



High dive efficiency in shallow water

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Abstract

Dive studies across mammals, birds, reptiles and fish often focus on deep dives, and shallow water diving has tended to be overlooked. For air-breathers, foraging in shallow water poses challenges since the lungs generate buoyancy, and shallow divers must trade off the extent of inhalation against the negative buoyancy needed to avoid floating to the surface. Using high-resolution depth loggers, we addressed this knowledge gap around the ecology of shallow water diving at a foraging site for hawksbill turtles (*Eretmochelys imbricata*) where depth was typically < 3 m. Contrary to predictions, dive durations were long, particularly at night (mean dive duration per turtle: 17–61 min, $n = 12$ turtles, $n = 2576$ nocturnal dives), despite warm water temperatures (24–37 °C). Dive efficiency (% time submerged) for hawksbills was 98%, the highest recorded for any air-breathing marine vertebrate including penguins (60–78%), seals (51–91%), cetaceans (68–87%), and other sea turtle species (68–95%). Hawksbills usually dive for much longer (42–286% increase) than green and loggerhead turtles when depth and temperature are accounted for. Hawksbill turtles likely forage in very shallow water to reduce predation risk from sharks: of 423 hawksbills captured by hand, none had any evidence of shark attack, although large sharks were present in nearby deeper water. Our results challenge the prediction that shallow water dives by air-breathers will usually be short and open the way for comparative studies of the ecology of shallow water diving in a range of other taxa. Our work emphasises the likely importance of predation risk in shaping patterns of habitat utilisation.

Keywords Biologging · Cheloniid · Depth use · Dive depth · Marine turtle · Indian Ocean

Introduction

For marine species, patterns of depth utilisation play a central role in their ecology and influence foraging success, risk of predation and energy balance (e.g. Sims et al. 2005; Heithaus et al. 2007; Teo et al. 2007). For air-breathing animals that forage underwater, maximising the time spent at foraging depth maximises the energetic return per unit foraging effort (Weise et al. 2010). Minimising time spent at the surface additionally reduces the risk of being predated upon for many species (Heithaus and Frid 2003). While there is a huge amount of work on patterns of depth use across a broad

range of taxa including fish, seabirds (e.g. penguins), marine mammals (e.g. seals and whales) and reptiles (e.g. turtles and sea snakes), these studies tend to focus on patterns of deeper diving to 10s or 100s of metres (e.g. Williams and Ponganis 2021), and the ecology of shallow water diving has tended to be neglected (but see Sims et al. 2005). For the deepest divers, such as sperm whales (*Physeter macrocephalus*) and elephant seals (*Mirounga* spp), adaptations to deep diving (100s of metres) include the primary oxygen stores being in the blood (haemoglobin) and muscle (myoglobin), with animals exhaling prior to submergence (Fahlman et al. 2017). Conversely, for shallower divers routinely descending to only a few 10s of metres, such as sea otters (*Enhydra lutris*), dolphins and cheloniid (hard-shelled) turtles, the lungs may be an important oxygen store for dives (Lutcavage and Lutz 1997).

Many breath-hold divers have been shown to adjust inspired air volume according to the depth of the coming dive in order to regulate the buoyancy created by air in the lungs (penguins: Sato et al. 2002; sea turtles: Hays et al. 2004; freshwater turtles: Peterson and Gomez 2008; sea

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lions: McDonald and Ponganis 2012). As gas compresses with depth due to increasing pressure, such divers are able to dive with a greater inspired lung volume when travelling to greater depths while still achieving neutral or negative buoyancy at the target depth. As a result, both the oxygen store and the duration of dives are expected to increase with depth for those divers using the lungs as an important portion of their oxygen store. In line with predictions, dive duration has been shown to increase with depth in multiple taxa (e.g. sea turtles: Hochscheid et al. 1999; dugongs *Dugong dugong*: Churchward 2001; penguins: Wilson 2003), with the strongest effect seen in sea turtles (Hays et al. 2004) which are the most lung-dependent of these divers (lung oxygen store as a percentage of total bodily oxygen stores—penguins: 19–53%, Ponganis and Kooyman 2000; sirenians: 33%, Ponganis 2011; cheloniids: 72%, Lutz and Bentley 1985).

The dual functionality of the lungs as both oxygen store and buoyancy regulator (Hochscheid et al. 2003) therefore presents a challenge for divers inhabiting very shallow environments. Shallow diving should be relatively inefficient, with individuals having to resurface after short intervals due to the limited lung oxygen store needed to remain passively submerged in shallow water (Matley et al. 2020). To date there has been relatively little consideration of dive duration during very shallow water diving by air-breathing species, although the available data largely support the prediction of short dives. Short dives were recorded in foraging sea turtles and dugongs inhabiting shallow lagoons in Greece and Australia, with mean dive durations of 2–4 min at 2 m depth in adult green (*Chelonia mydas*) and loggerhead turtles (*Caretta caretta*; Houghton et al. 2000; Thomson et al. 2012) and a mean duration of 3 min at 5 m mean depth in dugongs (Chilvers et al. 2004). Short dives were also observed in internesting green turtles in a shallow estuarine habitat in French Guiana, with the majority of dives < 5 min and < 2 m (Chambault et al. 2016). Elsewhere in Australia, however, green turtles have been recorded diving for over 20 min in shallow water (2–6 m depth, 26–29 °C: Hazel et al. 2009). Here, we use high-resolution, fast sampling depth loggers to assess the depth utilisation behaviour of a foraging population of hawksbill turtles within a shallow lagoonal habitat in the Chagos Archipelago, Indian Ocean. We calculate standard metrics of dive efficiency (Watwood et al. 2006; Schagatay et al. 2011), (i) the % of time spent submerged and (ii) the % of the dive cycle spent in the bottom phase of dives, that we then compare against other sea turtle species as well as diving mammals, birds and reptiles often diving to 10s or 100s of metres. In this way, we assess the relative performance of shallow diving hawksbill turtles.

Materials and methods

Recording dive behaviour

High-resolution time-depth recorders (TDRs) were deployed on hawksbill turtles foraging in Turtle Cove at the southern tip of the horseshoe-shaped lagoon of Diego Garcia atoll in the Chagos Archipelago, Indian Ocean (7.42 °S, 72.46 °E), during October 2012 ($n = 5$) and February to March 2021 ($n = 7$). Turtles were captured at low tide in shallow water (< 1 m) by approaching slowly and carefully from behind before seizing the carapace, whereupon turtles were carried ashore. The curved carapace length (CCL) and curved carapace width (CCW) were measured using a flexible tape, and mass recorded with a suspended scale (Pesola Macro line 50 kg scale, Pesola AG, Switzerland). Maximum precision TDRs (G5 data loggers, 10 bar sensors with 0.03 m resolution, Cefas Technology Limited, Lowestoft, UK) were attached proximally to the trailing edge of flippers, using wire ties to fix them onto flipper tags placed at the thin junction between adjacent thick flipper scales (Supplementary Information Fig. S1). The TDR data sampling rate was every 1–5 s for pressure/depth and every 30–60 s for temperature. TDRs were recovered after various intervals when the turtles were next encountered in the cove (SI Table S1).

Analysis of dive data

The first four hours of each deployment were excluded in case of altered behaviour following capture and attachment (Thomson et al. 2012). Overall data analysis and visualisation were performed in R (R Core Team 2021). Zero-offset correction was scripted directly in base R. Individual dive characteristics and post-dive surface intervals (PDSI) were measured using MultiTrace Dive (Jensen Software Systems, Hamburg, Germany) with a minimum duration of 5 min and a threshold depth of 0.2 m, as has been described for shallow divers by Hays et al. (2007).

Welch's t test was used to test for differences in diurnal vs. nocturnal dive depth and dive duration for individual turtles, and repeated measures ANOVA was used to test for a diel difference in dive duration at the group level. Linear modelling was used to explore relationships between dive depth and dive duration, and temperature and dive duration, and was performed in R using the package 'lm', as well as the 'MASS' package for Boxcox transformation. Inverse transformation (1/duration) was used to rectify skew in the residuals for two models (those for diurnal dive duration). Results for subsetted datasets are reported to minimise co-variant effects: mid-temperature

dive datasets exclude dives < 28 °C and ≥ 30 °C, and dives by immature turtles exclude data from the single subadult turtle.

Sequential dives were considered to be independent as each dive is separated by a surface interval. However, all statistical tests and linear models were repeated with reduced datasets consisting of every other dive per individual.

Evidence of shark attacks

Between 2012 and 2021, hawksbill turtles were captured in the shallows of the lagoon ($n=423$) and examined for any evidence of recent shark attack such as scars on the carapace or skin, or missing parts of flippers. Recent injuries were noted when they were a different colour from surrounding flesh.

Comparisons across taxa: sea turtles

Sea turtle dive profiles are often categorised by shape, so comparisons were made specifically for U-shaped dives in order to minimise variability in activity levels across dives. U-shaped dives or U-dives have a steep descent followed by a flat bottom phase and a steep ascent, and are associated with bottom feeding and resting (Hochscheid 2014). Comparative data points were collected from the literature where individual or group mean depth and duration were provided for U-shaped dives in non-migratory cheloniid sea turtles in warm waters. Where mean data included a variety of dive types, depth and duration data were instead taken for flat-bottomed U-shaped dives shown in example dive profile figures, to allow inclusion of studies not providing mean data specific to U-dives. Where dives were classified into active/foraging and resting U-dives (e.g. Ballorain et al. 2013), or Type 1a (flat-bottomed U-dives) and Type 1b dives (U-dives with variability in bottom phase depth; Houghton et al. 2002), data were included for resting U-dives/Type 1a only. Where temperature categories were given, only the warmest category was included to enable comparison to conditions in Diego Garcia. See SI Section S1. Linear-plateau regression models were fitted using the nls package in R (R Core Team 2021) with a custom ‘if-else’ function describing the linear-plateau model (Gradycylinder.org 2022). Where nls failed to choose a plateau value (hawksbill turtles only), the most conservative model with the lowest R^2 value was chosen. This value also matched the quadratic-plateau model that successfully fitted using nls; however, the quadratic term did not significantly enhance the model and so was not included.

Comparisons across taxa: diving vertebrates

Diving efficiency is discussed in the literature in relation to either the proportion of time spent in the bottom phase of dives (e.g. Watwood et al. 2006), or the percentage of time spent submerged versus at the surface (e.g. Schagatay et al. 2011). Here, we present data for both measures of dive efficiency in foraging hawksbill turtles and compare our findings with data sourced from published studies of other air-breathing marine vertebrates. Dive efficiency in terms of the proportion of time spent in the bottom phase of dives varies with dive type and the depth an animal must travel to in order to reach the bottom phase of dives. We therefore compare dive efficiency across taxa using percent time spent submerged, to broaden comparability and to remove depth-bias.

Results

Diving performance of hawksbill turtles

Dive data were recorded for twelve hawksbill turtles (CCL: 36.2–70 cm, mass: 3.7–29.5 kg) for a total of 124 days (median: 5.0 d per individual, range: 0.6–51 d). The majority of dives were U-shaped dives, with occasional V- or W-shaped dives (see Fig. 1a, b for example depth profiles). A total of 7458 U-shaped dives of over five-minute duration were extracted from the dive records (median: 285 dives per individual, range: 23–3516; Fig. 1, SI Table S1; Stokes et al. 2023). Often the depth of consecutive dives paralleled the change in tidal height, i.e. dives became deeper as the tide came in and vice versa (Fig. 1a, b). Even though the threshold depth for recording a dive was very shallow (0.2 m), due to the high sensor resolution even these shallow dives were clearly evident in the dive records and were often many minutes long (Fig. 1b).

Mean bottom depth of U-dives for each individual ranged from 0.55–1.52 m for diurnal dives (mean \pm SD: 0.86 ± 0.41 m) and 0.37–2.38 m for nocturnal dives (mean \pm SD: 0.81 ± 0.47 m), i.e. turtles exhibited shallow dives both day and night (Fig. 1c; SI Table S1). Diurnal dives were significantly shorter (mean \pm SD, range in means per individual: 9 ± 5 min, 7.3–21.8 min) than nocturnal dives (24 ± 11 min, 17.1–60.9 min; repeated measures ANOVA, $F_{(1,11)} = 49.72$, $p < 0.001$; Fig. 1d; SI Table S1). This was also true for 11 out of 12 turtles when testing at the individual level (Welch’s t test, $p < 0.001$, SI Table S1), the one non-significant result being due to the low number of dives recorded ($n=3$ diurnal U-dives, $n=20$ nocturnal U-dives). Post-dive surface intervals (PDSI) were consistently short (Fig. 1f), with mean PDSI per individual ranging between 0.1 and 0.5 min (SI

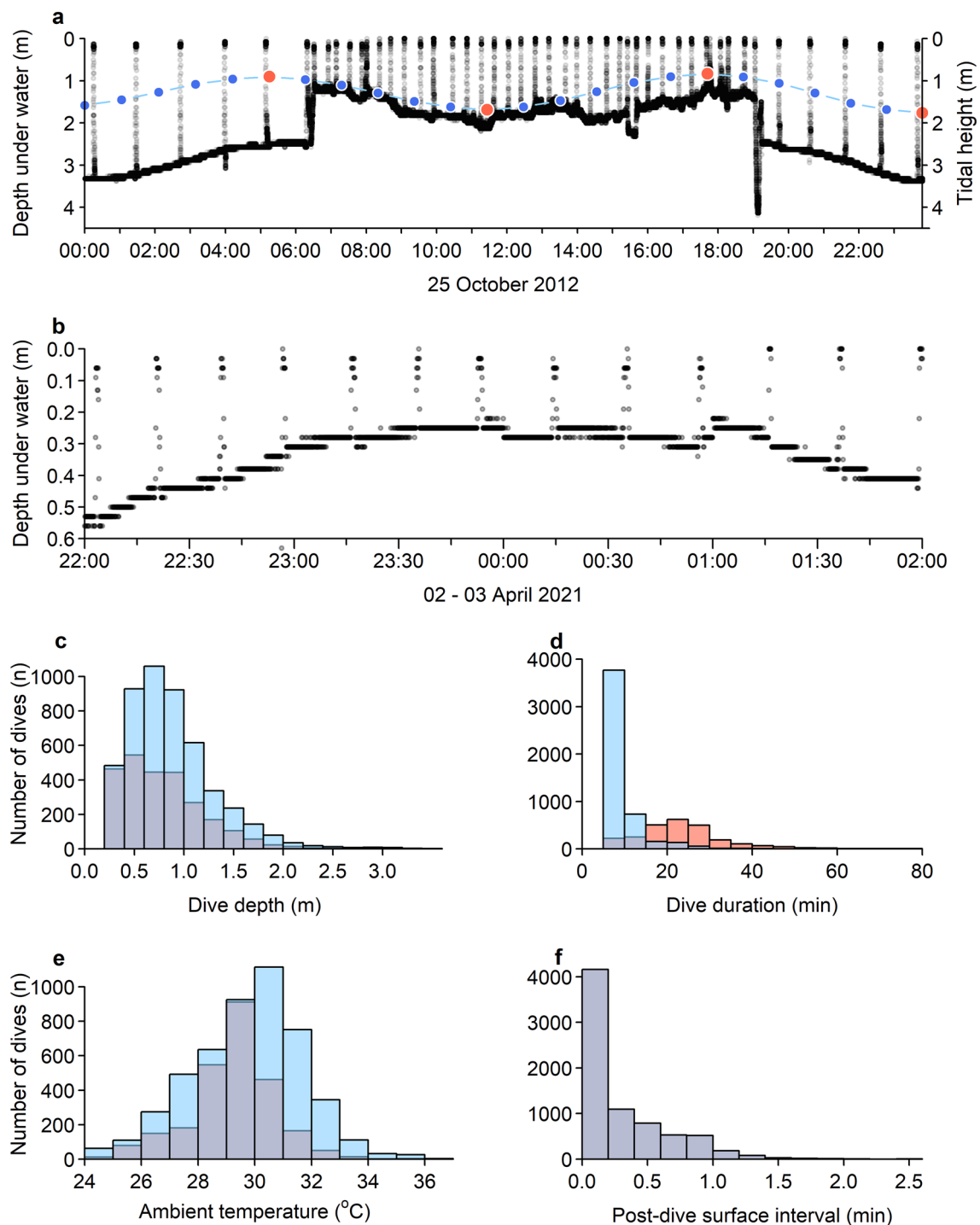


Fig. 1 **a** An example 24 h depth profile for a hawksbill turtle. Blue dot-dash shows tide heights at the lagoon mouth as calculated using the rule of twelfths from high and low tide times (shown in red). **b** An example 4 h depth profile showing a bout of very shallow diving (0.25–0.5 m), with U-shaped dives up to 22 min clearly delineated (depth changes with tidal height). Distributions of **c** mean bottom depth of dive **d** dive duration **e** mean ambient temperature during

dive and **f** post-dive surface intervals for $n=7458$ U-shaped dives. Depth use had similar distribution across diurnal and nocturnal dives (panel c), while dive duration is markedly longer in nocturnal compared to diurnal dives (panel d). Blue bars: diurnal dives, red: nocturnal dives, purple: overlap between diurnal and nocturnal dives (**c–e**) or all dives (**f**)

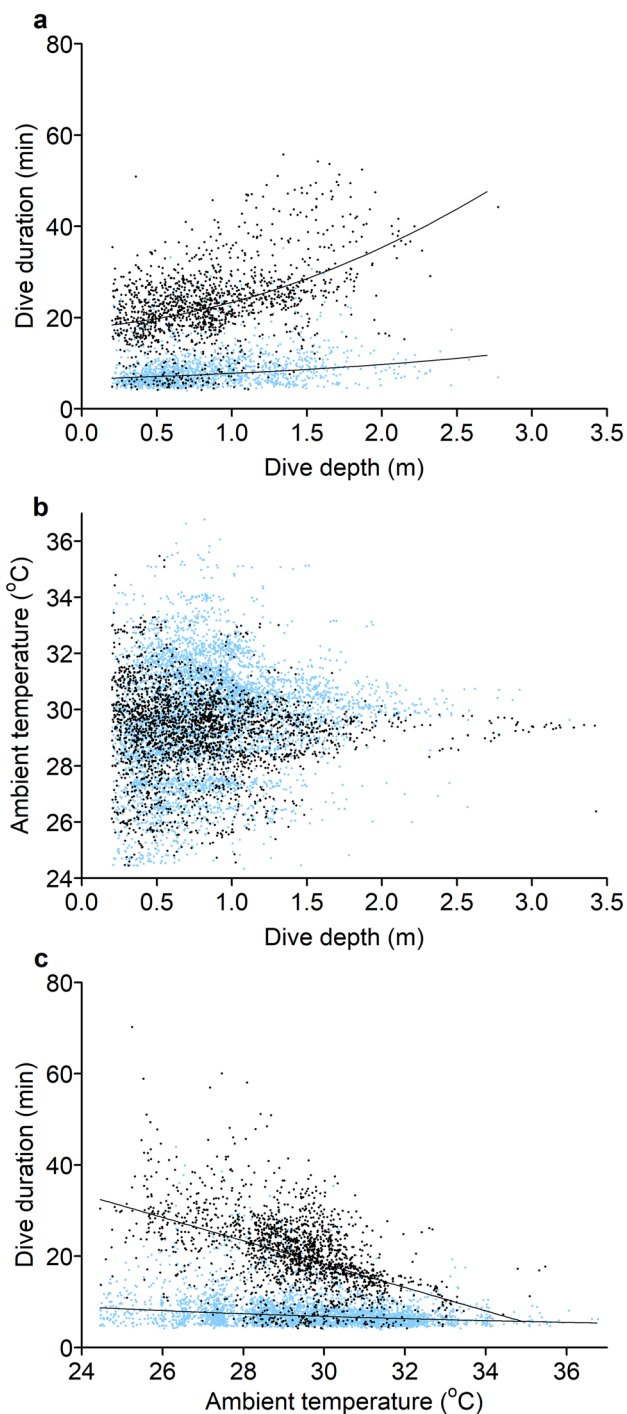


Fig. 2 Dive depth, dive duration and ambient temperature for hawksbill turtles foraging in Diego Garcia lagoon. **a** Mean bottom depth and duration of mid-temperature U-dives by immature turtles. **b** Mean ambient temperature during dive versus mean bottom depth for U-dives. In the shallowest water there was a much greater range of temperatures. **c** Dive duration during U-dives as a function of ambient temperature. Diurnal dives are shown in blue, nocturnal in black. Regression equations are given in Table 1

Table S1). So the mean PDSI for each individual was much shorter than the mean dive duration, with this ratio ranging from 0.01 to 0.03 across the 12 individuals.

Dive duration increased with depth as expected, particularly at night (Fig. 2a, Table 1). Although turtles occupied a very narrow range of depths, they experienced a large variation in ambient temperature (Figs. 1c, e, and 2b). For dives to < 1 m the ambient temperature varied widely between 24 and 37 °C, and dive duration decreased markedly with increased temperature (Fig. 2c, Table 1). For example, diurnal and nocturnal dives at 25 °C averaged 9 and 32 min respectively, decreasing to 6 and 13 min at 32 °C (Fig. 2c).

Diel differences in depth use were not consistent among turtles, i.e. some individuals performed deeper dives during the day ($n=6$) and others during the night ($n=3$; Welch's t test, $p < 0.05$, SI Table S1). All statistical tests and linear models that were significant with all dives included remained significant when repeated with every second dive removed, other than differences in mean diel depth for two turtles (T6 and T10) that were significant to $p < 0.05$ with all dives included (those with a single asterisk for significance level in SI Table S1). Diel depths were significantly different for 7 out of 12 turtles when using the reduced dataset, compared to 9 out of 12 turtles when using the full dataset (SI Table S1).

Evidence of shark attacks

In an estimated 190 h of in-water captures of turtles in this shallow lagoon environment we frequently observed small piscivorous sharks, namely small black tip sharks (*Carcharhinus limbatus*) and sickle fin lemon sharks (*Negaprion acutidens*), which do not predate on turtles. No larger sharks or other species of shark were seen in this shallow area of the lagoon. For 423 hawksbill turtles captured and assessed, there was no evidence of any recent shark injuries.

Comparisons across taxa: sea turtles

When comparing U-dive depths and durations from the current study to those from other published sources, hawksbill dive durations were longer for any given depth under 25 m than loggerhead or green turtle dive durations, with a clear separation of dive data by species (Fig. 3, SI Table S2). Modelled dive duration was 42–286% higher for hawksbills when compared to green and loggerhead turtles (equations given in Table 2). For example, for dives to 1, 5, and 10 m the fitted models gave mean dive durations of around 20, 33 and 49 min for hawksbill turtles, 7, 15 and 25 min for greens and < 1, 15 and 32 min for loggerheads.

Table 1 Relationships describing hawksbill U-dive parameters in Diego Garcia, Chagos Archipelago

Parameters	Diel phase	Dataset	Equation	Test statistics	R^2
Dive depth, dive duration	Nocturnal	Mid-temperature dives by immature turtles	Duration = $17.80 + 2.35 * \text{depth} + 3.22 * \text{depth}^2$	$F_{(1404,1405)} = 13.06$ $p < 0.001$	0.20
	Diurnal		$1/\text{duration} = 0.154 - 0.0255 * \text{depth}$	$F_{(1497,1498)} = 106.66$ $p < 0.001$	0.07
Ambient temperature, dive duration	Nocturnal	Dives to < 1 m, immature turtles	Duration = $97.08 - 2.62 * \text{temperature}$	$F_{(1894,1895)} = 630.56$ $p < 0.001$	0.25
	Diurnal		$1/\text{duration} = -0.0266 + 0.00578 * \text{temperature}$	$F_{(3393,3394)} = 304.99$ $p < 0.001$	0.08

Low R^2 values are due to variability in activity levels during dives, particularly diurnally

Comparisons across taxa: diving vertebrates

Dive efficiency was found to be consistently high across all individuals (percent time spent submerged: mean \pm SD, range in means per individual: 98.1 ± 0.02 , 96.6–99.6%; percent time in bottom phase of dives: 93.4 ± 0.04 , 92.4–97.5%; SI Table S1). Dive efficiencies recorded here are high compared to previously published data for reptile, bird and mammal breath-hold divers (Fig. 4, SI Table S3). For example, among marine mammals including phocid and otariid seals, cetaceans, the walrus (*Odobenus rosmarus*) and humans, dive efficiency ranged from 50 to 91%, being highest in hooded seals (*Cystophora cristata*). Among seabirds, dive efficiency ranged from 43 to 78% and was highest in the gentoo penguin (*Pygoscelis papua*). Among marine reptiles, dive efficiency ranged from 68 to 98% and was highest in hawksbill turtles from the current study.

Discussion

There is a wide body of literature showing that many marine vertebrates, including air-breathers, often reside in shallow water for a multitude of reasons including foraging, resting, breeding and migration (e.g. Sims et al. 2005; Cerritelli et al. 2022). It might be expected that shallow dives in air-breathers come with a trade-off of short duration, due to the constraints on inhalation as part of lung-controlled buoyancy regulation (Hays et al. 2004). However, our results are noteworthy in showing that highly efficient diving is possible

for a breath-hold diver on very shallow dives, and hence the habitat of shallow water seabeds can be occupied on long dives.

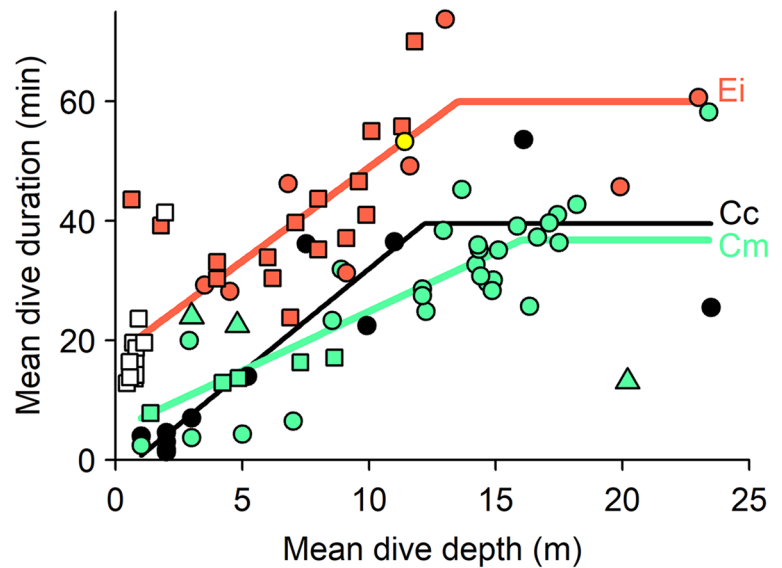
Most studies of diving in air-breathing marine vertebrates consider dives to 10s or 100s of metres and so generally the threshold depth for defining a dive is typically 2–5 m (e.g. Weise et al. 2010; Zimmer et al. 2010), i.e. much deeper than used here (0.2 m). This selection of a dive threshold works well for deeper diving animals, where often the pressure sensor used will have much greater measurement range, often capable of recording dives to 1000 m or more (e.g. Houghton et al. 2008). As a consequence, these sensors have lower precision for recording near-surface activity. In contrast, the depth loggers we used have very high resolution (3 cm) but have a limited measurement range, with a maximum of about 100 m in our case. These sorts of high-resolution depth loggers have been shown to reliably record shallow diving and have been used, for example, in studies with semi-aquatic divers such as mink swimming in rivers (Hays et al. 2007; Harrington et al. 2012), where dives were similarly defined as excursions to > 0.2 m.

Hawksbill turtles, like many fish (e.g. Sims et al. 2005), marine birds (Grémillet et al. 1998) and marine mammals, such as dugongs and manatees (Chilvers et al. 2004), likely occupy the seabed for foraging and/or resting. Certainly the U-dives we recorded are indicative of benthic diving, as has been noted in a number of other sea turtle studies (Seminoff et al. 2006; Thomson et al. 2011). This inference of benthic dives from the dive shape is further supported by the often close parallel between the depth of consecutive dives and the change in tidal height, i.e. the turtles

Table 2 Equations linking dive depth and duration for U-shaped dives in cheloniid turtles

Species	Equation (pre join-point)	Join-point	Plateau	Test statistics	R^2
<i>Eretmochelys imbricata</i>	Dive duration = $17.58 + 3.14 * \text{depth}$	13.50	59.95	$F_{(32,33)} = 67.4$ $p < 0.001$	0.68
<i>Chelonia mydas</i>	Dive duration = $5.00 + 1.98 * \text{depth}$	16.02	36.78	$F_{(26,27)} = 60.1$ $p < 0.001$	0.70
<i>Caretta caretta</i>	Dive duration = $-2.75 + 3.47 * \text{depth}$	12.19	39.55	$F_{(8,9)} = 41.5$ $p < 0.001$	0.84

Fig. 3 Depth and duration of cheloniid U-shaped dives. Eleven immature and one subadult hawksbill turtle in Turtle Cove, Diego Garcia (white squares), against other cheloniid populations sourced from published literature: mean depth and duration of U-shaped dives per individual or per study group. Red: hawksbill turtles (white distinguishes current study hawksbill turtles), green: green turtles, black: logger-head turtles, yellow: flatback turtle; circles: adults, squares: juveniles, triangles: mixed adults and juveniles. Regression equations given in Table 2



essentially provided the same sort of data as a tide gauge. Frequent dives to the seabed are expected in hawksbill turtles, as well as other sea turtles, since they both rest and feed on the seabed (Houghton et al. 2003). For example, elsewhere hawksbill turtles have been documented feeding on sponges on coral reefs (van Dam and Diez 1997), while a complete lack of motion associated with benthic sleeping has been shown for hawksbill turtles in the Seychelles (Houghton et al. 2003). Consistent with other studies of cheloniid turtles (e.g. Makowski et al. 2006; Witt et al. 2010), we observed longer U-dives at night indicative of benthic resting, with the longer dives likely facilitated by the lower metabolic rate of quiescent turtles compared to those foraging during the day. In contrast with studies finding a consistent pattern of diel depth use across turtles (e.g. deeper nocturnal depth use: green turtles, Ascension Island, Hays et al. 2002a, b; green turtles, Florida, Makowski et al. 2006; deeper diurnal depth use: green turtles, Hawaii, Brill et al. 1995; hawksbill turtles, Cayman Islands, Blumenthal et al. 2009), turtles at this site selected nocturnal depths that were either deeper or shallower than those they occupied during the day, depending on the individual turtle.

As U-dives are generally to the seabed, they give a good idea of the bathymetry encountered during diving. Hence, we can confidently conclude that the equipped hawksbills occupied very shallow depths (typically shallower than 3 m). This is in line with GPS tracking from this lagoon that has shown long-term occupation of very shallow areas (Hays et al. 2021). Certainly the instrumented turtles had ready access to deeper water, but they chose not to occupy these areas. For example, within the Diego Garcia lagoon only a few km from where animals were equipped there is deeper water (max depth 31 m) with abundant sponge and coral

cover (Hamylton and East 2012 Fig. 7), i.e. the types of preferred foraging habitat for this species. Hence, we conclude that occupation of shallow water by the turtles was through choice, rather than simply a consequence of limited available foraging habitat.

Depth selection in sea turtles and other marine vertebrates may often be linked to forage availability, maximising resting time, thermoregulation and avoiding predation (Hays et al. 2002a; Heithaus et al. 2007; Schofield et al. 2009). In our study one possibility is that the extremely shallow water leads to the exclusion of large sharks and so creates a low predation risk foraging environment for hawksbill turtles. Our evidence supports this possibility, with no large sharks seen in the shallow areas occupied by the equipped turtles, even though large sharks are found in deeper areas nearby (Winterbottom and Anderson 1997; Dunn et al. 2022). Furthermore, none of hundreds of captured hawksbill turtles showed any evidence of shark injuries, in contrast to other locations where sea turtles are frequently observed with missing rear flippers consistent with shark predation (Heithaus et al. 2002; Hill et al. 2017). So our observations are consistent with very shallow water offering hawksbill turtles a refuge from shark predation and, as such, our findings add to the growing body of evidence for the importance of predators in shaping habitat selection (Heithaus et al. 2008; Courbin et al. 2022; Siegal et al. 2022). A further reason facilitating the very shallow water occupation may be the long-term protection of turtles in Diego Garcia, with hawksbill turtles being fully protected since 1970 (Mortimer et al. 2020).

Despite the length of the shallow dives, the short post-dive surface intervals suggest these dives were aerobic, since long surface intervals are required to remove lactate build up from anaerobic metabolism (Costa et al. 2004).

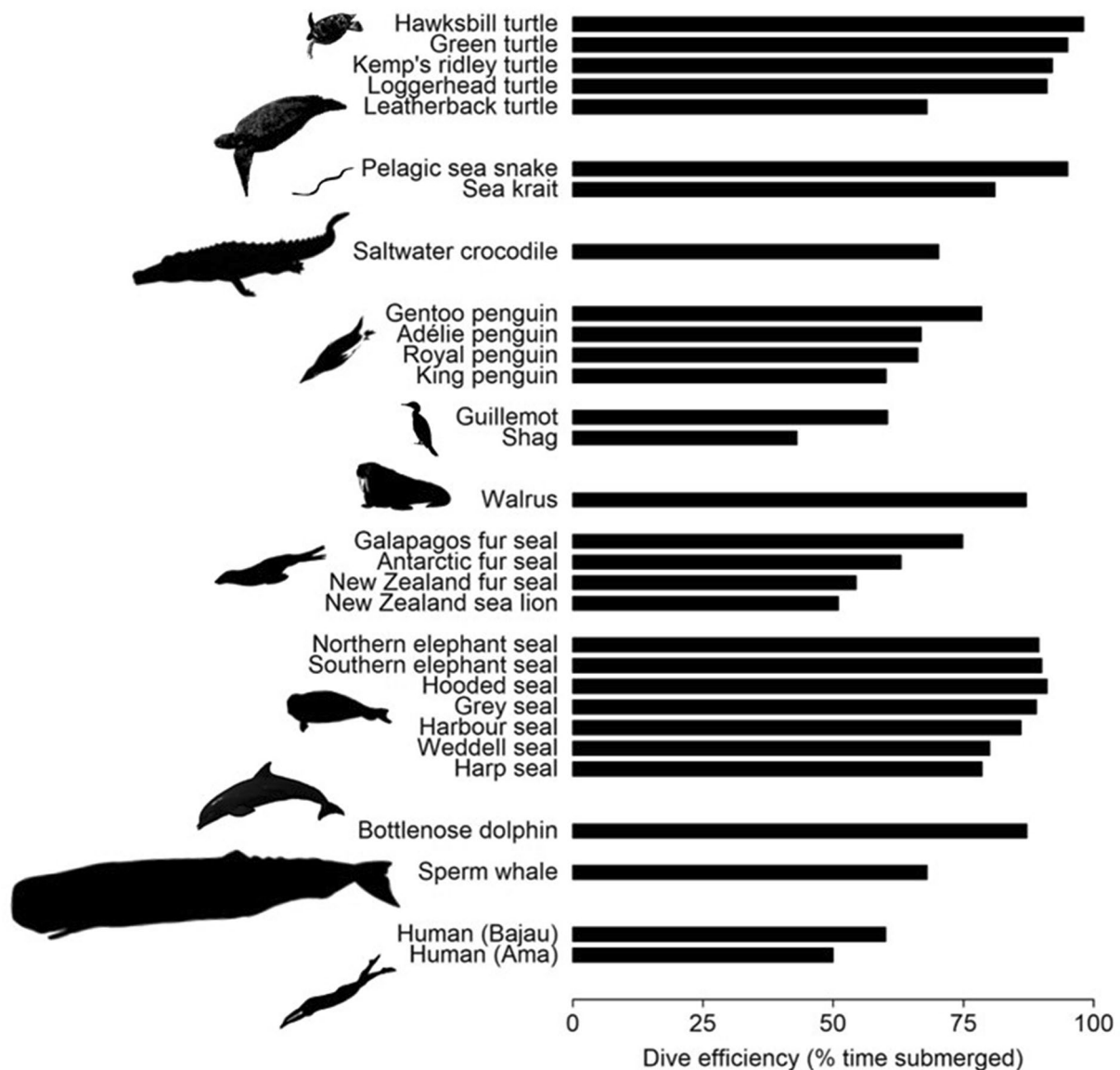


Fig. 4 Dive efficiency across various reptilian, avian and mammalian breath-hold divers (percentage of time spent underwater vs. at the surface)

Anaerobic metabolism in diving sea turtles seems to occur mainly under duress, for example in forced experimental submergences (Lutz and Bentley 1985) or entanglement in fishing nets (Snoddy and Southwood Williard 2010; Miguel et al. 2020). Our conclusion of routine aerobic diving supports this consensus view that sea turtles, in line with other air-breathing divers including mammals and birds, are usually diving aerobically (Southwood Williard 2013). Aerobic diving leads to higher overall dive efficiency as it negates the need for long surface intervals and is a far more efficient form of energy conversion, with each glucose molecule creating 19 times more ATP via aerobic pathways than anaerobically (Southwood Williard 2013).

One reason for long aerobic dives at shallow depths can be because of exceptionally cold water, since metabolic rate reduces at lower temperatures and hence aerobic dive limit increases (e.g. Hochscheid et al. 2004; Luschi et al. 2013). However, this was not the case in the current study since turtles experienced very high temperatures. For example, in a review of water temperatures at breeding sites, temperatures ranging from 22 to 28 °C were described (Hays et al. 2002b), compared to ambient temperatures exceeding 30 °C recorded here for shallow diving hawksbill turtles. As noted by others (Hochscheid et al. 2004; Madrak et al. 2022), we have shown that dive duration increased at lower temperatures, but even at warm temperatures of around 32 °C, nocturnal dives were still around 20 min. Our findings therefore suggest that at

shallow foraging sites that are cooler, hawksbill turtles will routinely dive for even longer than we recorded, i.e. long dives in shallow water can likely occur broadly in this species.

While the high variability of sea turtle metabolic rate with temperature (Southwood et al. 2006), activity levels (Williams et al. 2019) and digestive status (Jones et al. 2009) complicates comparisons of dive durations across studies and species, nevertheless, when combined with other dive data from hawksbill turtles, our findings highlight that this species consistently dives for longer than green and loggerhead turtles when depth and temperature are accounted for. The reasons for these long, shallow dives are enigmatic. At least three hypotheses can be suggested: (a) that hawksbills have lower mass-specific metabolic rates than green and loggerhead turtles, (b) they have larger mass-specific oxygen stores or (c) they have greater gas-free weight in water (for example due to lower fat stores), so that a larger lung volume will still attain neutral buoyancy in shallow water. Teasing apart these various alternatives is not straightforward. Measurements of lung volumes suggest hawksbills are not unusual in this regard (Hochscheid et al. 2007). There are no data on gas-free weights in water for sea turtles, i.e. the animal weight that the lungs need to support which will drive lung volume in attaining neutral buoyancy. Likewise there are no measurements of relative fat stores across species as yet. Recent evidence has shown differences in mass-specific blood volumes and hence oxygen stores across cheloniid turtles, showing that species may have different adaptations for diving (Arango et al. 2021) although data for hawksbill turtles are lacking.

Our cross taxa comparisons revealed high dive efficiency in hawksbill turtles, comparable to other air-breathing marine divers. Metrics of dive efficiency will be influenced by the threshold used to define depths. For example, when looking at the % time submerged, a deeper dive threshold will lead to calculations of lower dive efficiency. So our calculated high % of time submerged will be due, at least partly, to our shallow threshold (0.2 m) to define a dive and this metric will not be strictly comparable to other divers where this threshold is typically much deeper (2–5 m; Weise et al. 2010; Zimmer et al. 2010). Nevertheless, even when we looked at the % of the dive in the bottom phase, hawksbills still had high dive efficiency compared to other divers. Deeper divers will clearly need to spend longer in transit from the surface to the bottom phase of their dives, which will lower their dive efficiency compared to hawksbills. Regardless of the caveats of these dive efficiency metrics, it is clear that hawksbills can spend a high proportion of their time submerged, even when diving in very shallow water.

There are several reasons why cheloniid turtles, in general, might show high dive efficiency compared to marine mammals and birds. Cheloniid turtles tend to dive to

shallower depths than many marine mammals and hence energy expenditure during descent and ascent is likely reduced; they tend to feed on sessile invertebrates or plants and hence energy expenditure in prey pursuit is minimised; unlike endotherms, they do not expend energy warming cold prey in their stomachs; being ectothermic, their rates of oxygen consumption are considerably lower (Hayward et al. 2016). In contrast, leatherback turtles (*Dermochelys coriacea*) have lower dive efficiency and tend to be regionally endothermic, dive deeper and re-warm cold prey in their stomachs (Casey et al. 2010), making them more akin to diving birds and marine mammals. Optimisation of energetic gains can be achieved by either reducing the metabolic cost of foraging or maximising energy intake, and predators of mobile prey are known to switch between these strategies based on prey patch density in order to achieve maximal overall energy efficiency (e.g. blue whales, *Balaenoptera musculus*, Hazen et al. 2015). Hawksbill turtles and other benthic grazers employing lower cost feeding mechanisms are likely to minimise the metabolic cost of foraging dives by maximising dive efficiency, while species in pursuit of active prey may finish a dive before oxygen stores are depleted if prey are not encountered (Thums et al. 2013), or are likely to have lower dive efficiency due to the higher energetic demands of catching mobile prey.

In conclusion, while generally across studies with marine mammals and birds the focus has been on diving to 10s of metres or more (Williams and Ponganis 2021), our work highlights that shallow water habitats may be used very efficiently by air-breathing divers, both to forage and also likely reduce predation risk, highlighting the need for further consideration of shallow water diving across other diving species.

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Declarations

Conflict of interest The authors declare no competing or financial interests.

Ethical approval This study was approved by Swansea University and Deakin University Ethics Committees and the British Indian Ocean Territory Administration (BIOTA) of the UK Foreign, Commonwealth and Development Office. The study was endorsed through research permits (0002SE12, 0002SE14, 0007SE15, 0002SE17, 0006SE18, 0009SE18, 0004SE19, 0011SE19, 0001SE21) from the Commissioner's Representative for BIOT, and research complied with all relevant local and national legislation.

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Additional data sources

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