments are briefly discussed with respect to their potential impact on spike diving behavior.

Ocean currents typically cause local magnetic variations of around 100 nT (Lilley et al. 2001); this may be important as the underlying total magnetic intensity gradient varies by 1–10 nT/km. North–south velocity profiles of ocean currents can be calculated directly from a vertical magnetometer profile in the ocean (Lilley et al. 2001; Fig. 12). In the ocean, the greatest water velocity is usually in the upper 500 m caused by wind-driven surface currents; consequent-

ly, this is the area with the highest level of local magnetic field variation. Water movements in the deep layer (>500 m in depth) are usually orders of magnitude slower and thus produce negligible magnetic fields locally (NASA, <http://www.oceanmotion.org>). Thus, a tuna could more accurately measure the main field at depths approaching 500 m without surface current noise, or a swift vertical profile to or from the depth where the gradient leveled off could provide information about the direction and strength of the surface current. To take advantage of this information, the tuna would need to be able to detect small changes in magnetic intensity of the order of 1–10 nT.

The normal daily variation of the Earth's magnetic field may be amplified up to ten times by the coastal effect (Hitchman et al. 2000). Figure 9a shows total magnetic field intensity recorded during November 2002 at a location near Perth in Western Australia (Gnangara) (Geoscience Australia). Interestingly, due to the pattern of daily variation, at ~30 min on the dark side of dawn and dusk when the deepest portion of the spike dive occurs, the magnetic intensity reaches its maximum values, which are nearly identical at these two times of day (Fig. 9b). This is a worldwide phenomenon; data from the northern hemisphere (Roquetes, northeastern Spain, Ebro Observatory) show

exactly the same effect (Fig. 9c). Therefore, obtaining magnetic measurements at these two times of day could provide tuna with independent map readings that minimize the effect of the regular daily variation, while a comparison obtained at these two times of day could be used to filter out unreliable map measurements such as those obtained during periods of magnetic storm activity.

In addition to (or instead of) a magnetic map, tuna may rely on map information from one or more other sensory modalities. For example, an olfactory map is used by pigeons (Wallraff 1996), sharks detect both electric and magnetic fields (Kalmijn 1982), and salmon fry have a celestial and magnetic compass (Quinn 1980). Tuna may also use an acoustic map or make navigational decisions based on temperature stratification and associated gradients at depth. The most definitive temperature signal with depth is usually the thermocline, which is a sharp change in temperature between the surface layer (also called the mixed layer) and deeper water. The thermocline depth varies spatially and temporally and is usually between 50 and 500 m in depth (Kara et al. 2000). The vertical temperature profile, thermocline, and other ocean features vary predictably with latitude and longitude and, therefore, provide a potential source of geographic (map) information

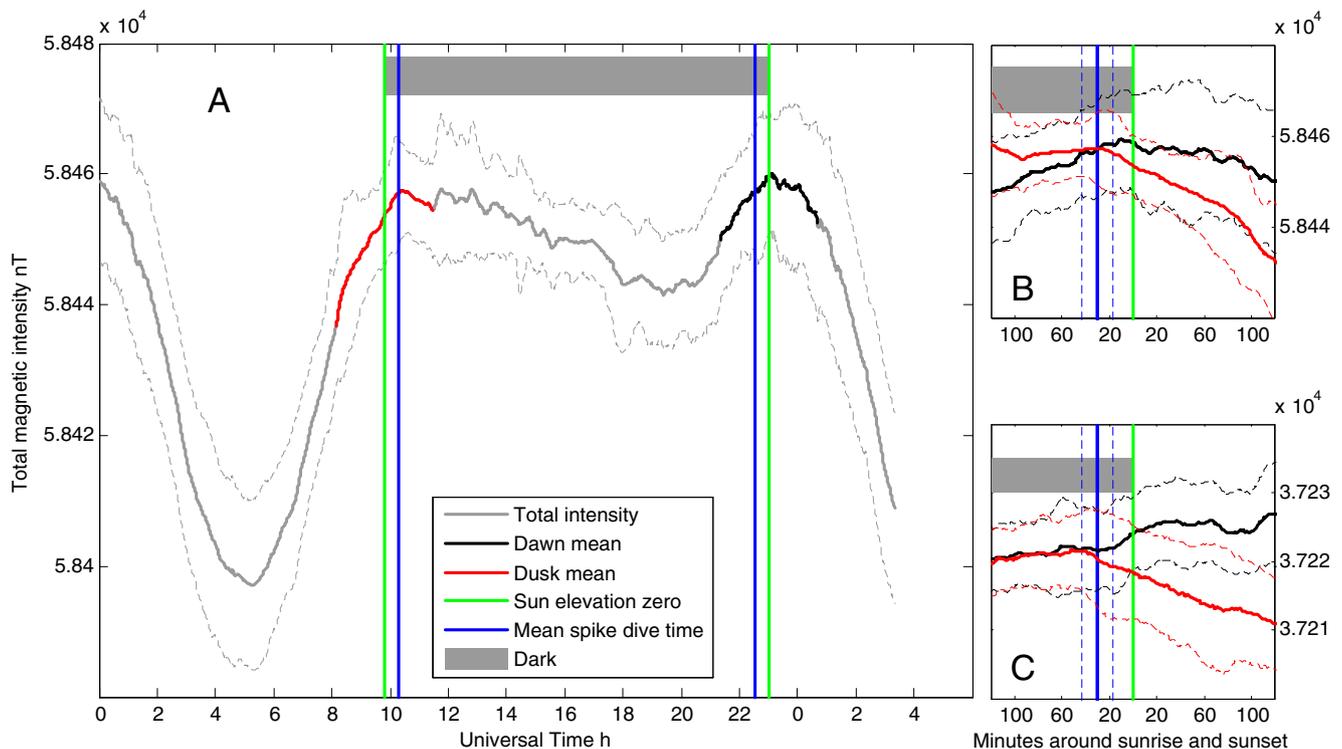


Fig. 9 Total magnetic field intensity throughout the day showing quiet daily variation. **a** Mean and one standard deviation of total intensity for all days of November 2002 measured near Perth in Western Australia. Dawn and dusk are indicated. **b** Same data as **a** with the dusk values reversed and overlaid over dawn. Mean spike

dive time is shown with one standard deviation for all fish in study. **c** A similar plot for data collected from Ebro Observatory in Spain. It is clear that the period just before dawn combined with the period just after dusk is globally of unique value in consistent measurement of magnetic intensity within a 24-h period

used for navigation that could be measured during the rapid ascent/descent portion of the spike dives.

Alternative explanations for spike diving

If spike diving is not related to navigation, it may have some other purpose, such as hunting. A closely related species of tuna (*Thunnus obesus*) has been observed following the vertical migration of the DSL (Josse et al. 1998); in this case there was no spike dive. The timing and profile of DSL migrations, as revealed by sonar, are similar to the gradual ascent/descent phase of the spike dive (Onsrud et al. 2004; Fig. 2). The gradual ascent and descent on the dark side of dawn and dusk may be evidence that tuna regularly follow the migration of the DSL but suspend this behavior to initiate spike dives at precise times of day. Thus, the sudden move toward or away from the DSL, from or to the surface, at precise times on the dark side of sunrise and sunset remains unexplained by this hunting hypothesis, especially since the tuna regularly move deeper before and after the spike, in daylight and darkness, so the deepest point of the spike appears not to represent a thermal or visual limit to the tuna following the DSL.

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