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Vertical niche overlap by two ocean giants with similar diets: Ocean sunfish and leatherback turtles

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ABSTRACT

We used satellite tags to record the patterns of depth utilisation for four ocean sunfish (*Mola mola*) and two leatherback turtles (*Dermochelys coriacea*) moving in broadly the same area off South Africa. Individuals were tracked for between 2 and 8 months and dive data relayed via satellite. For all the sunfish and one of the turtles, we received binned data on depth distribution, while for the second turtle we received individual dive profiles along with the proportion of time spent diving. Leatherback turtles dived almost exclusively within the upper 200 m, spending only 0.6 and 0.2% of their time >200 m. There were times when sunfish likewise occupied these relatively shallow depths. However, there were also protracted periods when sunfish spent the majority of their time much deeper, with one individual remaining around 500 m for many hours at a time. These results suggest that sunfish sometimes exploit deeply distributed prey which is beyond the foraging range of leatherback turtles. We conclude that while both species are believed to feed predominantly on gelatinous zooplankton, the fact that sunfish do not need to come to the surface to breathe means that they can occupy an expanded vertical niche compared to the leatherback turtle.

1. Introduction

There are many examples of convergent evolution by taxonomically dissimilar species towards foraging on similar prey. However, while diets may be similar across taxa, some aspects of behaviour may still be constrained by phylogeny. For example hirundine birds (e.g. swifts and swallows) and many insectivorous bats feed on flying insects. However the daily patterns of activity by these bird and mammal aerial insectivores are constrained by their flying ability and prey perception abilities. Hirundines feed visually and forage during daylight, using their fast flying speed to avoid aerial predators such as sparrow hawks. In contrast, insectivorous bats flying during the daylight are highly susceptible to aerial predators and this is thought to constrain their pattern of activity to darkness where they use echolocation to find their prey (Speakman et al., 2000; Duverge et al., 2002). In marine systems an analogy to aerial insectivory is predation on zooplankton, i.e. animals feeding on highly abundant but relatively tiny prey. Planktivory is seen in a number of taxonomically unrelated marine species and, interestingly, in many cases ocean planktivores are also giants: for example baleen whales feed on a variety of plankton including euphausiids (krill), while basking sharks also target crustacean zooplankton such as calanoid copepods and euphausiids. Two ocean giants, the ocean sunfish (*Mola mola*) and the leatherback turtle (*Dermochelys coriacea*) are both thought to feed heavily on gelatinous zooplankton such as scyphozoan jellyfish, salps and pyrosomes (Thys, 1994; Bjorndal, 1997), despite the relatively low nutritional energy content of these groups (Doyle et al., 2007). Leatherback turtles are the largest extant species of sea turtle with adults typically attaining a size of several hundred kilos (Georges and Fossette, 2006). Ocean sunfish are the largest bony fish with individuals attaining a size of up to 1500 kg (Freedman and Noakes, 2002). While they share attributes of size and diet, sunfish and leatherbacks are fundamentally different in that sunfish extract oxygen from the water with their gills, while leatherbacks have to come to the surface to breathe. This physiological dichotomy might be expected to lead to a relative constraint on the range of vertical depths that can be successfully exploited by these two species.

Sometimes gelatinous zooplankton are found near the surface (Houghton et al., 2006). In other cases gelatinous zooplankton undertake diel vertical movements, being closer to the surface at night and deeper during the day (Andersen et al., 1992, 1997). We would expect that similarities in depth use by sunfish and leatherbacks will vary across these different scenarios, with both species being expected to exploit shallow prey, but only sunfish exploiting deeper prey. However there is wide disparity in what is known about these two species. There have

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been many previous studies of the diving behaviour of leatherback turtles in a range of ocean basins (e.g. Eckert et al., 1989; Hays et al., 2006; Sale et al., 2006). For sunfish, published accounts of depth distribution have so far been limited to short term data-sets (a few hours) collected by direct acoustic tracking (Cartamil and Lowe, 2004) or short term deployments of data-loggers (Watanabe and Sato, 2008). Leatherback turtles show a range of dive behaviours, very occasionally diving to >1000 m, although most of their dives are restricted to the upper 200 m (Bradshaw et al., 2007a; Houghton et al., 2008). Leatherback turtles have also been shown to display a range of diel dive patterns (e.g. Sale et al., 2006). Sometimes (e.g. at high latitude in the North Atlantic), leatherbacks show a day and night near-surface distribution in the upper 50 m, presumably reflecting continuous near-surface distribution of their prey (Hays et al., 2006). However, nearer the equator in the Atlantic and during the breeding period when they are near their tropical nesting beaches, leatherback turtles display a diel pattern in diving, with lots of shallow near-surface diving at night and then infrequent diving during the day (Eckert et al., 1989; Hays et al., 2006; Myers and Hays, 2006). This diel dive pattern is widely thought to reflect turtles feeding at night on zooplankton that are exhibiting normal diel vertical migration with the suggestion that during the daytime in these cases prey are too deep for successful foraging by turtles. We might expect that in these circumstances prey that is deeply distributed in the daytime might still be available to sunfish.

Understanding how depth use varies spatially and temporally in sunfish and leatherbacks may also have applied benefits. Both species are suspected to suffer high mortality in fisheries targeting more commercial valuable species such a swordfish, sharks, mackerel and tuna (e.g. Silvani et al., 1999; Lewison et al., 2004; Petersen, 2005; Petersen and McDonell, 2007). Information about sunfish and leatherback turtle depth use might potentially be used to design measures to reduce fishery bycatch. Additionally, as reports of harmful gelatinous zooplankton blooms increase (e.g. Doyle et al., 2008; Purcell et al., 2007), knowledge of how and which predators are capable of effectively foraging on and reducing such rising pest populations is becoming of greater importance worldwide.

Given these fundamental and applied interests, we compare the patterns of depth utilisation by ocean sunfish and leatherback turtles occupying broadly the same area. We re-analyse previous data collected for leatherback turtles off South Africa (Sale et al., 2006) and compare these with new data collected from ocean sunfish equipped with depth recording tags for many months.

2. Materials and methods

In 2004 and 2006 four ocean sunfish were equipped with Wildlife Computer PAT 3 and PAT 4 Pop-off Archival Tags (PATs) respectively. Surface basking fish were located by zodiac and a team of four to six snorkelers were deployed to surround and stabilize the fish while tags were manually attached behind the dorsal fins. Tags were secured externally using a large nylon dart attached to the tag using 300 lb test monofilament line and stainless steel crimps. Each PAT was programmed to pop-off after 6 months, upon which time depth data were relayed via Argos. However, in some cases PATs detached prematurely as indicated by time spent continuously at the surface and repeated Argos locations until the batteries exhausted.

Geolocations of the sunfish were estimated from light level and sea surface temperature (SST) data recorded by the PATs, using the methods described by Teo et al. (2004). Longitude was estimated by calculating the time of local noon from the light level data using WC-GPE (v1.02.0005, Wildlife Computers). Sea surface temperature data from the tags were then combined with corresponding light level longitude estimates to obtain daily latitude estimates. For a given day, the latitude at which the tag-recorded SSTs best matched the corresponding remotely sensed SSTs, along the light level longitude estimate, was considered the latitude estimate for the day. The SST matching process was constrained to the area that the fish could have realistically moved for each day (120 nm day^{-1}) and where the bathymetry of the area was deeper than the maximum diving depth of the sunfish for the day. We also improved the geolocation algorithm with the addition of the capacity to switch to cloud-free, microwave-based, remotely sensed SST data (TMI/AMSRE, ftp://ftp.discover-earth.org/sst/) during periods with high cloud cover, and an improvement to the algorithm used to ensure the movement path did not cross land. Depending on area and species, PATs have root mean square errors of approximately 0.55–1.30° and 1.16–1.89° for longitude and latitude estimates, respectively (Teo et al., 2004).

Depth was measured every 60 s by these PATs and then these data were binned into depth intervals. For three of the tags, the data were binned over 12 h intervals, but in one case the interval was 6 h (Table 1). Times are given in GMT which was local time minus 2 h. The depth intervals were: <5 m, 5–10 m, 10–20 m, 20–50 m, 50–100 m, 100–150 m, 150–200 m, 200–300 m, 300–400 m, 400–650, 650–1000 m. In addition, PATs relayed information on the minimum and maximum depth obtained during each binning interval, i.e. either 6 h or 12 h. Due to limited bandwidth of the Argos system, not all binned depth data actually collected by the PATs were received.

The leatherback turtle data we consider here have previously been described by Sale et al. (2006). In short, satellite tags were attached to female turtles that had just completed nesting on beaches in Kwa-Zulu Natal, South Africa. Two types of satellite transmitter were attached. An ST-6 transmitter (Telonics Inc., Mesa, AZ, USA) provided depth data for 4-h intervals that was compressed into pre-selected depth bins. In essence these data were similar to those provided by the PATs attached to sunfish, with the depth intervals for the turtle data being: 0–10 m, 10–30 m, 30–70 m, 70–120 m, 120–200 m, 200–300 m, 300–500 m, 500–1400 m. Secondly a Satellite Relayed Data Logger (SRDL) (Sea Mammal Research Unit, University of St. Andrews, UK) provided actual dive profiles including the maximum depth attained on individual dives as well as summary information detailing the proportion of time spend diving to >10 m.

To allow direct comparison with the sunfish data, we converted the ST-6 data into the depth ranges 0–10 m, 10–50 m, 50–100 m, 100–200 m and >200 m, by linear interpolation through the original bins. We converted the SRDL data into these same bins by using the dive profile information relayed for individual dives along with the summary information that detailed the proportion of time spent

Table 1
Details of the tag deployments

Species/id	Size (cm) (weight)	Unit attached	Binning interval for depth data	Number of intervals/dive profiles obtained	Date of first depth data	Date of final depth data
Sunfish/415	160 (213 kg)	PAT 3	12 h	34	26/1/04	12/7/04
Sunfish/418	160 (213 kg)	PAT 3	12 h	154	27/1/04	22/8/04
Sunfish/204	108 (67 kg)	PAT 4	6 h	132	12/3/06	24/8/06
Sunfish/205	110 (70 kg)	PAT 4	12 h	46	11/3/06	14/5/06
Leatherback/T1	168 (441 kg)	ST-6	4 h	805	1/2/99	7/10/99
Leatherback/18262	170 (455 kg)	SRDL	n/a	1267	29/1/03	15/7/03

Size for leatherback turtles refers to curve carapace length and for sunfish refer to total length.
Weights are estimated using previously published length weight relationships for ocean sunfish (Watanabe and Sato, 2008) and leatherback turtles (Georges and Fossette, 2006).

diving. Again the limited bandwidth of the Argos system meant that not all the depth data collected by either the ST-6 or SRDLs were actually received. Locations for both type of tag attached to turtles were calculated by Argos and filtered as described by Sale et al. (2006).

We used data from a further seven leatherback turtles (where we did not have depth data) in comparative analysis of speed of travel. These leatherbacks were again equipped with satellite tags while nesting in Kwa-Zulu Natal and their tracks are described in full in Lambardi et al. (2008) Given the inaccuracies of light-based geolocation estimates (Bradshaw et al., 2007b; Teo et al., 2004), to calculate the speed of travel for the ocean sunfish we simply used the time and distance between the tagging and pop-off locations. To provide a

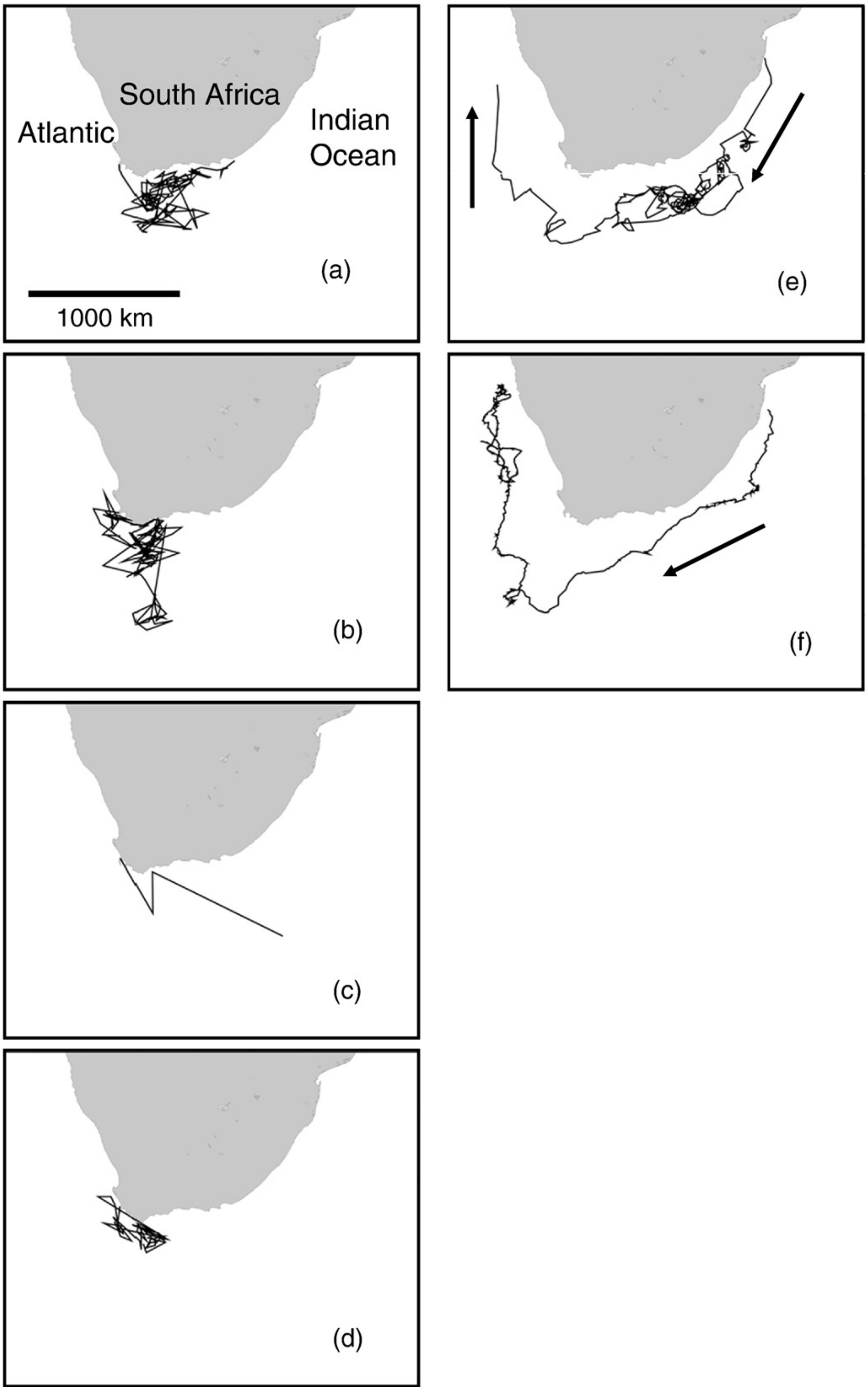

Fig. 1. Maps showing the tracks of (a–d) four ocean sunfish and (e–f) two leatherback turtles. Arrows show the overall direction of travel for the leatherbacks.

comparable speed estimate for the leatherback turtles, despite the continuous Argos positions we received, we simply used the tagging point and final location, assumed turtles could not cross land and used a maximum of two locations along the route to take account of any gross course changes.

3. Results

Depth data spanning several months were obtained for four ocean sunfish and two leatherback turtles (Table 1). The animals moved broadly within the same area off South Africa. Both leatherbacks

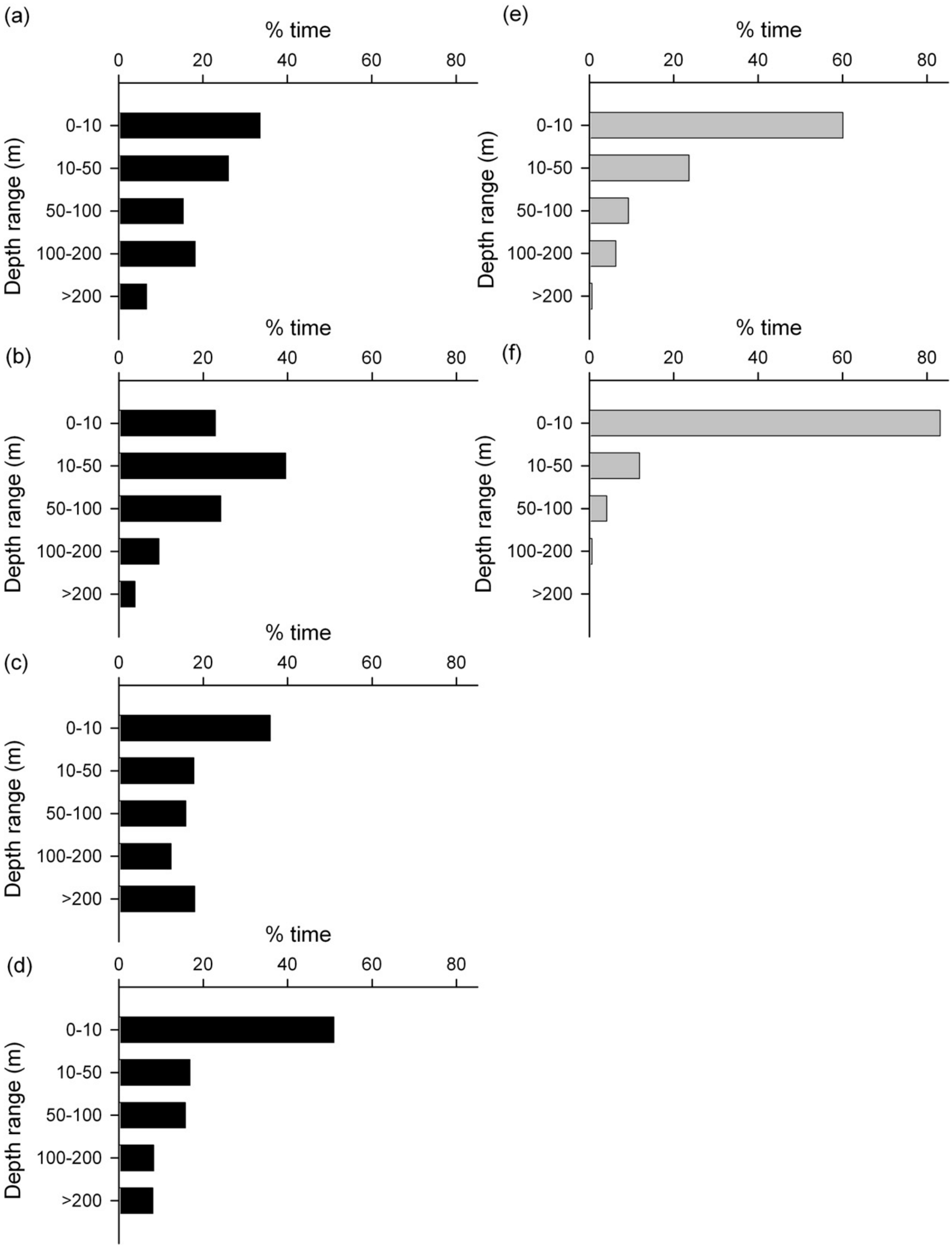

Fig. 2. Overall patterns of depth utilisation for all the individuals, (a–d) shows data for the sunfish 415, 418, 204 and 205 respectively. (e and f) show data for turtles T1 and 16282 respectively.

travelled down the SE coast of South Africa and then around Cape of Good Hope and into the South Atlantic. The sunfish remained for months in the same general area off the southern coast of South Africa (Fig. 1). The distances between tagging location and pop-off location for the four sunfish were 772 km, 333 km, 1174 km and 270 km equating to minimum speeds of travel of 4.6, 1.6, 7.1 and 4.2 km day^{-1}. By contrast the minimum distances distance between the start and end points of the two leatherback tracks were 3550 km and 3450 km, equating to speeds of travel of 15.9 and 20.5 km day^{-1}. For a further seven tracked leatherbacks, speeds of travel were 36.2, 11.0, 20.3, 28.3, 6.3, 10.4 and

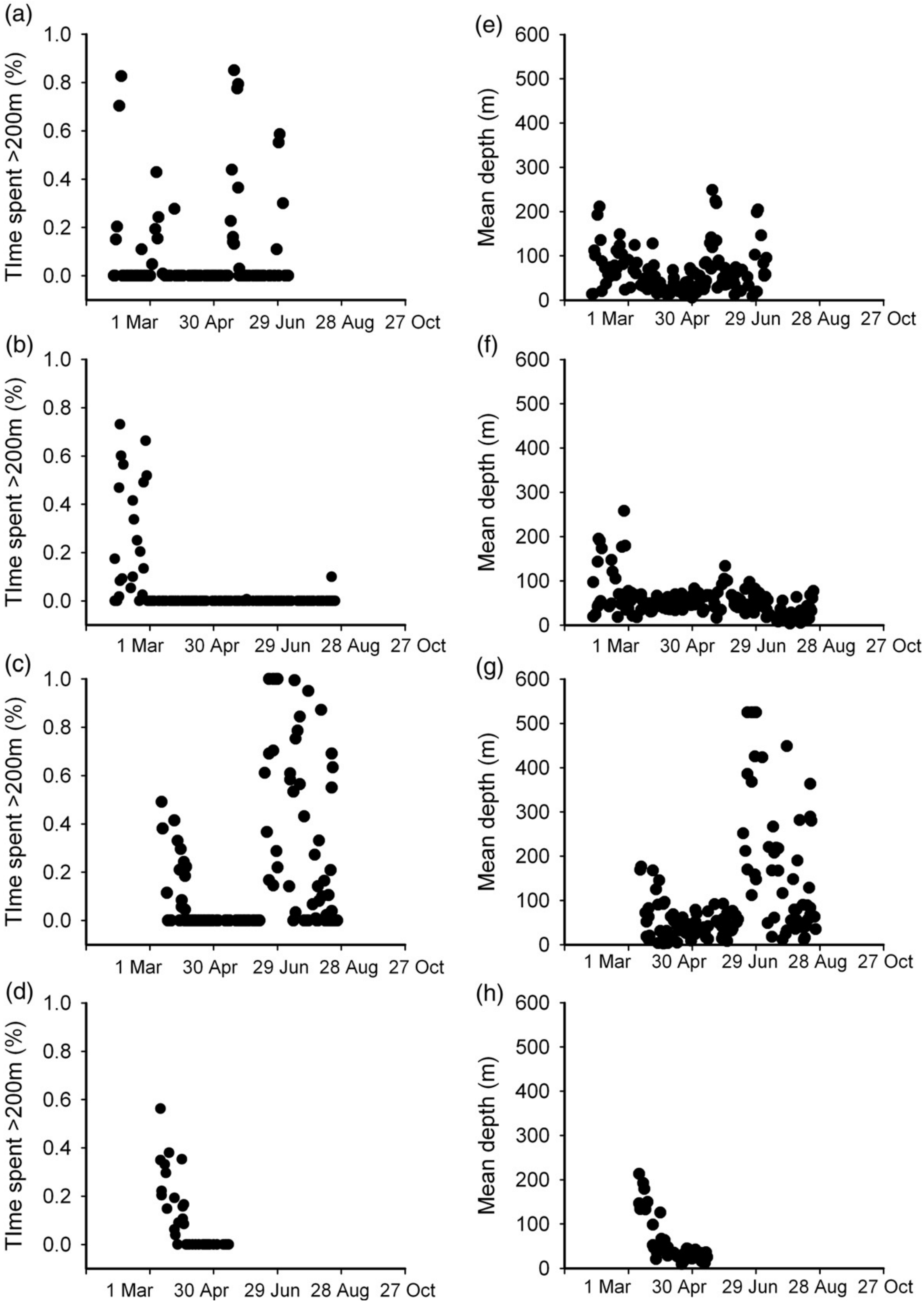

Fig. 3. For sunfish 415, 418, 204 and 205 the percentage of time spent >200 m at different times of year (a–d) and the mean depth (e–h). Each point represents a value of the time windows (6 h or 12 h) over which the depth data were binned (see Table 1 for details).

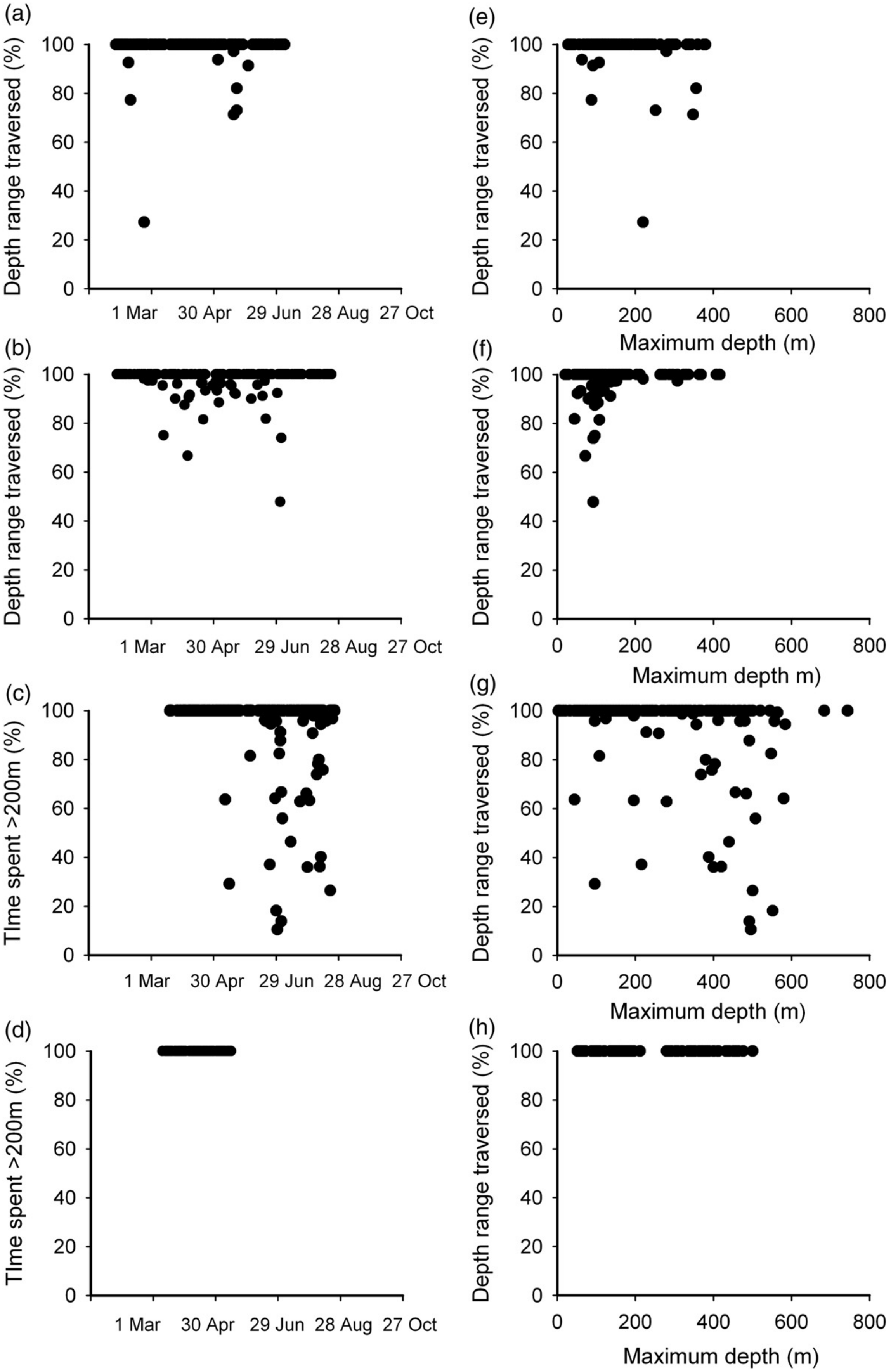

Fig. 4. For sunfish 415, 418, 204 and 205 the "% depth range traversed" (see text for details) versus the date (a–d) and the "% depth range traversed" versus the maximum depth. Each point represents a value of the time windows (6 h or 12 h) over which the depth data were binned (see Table 1 for details).

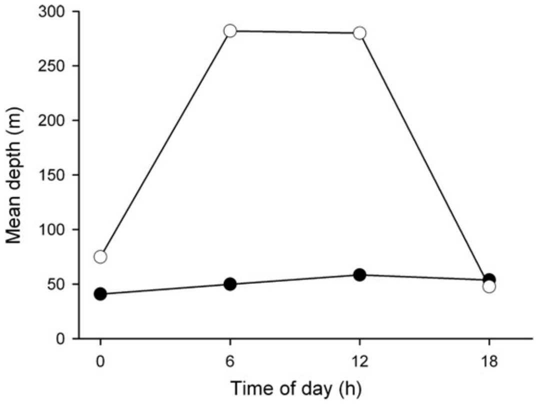

Fig. 5. For sunfish 204 the mean depth at different times of day. Open circles show data recorded between 12 March and 12 June, closed symbols show data recorded between 17 June and 24 August. Times are listed as GMT and refer to the start of each 6-h integration period for depth data. In mid-April, time of sunrise and sunset (in GMT) at the location of sunfish were 05:10 and 16:15 respectively.

76.5 km day^{-1}. On average leatherbacks traveled faster than ocean sunfish (means 25.0 km day^{-1} and 4.1 km day^{-1} respectively, $T_8 = 2.9$, $p = 0.02$).

The overall patterns of depth utilisation showed that both species spent long periods near the surface (Fig. 2). However, there were also very clear differences between the species in their depth distribution. For example, the percentages of time spent >200 m by the four sunfish were 6.7%, 3.9%, 18.0% and 8.1% respectively which was, on average, 92 times that spent at this depth range by the two leatherbacks (0.6% and 0.2%). Overall the mean depth of each of the four sunfish across individual 6 or 12 hour integration windows for the depth data (85.4 m, 55.2 m, 104.4 m and 59.2 m respectively) was significantly greater than the mean depth of both the leatherback turtles (26.3 m and 12.2 m respectively) (One-way ANOVA $F_5 = 95.8$, $P < 0.001$; paired t-tests, $t_{>33} > 4.2$, $P < 0.001$ in all pair-wise comparisons).

We examined the depth of individual dives made by turtle 18262. This was the only turtle for which we had a record of individual dive depths. Throughout the period of tracking the vast majority (99.5%) of dives were shallower than 200 m. Of 1267 dive profiles recorded there were only seven deeper than 200 m and these occurred irregularly over time.

To consider how sunfish used deeper depths, we examined the proportion of time spent >200 m in each integration period (i.e. 6 or 12 h). This analysis revealed considerable temporal patterns in their use of deep water. While all four fish had times of the year when they spent long periods >200 m, these periods were not consistent across individuals (Fig. 3). Deep residence occurred mainly in February and May for sunfish 415, during February for sunfish 418 and during March for sunfish 205. Sunfish 204 spent long periods >200 m in both March and July–August. Between 21 June and 5 July, 14 6-hour records of depth distribution were received for this fish. Six of these 14 6-hour records showed the fish to be continually >200 m with mean depths between 423 and 525 m. This fish also had the deepest mean depth of any of the four sunfish.

For the four sunfish, we considered the extent of their vertical movements over short time scales by calculating the % of their maximum depth that they traversed within each integration period (i.e. 6 or 12 h), i.e.:

$$\%\,\text{depth range traversed} = (\text{maximum depth} - \text{minimum depth}) / \text{maximum depth}$$

The % of the depth range traversed was generally very high (<90%) for all the sunfish and was not related to the maximum depth (Fig. 4). In essence this result means that even though sunfish had a range of preferred depths that changed over time, over short time-scales (a few hours) they were also generally moving up and down the water column and coming close to the surface.

To examine patterns of diel vertical migration (DVM) by sunfish we focused on sunfish 204 since this was the only individual where the time window for depth bins was 6 h. This individual showed a marked temporal variation in dive behaviour with more time spent at greater depths after 12 June. We therefore examined the extent of DVM both before and after this date. For each 6 hour period of the 24-h cycle, we calculated the mean depth. Between 12 March and 12 June when this sunfish occupied shallow depths, there was no evidence of DVM with similar depths occupied throughout the day and night. However between 17 June and 24 August there was a clear pattern of DVM with mean daytime depths of around 280 m and mean night time depths of around 50 to 75 m (Fig. 5). Although the 12 h binning intervals for depth data made it difficult to assess the extent of DVM for the other

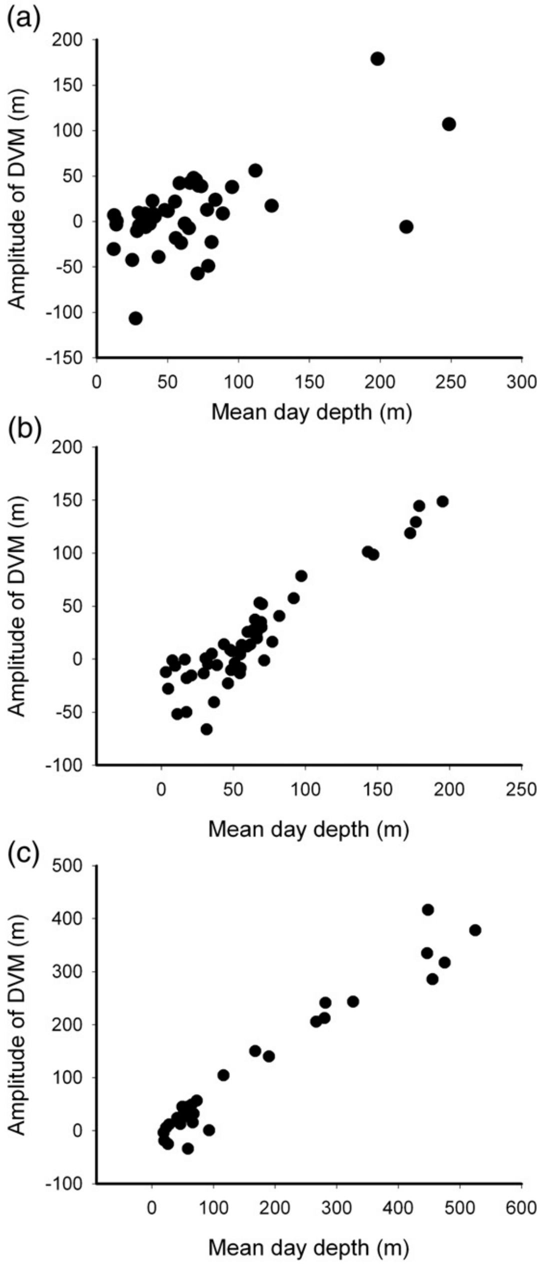

Fig. 6. The amplitude of DVM (the difference between the mean daytime and the mean night-time depths) versus the mean daytime depths. Each point represents a successive time intervals when there were depth data for a 6 or 12 h period in both the day and night. (a) sunfish 415 ($F_{1,40} = 19.7$, $P < 0.0001$, $r^2 = 0.33$); (b) sunfish 418 ($F_{1,48} = 304$, $P < 0.0001$, $r^2 = 0.86$); (c) sunfish 204 ($F_{1,27} = 510$, $P < 0.0001$, $r^2 = 0.95$).

three sunfish, for sunfish 415 and 418 the two binning intervals were largely during the day (04:00–16:00) and night (16:00–04:00) respectively. Sunfish 418 also showed a period of deep water occupation at the start of the tracking period. During this time (27 January to 27 February) there was a large and significantly different mean depth occupied during the day (mean 159.2 m) and night (mean 45.9 m) ($t_{13}=6.7$, $P<0.001$).

To examine more closely this suggestion that DVM was more pronounced at times when the sunfish were deeper, we looked at all three data sets that had some element of diel timing to the depth data (sunfish 415, 418 and 204). Where there were successive time intervals when there were depth data for a 6 or 12 h period in both the day and night, we calculated the difference between the mean daytime and mean night-time depths, i.e. the amplitude of DVM. We then plotted this day-night difference against the daytime depth. For all three fish, there were highly significant relationships between the mean daytime depth and the amplitude of DVM (Fig. 6). So while Fig. 4 shows active vertical movement within individual 6 or 12 h data integration windows, Fig. 6 shows systematic differences in day versus night vertical distribution.

4. Discussion

The advent of small reliable data-loggers and transmitters has allowed a huge number of studies to record both horizontal and vertical movements of a whole gamut of marine species (e.g. Hays, 2008; Hindell, 2008). To date most studies have tended to be autecological: focussing on single species. However, a central focus now is to try and compare results across taxa and identify commonalities and differences between species. Such synecological studies may shed light on fundamental foraging rules that apply across taxa and how physiology and anatomy constrain behaviour (e.g. Sims et al., 2008). Set against this backdrop, our comparison of the depths occupied by ocean sunfish and leatherback turtles reveals how physiology may constrain behaviour.

While we focussed on the vertical dimension, geolocation of animals showed that they were tracked moving in broadly the same area. We have shown previously how the horizontal movements of leatherback turtles in this area are tightly coupled to mesoscale features: in short leatherbacks are advected by the southerly flowing Aghulas current when they leave their nesting beaches and may then be entrained for long periods in mesoscale eddies (Luschi et al., 2006; Lambardi et al., 2008). The sunfish tracks were based on light and temperature based geolocation, which typically has relative large errors with individual location estimates often being >100 km from the true position (Teo et al., 2004). Nevertheless the tracks clearly show that the fish showed prolonged residence off South Africa. For leatherback turtles tracked in the North Atlantic and Pacific, very extensive pan-oceanic movements have been identified (Hays et al., 2006; Shillinger et al., 2008). Similarly for some fish including bluefin tuna in the North Atlantic (Block et al., 2005), great white sharks equipped with satellite tags off South Africa (Bonfil et al., 2005); and tiger sharks equipped with satellite tags in Australia (Heithaus et al., 2007), pan-oceanic movements have been identified. The long distance movements in these diverse groups may be associated with the search for widely distributed prey that may be far from breeding areas. The fact that ocean sunfish remained broadly off South Africa, implies that this area likely provides a suitable year-round habitat for these species. However, leatherback turtles, despite their similar diets to sunfish, tended to travel more extensively. This difference might be related to the more restricted vertical foraging niche for leatherbacks as discussed below.

The key drivers dictating a suitable habitat for these species are presumably a suitable water temperature and prey availability. Sea surface temperature off South Africa in the area occupied by leatherbacks remains >15 °C year-round (Sale et al., 2006), which is thought to be the lower thermal limit for prolonged occupation by leatherbacks (McMahon and Hays, 2006). The thermal climate envelope for sunfish has not yet been defined, but may be revealed through continued deployments of satellite tags onto fish in other areas of the world that span the range for the species.

Both sunfish and leatherback turtles are thought to feed predominantly on gelatinous zooplankton. However, it should be noted that direct observations of feeding in both groups are rare and hence it is possible that both species may have more catholic diets than presumed. Jellyfish are certainly very abundant off South Africa and this might explain the co-occurrence of leatherback turtles and ocean sunfish in this area. Indeed in the Benguela system off South Africa it has recently been reported that jellyfish abundance now exceeds the abundance of finfish (Lynam et al., 2006). This switch from a fish to jellyfish dominated ecosystem is thought to be a least partly due to overfishing (Pauly and Maclean, 2003), with the implication that jellyfish biomass may be on an upward trend in some parts of the world (Purcell et al., 2007). If this trend does occur widely, we can broadly predict an improved foraging environment for ocean sunfish and leatherback turtles: they may be inadvertent benefactors from overfishing.

While the vertical distribution of gelatinous zooplankton is fairly poorly defined, it is known that they may occur at a range of depths (Andersen et al., 1992, 1997; Houghton et al., 2006). Our results suggest that sometimes gelatinous zooplankton may be found maximally near the surface, when they may be targeted by both sunfish and leatherbacks, but at other times the deep occurrence of sunfish implies a much deeper distribution of gelatinous zooplankton.

It might be argued that the difference in depth distribution between sunfish and leatherbacks is an inevitable consequence of the need for the turtle to ascend to the surface and breathe. This requirement means that even if both animals are targeting the same depth zones, then because of time spent in transit as well as time spent at the surface, the amount of time spent at the targeted foraging depth will inevitably be much lower in the turtle. However this explanation alone cannot explain the different depth distributions because when the analysis of leatherbacks data considered only the maximum depth of each dive it was clear that dives are still shallower than the depths occupied by sunfish. We are aware that we have only one long record for a turtle off South Africa where individual dive profiles were recorded. However, we have collected a much larger sample size in the North Atlantic. For example for nine leatherbacks each tracked from a minimum of 8 months in the North Atlantic, we obtained a total of 17,618 dive profiles of which only 279 (1.6%) were deeper than 200 m (Bradshaw et al., 2007a). This dataset reiterates the patterns seen off South Africa with only very rare dives >200 m by leatherbacks. In short it is clear that while leatherbacks rarely target depths >200 m, these depths may be targeted by sunfish for protracted periods.

Freed from the constraint to return to the surface to breathe, sunfish can spend extensive periods of time much deeper than leatherback turtles. It may also be that deep dives are energetically more costly for turtles than they are for sunfish or that sunfish are taking advantaging of deeper prey species that are simply easier to catch or more desirable, allowing them to reap caloric benefits that may outweigh additional dive costs. However, it was noteworthy that over the 6 or 12 h integration interval for depth data, the sunfish generally travelled between their maximum depth and the surface. The implication is that there is active vertical movement by sunfish even when they are targeting a specific depth. It has been suggested that a range of marine species may engage in vertical movements whereby they generally stay at the same depth with occasional large steps to different depths (Sims et al., 2008). This pattern of vertical movement may be an optimal search strategy for patchily distributed prey. It may be that sunfish are following this same pattern. Alternatively there have been other suggestions for why fish might come to the surface from deep water including the need to re-warm or to re-oxygenate after being in sub-oxic depths for prolonged periods (e.g. Holland et al., 1992; Dagorn et al., 2000). However, off South Africa, deep water to 500 m is fairly well oxygenated (5–6 ml O_2/l) (Boyer et al., 2006), suggesting that re-oxygenation is probably not the ultimate reason for surfacing by sunfish in this area.

There may also be seasonal changes in the extent of DVM in line with seasonal changes in the length of the day and night with zooplankton spending less time near the surface during the summer (Hays, 1995). Furthermore, zooplankton may respond to the ambient light level changes from day to day such that their depth of daytime residence is deeper when surface light conditions are brighter (Buskey et al., 1989). These factors might be expected to drive deeper foraging by sunfish during the summer. However, there were differences between individual sunfish in when they foraged deeply, suggesting that consistent seasonal changes in the depth of their prey did not fully explain when the fish spent longer at greater depths. It is known that the oceanographic conditions off South Africa are characterised by many intense mesoscale features (Lambardi et al., 2008) and this in turn would be expected to drive marked spatial patchiness in plankton populations and indeed patchy distribution of gelatinous zooplankton has been revealed by acoustic surveys and net tows (Brierley et al., 2001; Lynam et al., 2006). Therefore a more parsimonious explanation for the different seasonal occurrence of deep water occupation by the sunfish is their individual responses to patchily distributed plankton prey which is sometimes distributed deeply but sometimes at shallower depths.

The one sunfish for which we had a short integration window for the depth data, clearly demonstrated that there was little diel vertical migration (DVM) when the overall depth distribution was shallow, but that there was marked DVM when the depth distribution was deeper. DVM had been very widely reported in a range of zooplankton and it has been widely shown how the diel diving behaviour of a range of predators (including some fish, marine mammals, penguins and turtles) may change both spatially and temporally, presumably in response to different vertical movements of their prey (for review see Hays, 2003). It is clear that likewise ocean sunfish show pronounced diel vertical movements, albeit at different times and locations, presumably tracking the vertical movements of their prey.

In conclusion, we have shown how for ocean sunfish and leatherback turtles, which have broadly the same diet of gelatinous zooplankton, there are times when there is vertical niche portioning with sunfish being able to target deeper prey. While leatherback turtles are only able to target prey that are relatively shallow (<200 m), ocean sunfish have a far more extensive capacity for foraging on target prey throughout the water column to depths greater than 500 m.

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