

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/258515419>

# Why we mind sea turtles' underwater business: A review on the study of diving behavior

**Article** in *Journal of Experimental Marine Biology and Ecology* · November 2013

DOI: 10.1016/j.jembe.2013.10.016

---

CITATIONS

19

---

READS

373

1 author:



**Sandra Hochscheid**

Stazione Zoologica Anton Dohrn

72 PUBLICATIONS 1,027 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Restauro Ambientale e Balneabilità del SIN Bagnoli-Coroglio (ABBaCo) [View project](#)



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/authorsrights>



Contents lists available at ScienceDirect

## Journal of Experimental Marine Biology and Ecology

journal homepage: [www.elsevier.com/locate/jembe](http://www.elsevier.com/locate/jembe)

## Special issue: Charismatic marine mega-fauna

## Why we mind sea turtles' underwater business: A review on the study of diving behavior

Sandra Hochscheid<sup>1</sup>

Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Napoli, Italy

## ARTICLE INFO

Available online 2 November 2013

Keywords:  
Data logger  
Dive behavior  
Satellite telemetry  
Sea turtle  
TDR

## ABSTRACT

For most of their lifetime, sea turtles have to organize their underwater activities around the necessity to return to the surface to breathe. This group of animals has developed extraordinary diving capacities (over 10 h of single breath-hold dives and dive depths exceeding 1200 m) that allow them to exploit oceanic and neritic habitats, and maintain their role in marine ecosystems, despite the numerous threats imposed on them by human activities. Understanding sea turtle behavior, and the extent of flexibility with which they respond to environmental changes, has been a key element of studies on sea turtle diving behavior for over 25 years. Here, I review the major outcomes of these studies, summarizing published data on dive durations and depths, and identifying the factors that influence the shape and temporal patterns of sea turtle diving. By carefully assembling existing published information in this research field, some unique features emerged (such as the ability of some turtles to rest for extended periods in the middle of the water column), as well as knowledge gaps that require further investigations (such as the behavior and diving capacity of small juvenile turtles). In addition to simply collecting and presenting existing data, this review also highlights the needs for some level of minimum standardization, especially for studies involving electronic telemetry equipment, in addition to clarifying where future effort should be focused. Ultimately, this review is anticipated to serve as a reference guide for scientists and wildlife managers alike, who seek to mitigate threats to sea turtles through specific knowledge-based conservation strategies.

© 2013 Elsevier B.V. All rights reserved.

## 1. History of studying diving behavior

Since the 1930s and 1940s, behavioral ecologists and physiologists have been intrigued by how air-breathing aquatic animals deal with the separation of two fundamental resources, food and oxygen, which may be separated by hundreds of meters of sea water on occasion.

The understanding of the physiology, behavior, and ecology of many marine species has been revolutionized by the development of telemetry techniques (Rupert-Coudert et al., 2009; Wilson et al., 2008), which involve attaching electronic devices to animals (Hooker et al., 2007; Rutz and Hays, 2009; Shillinger et al., 2012) and measuring their behavior from a distance (from the Greek word “tele” meaning remote, and “metron” meaning measure). In 1963, the first time depth recorder (TDR) was designed to measure the timing and depth of freely diving Weddell seals, *Leptonychotes weddellii*, to obtain detailed information about the underwater activities of these animals (Kooyman, 2004). During the 1970s and 1980s, other fur seal species were studied. In 1984, Eckert et al. (1986) and G. Kooyman were the first researchers

to place a TDR on leatherback turtles, *Dermochelys coriacea*, prompted by the lack of information about the behavior of turtles at sea, and to demonstrate the feasibility of applying depth recording technology developed for marine mammals onto sea turtles. This pioneering work by Eckert and co-workers initiated a succession of investigations about the diving patterns of leatherback turtles during their inter-nesting intervals (Eckert et al., 1989, 1996), which was followed by research on loggerhead turtles, *Caretta caretta*, by Sakamoto and colleagues in the 1990s (Sakamoto et al., 1990a, 1990b, 1993).

It goes without saying that the progress in technology had a major impact on the design, electronics and capacity of data-logging devices. The first TDR used on sea turtles by Eckert et al. (1986) was cylindrical, measured 5.2 × 20 cm and weighed 500 g. Battery life was between 7 and 16 days, depending on temperature. The accuracy of the pressure sensor was 2% of full scale after first 10 m and the maximum depth range was limited to 315 m. Nowadays, TDRs are considerably reduced in dimension (the smallest range from 25 to 30 mm length with 8 mm diameters) and weight (in air ≈ 3 g, in water 1–2 g), while battery life was enhanced (in units of months and years), as well as sensor resolution (<4 cm) and capacity (>1000 m). In addition, TDR technology has been greatly improved by combining these relatively simple devices with other sensors, that can, for example, register movements of body parts (Hays et al., 2007; Hochscheid et al., 2013)

E-mail address: [sandra.hochscheid@szn.it](mailto:sandra.hochscheid@szn.it).<sup>1</sup> Tel.: +39 081 5833222; fax: +39 081 5833294.

or overall body acceleration (Fossette et al., 2012; Okuyama et al., 2012; Wilson et al., 2008) or even film the animal's behavior during diving (Reina et al., 2005; Seminoff et al., 2006). The recent transition from TDRs to accelerometry and video-based assessments of diving behavior have shown great potential to more accurately determine energy management of diving animals and confirm behaviors assumed by TDRs. There are also numerous solutions for data recovery, aiming to circumvent the physical retrieval of the tag (such as dive information being relayed via satellite) or at least the recapture of the turtle (such as the use of pop-up tags, which are then retrieved by following radio signals or collection after being washed up on the beaches) (see also Section 3.1).

The ever ongoing technological development of telemetry tags led to an increase in the diversity and applicability of these devices. As a result, studies on sea turtle diving behavior have become more frequent. Over the last two decades (1993–2012), 70 studies were published in peer-reviewed journals; during the first decade (1993–2002), there were on average 2–3 publications per year, after which there was a noticeable increase in the number of publications, which has been averaging 6–7 per year since 2003. This calculation does not take into account numerous studies that are contained in master's and PhD theses, conference proceedings, technical reports, and other less readily available sources. However, it would not be possible to fully give credit to all these studies; thus, for this review, I focused on studies that have already been subject to critical review by internationally renowned experts.

The general aim of this review was to gather, summarize, and present current knowledge about sea turtle diving behavior, to inform those interested in the performance of air-breathing aquatic animals. However, in-depth understanding (literally and figuratively) about sea turtle behavior also sets the base for sound conservation strategies and for informing decision makers (Fossette et al., 2012; Schofield et al., 2009). I provide information about the depths to which different species of sea turtles dive to and for how long, elucidating patterns of behavior and what governs them. Ultimately, I shaped this review to serve as a useful reference guide, with the intention of encouraging further focused work in this research field, rather than critically disassembling the contents of published papers.

## 2. What is a dive?

According to Kooyman (1989), three conditions must be met for an animal to be diving: 1) there is a distinct break in the respiratory rhythm, where apnoeic periods become longer than when the animal is awake and on land (or with access to air); 2) exercise is involved when departing from the surface to depth by active swimming effort; and 3) there is a change in hydrostatic pressure corresponding to the change of depth. However, it soon became clear that there are exceptions to the rule, as is the case with, for example, Weddell seals, *L. weddellii*. This species is able to rest under water and sink passively during a submersion; hence, the exercise factor is missing. In addition, sea turtles also rest underwater, either on the sea floor or in mid-water (Hays et al., 2004a; Minamikawa et al., 2000), and are therefore not engaged in any physical activity. Yet, in both cases the animals would have to return to the surface by active swimming; hence, we may safely extend the exercise factor to apply to at least one of the two vertical traveling phases, either descent or ascent, to comply with the three conditions of diving.

A break in the ventilatory pattern might also be difficult to judge in sea turtles, which normally breathe only intermittently (Lutcavage and Lutz, 1997). The duration of short dives might fall within the range of these normal apnoeic intervals between two breaths. Hence, apnoea alone is not sufficient to describe whether a turtle is diving, not even if the head or only the nostrils are temporarily submerged, because that happens while the turtle is resting at the sea surface. We could agree that a sufficient change in depth is already achieved when

the turtle's whole body is fully submerged. Thus, the beginning and end of a dive is determined at the times that this condition becomes true and untrue, respectively.

Naturally, when we have clear sight of an animal we may intuitively infer whether the animal is diving or pursuing activities at the water surface/out of water (see, for example, Schofield et al., 2007). However, sea turtles are difficult to access at sea and are most of the time out of sight, so that direct observations are often not an option for the study of their diving behavior. For these reasons investigation are conducted by the means of technological support, which is where an accurate definition of diving becomes important, so that the devices can be configured accordingly and the recorded data deliver the desired results. In addition, the size and behavior of the animal, as well as the attachment location of the tag (Fossette et al., 2012), may influence the definition of a dive, and should thus be taken into consideration when assessing which behavior qualifies as a diving event.

In an ideal scientific world, all researchers using telemetry devices would use the same parameters to configure their tags, and all collected dive data from turtles would be genuinely comparable. However, in practice, this specification is impossible to apply, not only because tags have different properties, but also because, as we gain new knowledge about sea turtle underwater behavior, we adjust our set-ups to successfully capture previously unrecorded behaviors. Moreover, as I will illustrate in this review, a tag may yield higher quality results when its configuration is adapted to a certain life stage and habitat of a given species under study. Consequently, the available data pool about the diving behavior of sea turtles is highly heterogeneous because of the differences in the methodological set-up, the data analysis, and ultimate presentation. In the following methodological section, I explain how I have addressed the heterogeneous nature of the diving studies, to compile a comprehensive overview of the current knowledge about turtle diving behavior.

## 3. Methodology

### 3.1. Methods commonly used for the study of dive behavior

In this section, I briefly describe the various types of tags that are most commonly used in diving studies, and which were considered for this review. Basically, the tags belong to two groups, namely archival tags and satellite tags. Both tag types operate with their own integrated energy source. Archival tags are data-logging devices with generally high memory capacities that record and store data from their sensors, and which are retrieved by direct download to computer after tag recovery. Included in this category are simple TDRs (as described in Section 1) and any modified form, such as acceleration data loggers, and underwater cameras with integrated TDRs that may either record videos or take snapshot pictures. The second category contains tags that transmit recorded dive (and other sensor) data via satellite, thus physical tag recovery is not necessary. The satellites used for this purpose belong exclusively to the ARGOS system ([www.argos-system.org](http://www.argos-system.org)) and data collection is managed by the Collecte Localisation Satellites (CLS). The vast range of satellite tags considered here include simple ARGOS tags with integrated pressure sensors, satellite relay data loggers (SRDL), and Pop-up archival transmitting tags (or simply Pop-up tags).

### 3.2. Resources used for this review

The data presented in this review were obtained from publications in peer-review journals that are contained in the Science Citation Index Expanded (1975–present), by means of a search in the Web of Knowledge (Thomson Reuters© 2013). A topic based search with the following search terms was conducted: Topic = ((“div\* behavio\*”) and (“marine turtle\*” or “sea turtle\*”). Out of the resulting 98 papers, 28 were discarded because they were not directly focusing on underwater



behavior, but with related topics instead. I further selected only those papers that used any type of archival tag or satellite tag, as described above or, in a few cases, those papers that were based on direct observations, but where the observer had the possibility to determine dive depth of the turtle under study. This selection was necessary to collect data obtained with similar methodologies, and which contained the depth factor in the dive records. Although there are numerous studies that present and discuss diving behavior using submergence times alone, these were generally not considered because depth information was missing (i.e. failure to comply the definition of a dive, see Section 2).

### 3.3. Data processing and analysis

Of the 70 papers about diving behavior, 57 presented data on dive durations and depths that I used to produce a summary table (Table 1) on general diving parameters. For each study, I took note of the species, the type of tag used, the habitat type, the number of turtles studied, the study location, and the life stage of the turtles. Whenever available, additional information about the turtles was also collected, including sex, size, and body mass. At least two of the following dive parameters needed to be presented in the paper to be included in this table: number of dives, dive duration, average or median dive depth, maximum dive duration, and/or maximum dive depth. When these values were only presented for individual turtles, I calculated the mean from the individual means. In some publications, data about the maximum dive depth and duration were not provided, but could be estimated from the figures (using the measurement tool in Adobe Acrobat 9 Pro (version 9.5.5, Adobe Systems Inc.) for pdf files or a ruler for papers that were only available as hardcopies). All estimated values that were not directly obtained from these original sources were identified in the table as such.

## 4. General overview on diving in sea turtles

Data were collected and summarized from 57 studies (Appendix 1) published between 1986 and the beginning of 2013. Overall, a total of 538 turtles were studied, of which only 19 (3.5%) were directly observed, while 355 (65.3%) were equipped with TDRs, 82 (15%) were equipped with TDRs in combination with video recording devices, 63 (11.5%) were equipped with satellite tags with pressure sensors or integrated data loggers, and 25 (4.6%) were other types of tags. Divided by sex, 245 (46%) of the studied turtles were adult females, only 16 (3%) were adult males, and 277 (51.5%) were post-hatchling to late juvenile stages for which the sex was unknown. Green turtles were the most studied species, with 209 turtles in 20 publications, followed by leatherbacks (149 turtles in 16 publications), hawksbills (82 in 9 publications), loggerheads (53 in 11 publications), and olive ridleys (20 in 3 publications). There was just one published study for each of flatbacks and Kemp's ridleys, using 22 and 3 turtles, respectively. For known problems of data recovery, the actual number of turtles for which dive data was retrieved differed from the sampling effort; hence, 417 datasets (77% of all instrumented turtles) were available for this general overview.

Since turtles are most accessible when they emerge on land to nest, it is not surprising that most of the dive data available (33%) were collected from females in neritic inter-nesting habitats. Neritic developmental habitats were the second most studied habitat type (23%), followed by neritic foraging grounds of adult turtles (11%), and oceanic inter-nesting habitats (10%). Apart from the latter, oceanic habitats were in general quite underrepresented, which most likely reflects the logistical problems of studying turtles in remote ocean areas.

The maximum recorded dive duration and depth for each species are listed in Table 2, with the corresponding references. As already known, the deepest diving species is the leatherback turtle, which reaches

depths of 1250 m, followed at some distance by olive ridleys, loggerhead turtles, and then green turtles. Neither Kemp's ridleys nor flatback turtles seem to exceed 100 m dive depth, although there is some data deficiency. The longest breath-hold dives were recorded for turtles overwintering in the Mediterranean Sea (Broderick et al., 2007), in which loggerhead turtles dove for slightly more than 10 h and green turtles remaining submerged for about half that time. Maximum dive durations for other species ranged between 82 and 217 min, with the exception of flatback turtles, for which data are only available for post-hatchling turtles that dove for relatively short times (maximum dive duration = 5.8 min).

The standard dive parameters of sea turtles are influenced by various factors, including environmental temperature, turtle size, and habitat; hence, there is broad variation in the average values for dive duration and dive depth in the literature. Yet, the range of average dive durations (1–44 min) overlaps fairly well among four species, not counting the extreme values measured during the overwintering period for loggerhead and green turtles (Fig. 1A). Average dive depth ranged between 2 and 54 m for loggerhead, green, hawksbill and olive ridley turtles, while the leatherback turtle had the widest mean depth range extending to 150 m (Fig. 1B).

### 4.1. Factors influencing dive behavior

#### 4.1.1. Temperature

Turtles are exposed to thermal variations in their environment, both in the short-term (e.g., diving through thermocline and resting at surface) and in the long-term (e.g., migration through different ocean regions and seasonal changes). The temperature effects on turtle physiology, in particular metabolic rate, circulation, respiration, and enzyme activity, are well documented (Hochscheid et al., 2002, 2004; Kraus and Jackson, 1980; Moon et al., 1997; Penick et al., 1996; Southwood et al., 2003a) and warrant no further details here. Despite the obvious importance of temperature in the life history of sea turtles, this factor has received rather limited attention in the analysis of dive behavior (12 out of 70 papers reported on temperature related changes in behavior). The dive patterns that are recorded under varying thermal regimes are a response to underlying physiological mechanisms, but may also be a means of thermoregulation if a turtle actively seeks out temperature ranges or, where available, microclimates. Although the choice of the latter may be reduced in the marine environment, especially for turtles diving within the mixed layer, there is first evidence that female turtles prefer microhabitats with higher temperatures presumably to enhance egg maturation rates (Sato et al., 1998; Schofield et al., 2009). Yet, many studies reported on turtles that were exposed to varying temperature conditions not of their choice, as, for example, turtles that forage in pelagic waters and dive through the thermocline (Hochscheid et al., 2010; James et al., 2006a; Sakamoto et al., 1990b). Repeated diving into cold waters eventually causes the body temperatures of these ectothermic animals to drop and, hence, turtles compensate behaviorally, either by increasing their body temperatures again or by avoid excessive heat loss. In Canadian waters, leatherback turtles may dive continuously in cold relatively shallow waters, but dives are short enough (mean dive duration = 6 min) so that internal temperatures are probably maintained through thermal inertia and body insulation (James et al., 2006a; Paladino et al., 1990). In comparison, leatherback turtles inter-nesting in the Pacific Ocean off Costa Rica raised their body temperatures through diving in shallower warmer waters (Southwood et al., 2005), while loggerhead turtles diving in the Mediterranean spent extended times at the surface after diving in deep cold waters (Hochscheid et al., 2010).

In the long-term, particularly for seasonal changes, dive duration is negatively correlated with temperature (Bentivegna et al., 2003; Broderick et al., 2007; Godley et al., 2002; Hatase et al., 2007; Hazel et al., 2009; Hochscheid et al., 2005a; Southwood et al., 2003b; Storch et al., 2005; Thomson et al., 2012). Because of the metabolic depression

**Table 1**  
Summary of diving behavior data for sea turtles presented in 57 publications (Ref – for complete citation refer to numbered reference list in Appendix 1). Methods: SRDL = satellite relay data logger, SATpres = satellite tag with pressure sensor, Observation = direct observation, TDR = time–depth recorder, Video = video camera, UTPR = underwater timed picture recorder, PSAT = pop-up satellite tag, AccDL = Acceleration data logger; Habitat types are NINT = neritic inter-nesting habitat, OINT = oceanic inter-nesting habitat, NDEV = neritic developmental habitat, ODEV = oceanic developmental habitat, NFG = neritic foraging ground, OFG = oceanic foraging ground, OW = overwintering ground, MIG = migratory path; N = the number of turtles equipped and the number of datasets available are given in parenthesis; Sex is given as female (f), male (m) and unknown (UK) and numbers are given when the studied turtles were composed of more sex categories; Size is given as curved carapace length (CCL), except where noted otherwise, and body mass (M<sub>b</sub>) and is in most cases referring to the mean across all individuals used in the study (in some cases minimum and maximum were given where a large range of turtle sizes were studied); water temperatures (T<sub>w</sub>) are means over the entire study period or over time intervals relevant to the study, as given by the authors (in some cases minimum and maximum were given where turtles experienced a wide range of temperatures); Dive duration and depth are given as mean (except where noted otherwise) and maximum (max) values; see also Section 3.3 for further information on how data were summarized.

Species	Ref	Method	Habitat type	N	Life stage	Sex	CCL (cm)	M <sub>b</sub> (kg)	T <sub>w</sub> (°C)	N dives	Dive duration (min)		Dive depth (m)		Notes
											Mean	Max	Mean	Max	
<i>Caretta caretta</i>	4	SRDL + other tags	OW	10 (1)	Adult	f				135	307.2	614.4			
	16	SATpres	NFG + OFG	2 (1)	Adult	f	84.8	82	18–29	1175	28.8	320.1	150		Data for smaller turtle
	23	SRDL	OW	1 (1)	Adult	f	73.5	52	14.7	1952	5.5–341 <sup>b</sup>	410	174.5		
	25	Observation	NFG	4 (4)	Adult	m				96	2.3	11			Shallow habitat
	27	TDR	NINT	5 (2)	Adult	f				347		55 <sup>c</sup>	8.7	70	Data for Profile A <sup>d</sup> dives
	33	TDR	NINT	1 (1)	Adult	f	88.1			1319	26	97 <sup>c</sup>	5.2	120 <sup>c</sup>	Data for Profile F dives
	34	TDR	NINT	9 (6)	Adult	f	81.4 <sup>a</sup>	74.4			26.1		6.1		Only turtles from experiment 1 and only Profile E dives
	36	SRDL	ODEV	2 (2)	Juvenile + sub-Adult	UK	72							178	Only time at depth histograms
	39, 41	TDR	OINT	1 (1)	Adult	f	89.4		12–25.5	17			54	233	Means for dives following deep diving
	40	TDR	NINT + OINT	4 (2)	Adult	f	81.6 <sup>a</sup>		23.2–25.7	341	36.5–25.5 <sup>b</sup>	11, 23.5 <sup>b</sup>	39 <sup>c</sup>		
	52	Video + TDR	NDEV	14 (14)	Adult + juvenile	UK = 9, m = 5			87	7.08		4.8			
<i>Chelonia mydas</i>	3	TDR	NDEV	6 (5)	Juvenile	UK	52.9	20.9			3.8	46 <sup>c</sup>	2.1	28	
	4	SRDL + other tags	OW	10 (1)	Adult	f				81	100.2	307			Winter dives only
	5	TDR	NINT + OINT	10 (10)	Adult	f	96.1 <sup>a</sup>		27.3, 29.1	3131	32.7	71.8	17.1	65.2	Data for Profile A dives in bouts
	13	Video + TDR	NDEV	6 (6)	Juvenile	UK			23.4–28.6				2.1	2.9	Shallow habitat
	14	UTPR	NINT	2 (2)	Adult	f	96	102		2899	6.0	28	2.8	13.1	
	15	TDR	NINT	1 (1)	Adult	f				86			4.6		Data for Profile A dives
	20	TDR	NINT	6 (2)	Adult	f	119.1			4247	32.3	55 <sup>c</sup>	13.2	32 <sup>c</sup>	
	21	TDR	MIG	9 (5)	Adult	f				182	22.7		28.7		Data for Profile E dives
	17	TDR	NINT	25 (6)	Adult	f	61.3			1377	33.3	56 <sup>c</sup>	15.2		Data for non-weighted turtles and Profile A dives
	18	Video + TDR	NDEV	5 (5)	Juvenile	UK	82.6	71.5	25.4	78	7.7	17.7	21.7	37.1	
	22	TDR	NDEV + NFG	25 (19)	Adult + juvenile	m = 2, f = 5, UK = 18	49–118		13.8–30.3			156		7.9	
	24	TDR	NINT	4 (2)	Adult	f			26–32	2285	7–11 <sup>b</sup>	40	4.4–7.8 <sup>b</sup>	24.8	

(continued on next page)

Table 1 (continued)

Species	Ref	Method	Habitat type	N	Life stage	Sex	CCL (cm)	M <sub>b</sub> (kg)	T <sub>w</sub> (°C)	N dives	Dive duration (min)		Dive depth (m)		Notes
											Mean	Max	Mean	Max	
<i>Dermochelys coriacea</i>	31	TDR	NDEV	6 (4)	Juvenile	UK	36.7 <sup>a</sup>	9.9		336		25 <sup>c</sup>	3.2	6.1	Data for daytime dives
	38	TDR	MIG	3 (3)	Adult	f=1, m=2					39.1	215	38.8	138	
	43	TDR	ODEV	33 (33)	Post-hatchling	UK	6.2–7.9 <sup>a</sup>	0.04–0.07	299	1.4	4.3	2.5	9.3		
	46	Video + TDR	NDEV + NFG	34 (32)	Adult + juvenile	UK	79.6 <sup>a</sup>	75.1		1065	16.1	48	28.4	54.5	Summer dives only
	47	TDR	NDEV	7 (6)	Juvenile	UK	50.3	15.4	26.2	2080	13.1		2.9	19.5 <sup>c</sup>	
	51	PSAT	ODEV	1 (1)	Juvenile	UK	70		22–28					91	
	52	Video + TDR	NDEV + NFG	12 (12)	Adult + juvenile	UK = 10, m=2			132	5.3		6.0			
	57	AccDL	NINT	4 (4)	Adult	f	98.25			348	43.8	71 <sup>e</sup>	20.5	59 <sup>c</sup>	Data for Profile A daytime dives
	6	TDR	NINT + OINT	3 (2)	Adult	f	145.1				12.9	37.4	103.2	475	Data for daytime dives
	7	TDR	NINT + OINT	6 (6)	Adult	f	154.7	335.9			9.9	37.4	61.6	1300	Max depth estimated since out of range of depth sensor
	8	TDR	NINT	5 (3)	Adult	f	153.3			2422	10.1	27.7	33.1	62	
	9	TDR	NINT + OINT	5 (5)	Adult	f	154.4			845	6.1	23	45.4	56.8	Data from pre-nesting females
	11	TDR	NINT	16 (10)	Adult	f				20,607	4.4	28.2	9.4	83.8	
	10	TDR	NINT	12 (4)	Adult	f				1009	6.6		11.8		
	12	AccDL	NINT + OINT	5 (2)	Adult	f	161.5			81	17.3	33.6	151.8	462.4	
	19	3 SRDL + 1 TDR	MIG	4 (4)	Adult	f				2548	11.0	63 <sup>c</sup>	51.7	640	Data for dives in Caribbean
	28	SRDL	OFG	13 (13)	Adult	f=12, m=1			11–28	26,185			52.9	1250	N of dives here is sum of dives in Table 1 of the cited reference
	30	SRDL	NFG + OFG	1 (1)	Adult	f	148		17.5	1312	6			96	
	37	Video + TDR	NINT	11 (11)	Adult	f				465	7.1	27 <sup>c</sup>	16	64 <sup>c</sup>	
	42	2 SATpres + 2 SRDL	OFG	4 (4)	Adult	f			14.3–27.5	1781	10.4	82.3	70.5	940	Mean depth for daytime diving of Turtle 3 only
<i>Eretmochelys imbricata</i>	43	TDR	ODEV	34 (21)	Post-hatchling	UK	7.25 <sup>a</sup>	0.06		86	2.1	6	5.3	17.1	
	49	TDR	NINT	6 (4)	Adult	f	143.7	267.8		1041	7.4	67.3	19.1	124	
	48	TDR	NINT	6 (5)	Adult	f			15.7–29.8	4395	10.1	67.3	33	146	
	55	TDR	NINT	18 (19)	Adult	f		268		23,806	7.8	44.9	14.6	35.2	
	1	TDR	NINT	9 (11)	Adult	f				1450	31.2	74	5.7	20.6	
	2	TDR	NDEV	21 (18)	Juvenile	UK	41.6	7.7		n.a.	16	53	8	91	Data for daytime dives
	26	Observation	NDEV	11 (11)	Juvenile	UK	51				23.8	31	6.9	9	data for resting dives
	29	TDR	NINT	4 (4)	Adult	f	82.5			1758	38.6	79.5	11.3	55.3	Data for Profile A dives
	35	AccDL	NDEV	4 (4)	Juvenile	UK	46.3 <sup>a</sup>	9.6	24.9–30.1	1034	26.6	112.4 <sup>c</sup>	10.4		
	50	TDR	NFG	4 (3)	Adult	f		81.3	24.1–31.4	18,955		138 <sup>c</sup>	19.2	48 <sup>c</sup>	
<i>Lepidochelys kempii</i>	53	TDR	NDEV	6 (4)	Juvenile	UK	42	10.2		3353	19.2	81.1	6.8	72.1	Mean depth of resting dives
	54	Observation	NDEV	4 (4)	Juvenile	UK	52.5		25.63–31.05	187	27.4	62	8.2	26	
	56	TDR	NDEV	19 (9)	Juvenile	UK	42.3				7.5	61.5	5.1	23.3	Dive duration for daytime dives
	45	TDR	NDEV	3 (1)	Juvenile	UK	41 <sup>d</sup>	10.8		1922	4.8	22.1		4	Shallow habitat
	32	SRDL	NFG + OFG	4 (4)	Adult	f	68.7		23–29	17,328	35.9		39.8	200	
	Lepidochelys olivacea													254	
	36	SRDL	ODEV	2 (2)	Juvenile + sub-adult	UK	57.5								
	51	PSAT	ODEV	14 (11)	Juvenile	UK	59		22–28					408	
<i>Natator depressus</i>	44	TDR	NDEV	22 (22)	Post-hatchling	UK		0.06		192		5.8		11	

<sup>a</sup> These values refer to straight carapace length.

<sup>b</sup> These are median values or range of medians.

<sup>c</sup> These values were estimated from the figures in the cited publication.

<sup>d</sup> for Profile descriptions see Fig. 3.

**Table 2**

Maximum recorded values for dive duration and depth for each species. Apex numbers indicate the corresponding reference for these values.

Species	Max duration (min)	Max depth (m)
<i>Caretta caretta</i>	614.4 <sup>1</sup>	233.0 <sup>2</sup>
<i>Chelonia mydas</i>	307.0 <sup>1</sup>	138.0 <sup>3</sup>
<i>Dermochelys coriacea</i>	86.5 <sup>4</sup>	1250 <sup>5a</sup>
<i>Eretmochelys imbricata</i>	138 <sup>6b</sup>	91 <sup>7</sup>
<i>Lepidochelys kempii</i>	217 <sup>8c</sup>	n.a.
<i>Lepidochelys olivacea</i>	200.0 <sup>9</sup>	408.0 <sup>10</sup>
<i>Natator depressus</i>	5.8 <sup>11d</sup>	11.0 <sup>11d</sup>

## References

<sup>1</sup> Broderick et al. (2007).

<sup>2</sup> Sakamoto et al. (1990a).

<sup>3</sup> Rice and Balazs (2008).

<sup>4</sup> López-Mendilaharsu et al. (2009).

<sup>5</sup> Houghton et al. (2008a).

<sup>6</sup> Storch et al. (2005).

<sup>7</sup> Blumenthal et al. (2009).

<sup>8</sup> Gitschlag (1996).

<sup>9</sup> McMahon et al. (2007).

<sup>10</sup> Swimmer et al. (2006).

<sup>11</sup> Salmon et al. (2010).

<sup>a</sup> A maximum of >1300 m was already estimated by Eckert et al. (1989), but depth sensor range was only until 315 m.

<sup>b</sup> This value was estimated from Fig. 2 in Storch et al. (2005).

<sup>c</sup> This value was based on the saltwater switch function of a satellite transmitter; since this transmitter was not equipped with a pressure sensor, the study was not among the 57 selected diving behavior studies (see Appendix 1).

<sup>d</sup> These values were derived from post-hatching turtles weighing less than 100 g.

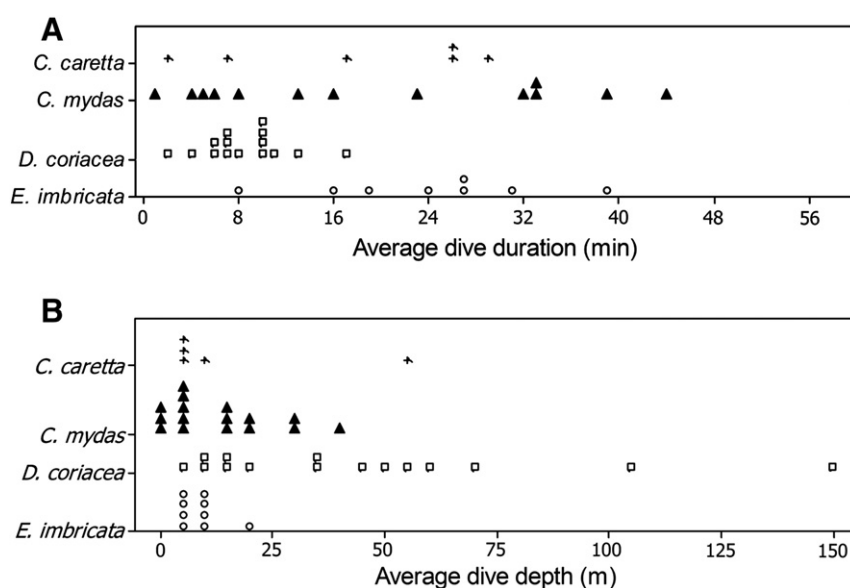
at the lower range of temperatures tolerated by sea turtles, body oxygen reserves are consumed much slower than at higher temperatures and last for longer periods underwater (Davenport et al., 1982; Hochscheid et al., 2004; Lutz et al., 1989; Southwood et al., 2006). Hence, the longest dive durations recorded for a diving turtle, and as it is, for any diving air-breathing vertebrate, were in the range of eight to 10 h during the winter period with water temperatures between 12 and 14 °C (Broderick et al., 2007; Hochscheid et al., 2007a; see also Hawkes et al., 2007). It has been proposed that these long dives, which typically occur in bouts lasting for several days up to weeks, are

still within the aerobic capacity of turtles, thus opposing the concept that turtles, at least some populations, hibernate. However, until a dedicated study with time–depth recording devices has been carried out on either green turtles in the Gulf of Mexico or loggerhead turtles in the Cape Canaveral Shipping Channel (i.e., the populations hitherto assumed to hibernate (Carr et al., 1980; Felger et al., 1976; Hochscheid et al., 2004; Southwood et al., 2003a)), the possibility that sea turtles may also stay underwater for extended periods using anaerobic metabolism, as some freshwater turtles do (Ultsch, 1989), cannot be excluded entirely.

While turtles that migrate through or forage in the open ocean may also experience seasonal temperature changes, they are as well subject to latitudinal temperature differences and temperature variations in association with oceanographic features such as eddies or frontal zones. Although several studies reported on behavioral changes by turtles that encountered different temperatures, the correlations between diving behavior and water temperature differed. For example, leatherback turtles foraging in the North Atlantic made short ( $\approx 5$  min) and shallow (30 m) dives throughout the day and night, but when they moved to warmer southern regions they exhibited diel diving patterns, with longer deeper nocturnal dives (James et al., 2006b). A similar behavior has also been observed by Sale et al. (2006) for leatherback turtles diving in the South Indian and Atlantic Oceans. In comparison, loggerhead turtles in the North Pacific adapted their diving behavior to the presence and depth of the thermocline, by exhibiting shorter and shallower diving behavior when temperatures drop below 15 °C at 20 m (Howell et al., 2010). In more tropical Pacific regions, olive ridley turtles changed their depth utilization when they encountered different oceanographic conditions to remain within the same temperature range of 22–28 °C (Swimmer et al., 2006). In summary, temperature–dive behavior relationships in the open ocean seem to differ among species and regions; yet, all studies proposed that diving activities are rather indirectly linked with temperature through associated prey distributions, which ultimately shape sea turtle behavior.

#### 4.1.2. Oceanographic features (current systems, frontal zones, and eddies)

While temperature effects on sea turtle diving behavior have been given surprisingly limited attention, even less is known about the influence of oceanographic features that characterize their habitats.



**Fig. 1.** Average dive durations (A) and depths (B) reported for four species of sea turtles. Note: for *Lepidochelys olivacea*, *Lepidochelys kempii* and *Natator depressus* not enough data were available to be plotted in this graph; extremely long dive durations for *Caretta caretta* and *Chelonia mydas* during the cold winter period were not included in this graph, since comparable data for other overwintering turtles were not available.



Yet, there is ample evidence for the importance of major current systems, mesoscale eddies, and frontal zones for the distribution and movement patterns of marine turtles throughout their life history (see, for example, Galli et al., 2012; Girard et al., 2009; Hays et al., 2010; Kobayashi et al., 2011; Lambardi et al., 2008; Luschi et al., 2003; Monzón-Argüello et al., 2012; Plotkin, 2010; Polovina et al., 2000). For example, Lambardi et al. (2008) showed that oceanic currents have profound effects on the shape of leatherback turtle movement routes, varying from straight line segments (in fast flowing currents) to convoluted looping legs, which were almost identical to those of passive drifters. Turtles are more likely to encounter and become entailed in complex dynamic ocean circulation systems in offshore areas, where studies on diving behavior are most difficult. Hence, to date, only limited detailed diving data in association with ocean circulation patterns are available, with some of these studies seeming contradictory. Sale et al. (2006) found that the diving activities of leatherback turtles around the southern African continent remained invariable when moving along main currents or looping within eddies. In contrast, Doyle et al. (2008) reported shallow diving within mesoscale features for the same species, and showed that diving behavior changed markedly upon leaving the mesoscale, becoming deeper (mostly >225 m, often even >500 m).

In their pioneering work in 1990, Sakamoto et al. (1990a, 1990b) used sophisticated multi-channel data loggers and made a detailed description of loggerhead turtle diving behavior in relation to frontal zones in the Kuroshio Ocean Current (NW Pacific). In particular, one turtle made irregular deep (to >100 m) and relatively short (<10 min) dives near the frontal zone when crossing over from warmer to cooler waters (and vice versa), which was discussed as thermoregulatory behavior to compensate for the experienced temperature changes. The authors also reported different diving behavior within the strong Kuroshio Current, where the turtle never exceeded 17 m depth and made long dives (30 min), which were three times longer compared to dives outside the Kuroshio Current. Twenty years later (Howell et al., 2010) showed that juvenile loggerhead turtles, also in the North Pacific, spent more time in warm-core eddies, but that their diving behavior was independent of eddy characteristics (warm- or cold core). Yet, dive behavior changed in relation to the placement of the turtles within the eddy edge, whereby dive depth and duration were deeper and longer, respectively, in stronger eddy currents.

Latitudinal differences in diving behavior (including inter-basin differences) may be related to how prey is distributed vertically in the water column (see, for example, Shillinger et al., 2011), which ultimately depends on the nature of the water masses and prevailing circulation systems. Changes in dive depth and duration were noted for leatherback turtles moving through different latitudes, with inferred high foraging success occurring at higher latitudes where dives were shorter and shallower compared to diving at low latitudes (Hays et al., 2006). In addition, loggerhead turtles are more abundant in areas that contain many frontal features where suitable prey items are assumed to aggregate (Kobayashi et al., 2011); consequently, diving behavior is expected to reflect sea turtle foraging mode in these hotspots. More examples of latitudinal and site-related differences in diving behavior are discussed in Section 5.4. Combined, these studies form a potentially stimulating field of research, aimed towards understanding the fine scale mechanisms through which turtles locate their prey in a highly dynamic environment.

Diving behavior might also be temporarily affected by severe short-term changes in oceanographic conditions, such as during hurricanes or typhoons. During the passage of hurricane George in the Caribbean, a hawksbill turtle made shorter dives, spent less time at the surface and was generally more active (Storch et al., 2006). In addition, a loggerhead turtle encountering a typhoon increased its diving frequency, as well as dive depth and time spent at depth (Sakamoto et al., 1990a). In both cases there was clear avoidance behavior to reduce disturbance by wave action, and the turtles remained in a state of agitation for the

duration of the event, but were unaffected in the long-term, resuming quickly their “normal” behavior after the passage. Other species of marine mega-fauna such as, for example, blacktip sharks *Carcharhinus limbatus*, also react in a similar way to storms actually responding to changes in barometric pressure (Heupel et al., 2003). Hence, it would be important to identify to what parameter turtles are responding.

#### 4.1.3. Turtle size

Turtles span a considerable size range from a few tens of grams as hatchlings up to just under a ton as adults in certain species. Following the universal scaling rules (Schmidt-Nielsen, 1984) and the established allometry of diving capacity in air-breathing vertebrates (Schreer and Kovacs, 1997), it may be expected that size also matters for the dive performance of sea turtles. Indeed, the importance of turtle size has been shown for oxygen consumption rates (Hochscheid et al., 2004; Prange and Jackson, 1976; Wallace and Jones, 2008), heat exchange (Paladino et al., 1990; Sato et al., 1995; Spotila and Standora, 1985), and respiratory properties (e.g. maximum lung capacity (Hochscheid et al., 2007b)), among other parameters, all of which impact turtle diving capacities to some extent.

However, size-related differences in diving behavior may be explained by both underlying physiological mechanisms and ecological differences, such as habitat use and niche occupation. Small post-hatchling green and leatherback turtles (1 to 10 weeks of age) lead an epipelagic lifestyle with average dive depths of 2.5 to 5 m, and as they grow they tend to dive deeper for longer (Salmon et al., 2004). The flatback turtle, which is the only species lacking an oceanic developmental phase, starts to dive to the seabed at an early age, but still no deeper than 11 m. In this species, variations in dive behavior were, in fact, weight but not age related (Salmon et al., 2010). Juvenile hawksbill turtles (2–22 kg) showed a significant positive correlation between body mass and both dive duration and depth, although the latter was only correlated at night (Blumenthal et al., 2009). The authors argued that the diurnal relationship was not significant because diving was influenced by too many other factors (forage distribution, predator avoidance, competition, etc.). However, maximum diurnal dive depth was significantly deeper in bigger turtles, possibly reflecting greater diving capabilities that allow larger animals to forage in relatively pristine deep ecosystems with abundant sponges. In contrast, at night, size-related behavior was more evident, which conforms to the theory that size-specific depth selection allows individual turtles to maximize their resting time by diving with fully inflated lungs, and hence, maximum oxygen stores (Hays et al., 2004a).

Intrigued by the multiple functions of marine turtle lungs, including respiration, oxygen storage, and buoyancy regulation, Hochscheid et al. (2007b) demonstrated the consequences of allometric relationships for maximum lung volume for the diving capacity (assessed via calculated aerobic dive limits, cADL) in marine turtles. Considering the body mass effects on oxygen storage capacities and oxygen consumption rates, the authors calculated a scaling exponent of 0.6 for aerobic dive limits. However, the analysis of average dive durations from free-ranging hard shelled turtles revealed that dive duration only increases with a mass exponent of 0.51 (obtained through bootstrap Model II regression revealing a 95% confidence interval of 0.364 to 0.683), although there was considerable scatter around the fitted regression line. Even though this work showed that (chelonian) marine turtles appear to conform to the general paradigm of enhanced dive capacity in larger animals (Schreer and Kovacs, 1997), the increase in dive duration was not proportional to increases in body mass. In an attempt to narrow down the confidence interval of the scaling exponent and to determine with more certainty whether dive duration scales as predicted by the cADL-mass relationship, I extended the available dataset with more recently published dive durations. Unfortunately, despite the increase in publications on dive behavior, few papers included information about the body mass of the studied turtles and/or presented data that met the previously established conditions

(a study in water temperatures above 22 °C). Overall, 20 average duration–mass data pairs were added to the original dataset, but there was no improvement to the variability in average dive durations, with body mass appearing to be even less of a predictor (simple least square regression  $r^2 = 0.08$ ) (Fig. 2). Applying the bootstrap (10,000 iterations) Model II regression (as in Hochscheid et al., 2007b), the slope of the scaling exponent was 0.67, which seems, at first sight, to approach the predictions of the cADL–mass relationship, but the 95% confidence interval was actually even larger (0.538 to 0.881). There is thus still need of further increasing this dataset, and since temperature has a profound impact on dive durations, future analyses might consider the combined impacts of size and temperature together.

There are several examples that size-related dichotomy in behavior might also depend on latitudinal or, generally, geographical distribution of individual turtles. In accordance with Bergmann's rule, Witt et al. (2007) found that the northern most (Northeast Atlantic) waters were predominantly used by bigger leatherback turtles, whereas smaller turtles were distributed in more southerly locations. This pattern is most likely driven by the gigantothermy of these largest marine reptiles, making colder northern waters only accessible for bigger turtles, due to thermal constraints. However, such a latitudinal gradient in leatherback turtle body size was not confirmed by Shillinger et al. (2011) in the Northeast Pacific, and neither paper reported on size-related differences in diving behavior. The perhaps best-known examples for behavioral polymorphism were described for loggerhead turtles, particularly adults, which diverged into neritic and oceanic foraging habitats. In the waters off Japan, larger loggerhead females used pelagic feeding habitats, whereas smaller turtles used neritic feeding habitats (Hatase et al., 2002). The same was found by Hawkes et al. (2006) studying post-nesting female loggerhead turtles at Cape Verde. These authors pointed out that both records of this unusual behavior came from insular nesting populations in temperate regions which may experience similar surface currents and productivity. Interestingly, in a continental nesting population of tropical Oman, there was no correlation between body size and foraging strategies albeit neritic and oceanic foraging areas were used all the same (Rees et al., 2010). At any rate, the link between diving behavior and turtle size is rather indirect due to different resource distribution and availability in these habitats, which require different diving strategies (see also Section 5.2). Recently, size and diving relationships were discovered for male loggerhead turtles that separated after the breeding season in Florida into northbound and southbound groups (Arendt et al., 2012). Although this study revealed association with body mass and dive duration in northbound males and surface interval in southbound males, this behavioral difference was not further explored and there seemed to be no mutual link between foraging variability and either body size or geographic area. However, a recent discovery by Schofield et al. (2013) revealed that also in the Mediterranean larger turtles forage at higher latitudes, indicating that size related geographic distribution and behavior are well worth further investigations.

## 5. Classification and characterization of dives

### 5.1. Dive types and profiles

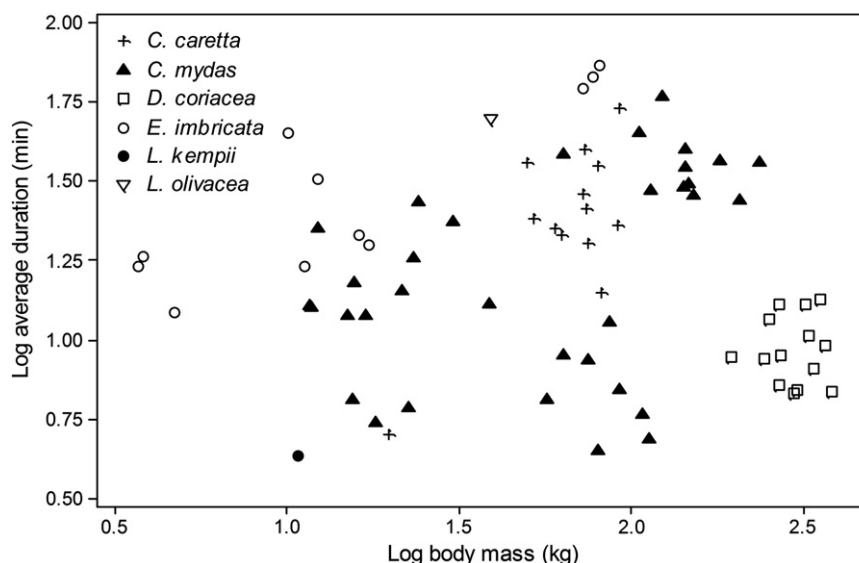
The study of behavioral patterns in diving animals largely relies on the analysis of times that an animal spends at certain depths. Time–depth data are usually obtained in the format of either continuous depth records at user-specified intervals or as histograms of time spent in depth classes. The former are also most commonly known as depth or dive profiles which result from the graphical output of depth plotted against time (Fig. 3). Dive profiles may be distinguished by their shape and have, thus, been described as, for example, U-, V-, and W-shaped dives (Fedak and Thompson, 1993; Hochscheid et al., 1999; Wilson et al., 1996). While these terms are easy to remember and to associate with particular dive profiles, capital letters may not

adequately represent the more complex dive patterns that sea turtles exhibit. Therefore, many authors simply started to number dive types. Fig. 3 shows schematic drawings of the most described dive profiles, while Table 3 lists all publications that have described and named these profiles. From here onwards, particular dive profiles are referred to by their panel letter in Fig. 3. The problem becomes immediately clear: not only are there multiple names for the same dive profile, but authors also typified dive profiles with names that were already assigned to other dives in previous publications. Depending on the authors, Type 2 dives, for example, have five quite different shapes, which leads to difficulties in the comparison of behavioral patterns.

It is worth noting that “dive profile” and “dive type” are not synonyms, because dive patterns have been categorized into different types based on specific dive parameters (e.g., TDD, MDD, bottom time, and ascent duration, Fossette et al., 2007) or through statistical analyses that group similar dives (e.g., K-means cluster analysis, Howell et al., 2010). Dive types have also been assigned to datasets consisting of depth histograms, but not profiles (Howell et al., 2010). At any rate, the importance of dive type classification is that of assigning a scope or specific activity to each type so that we may obtain a comprehensive picture of how turtles allocate time to various underwater activities. This direction requires that we are able to distinguish the various dive types and interpret the associated behavioral activity of turtles; however, both presumptions are not consistently fulfilled in the literature, at present.

U-shaped dives (Profiles A and B in Fig. 3), for example, have widely been recognized as typical profiles obtained from turtles resting on the seabed (refer to references given in Table 3). After Houghton et al. (2002), these flat-bottomed dives were divided in two sub-types, one with little to no variation in the depth readings during the bottom phase (Profile A in Fig. 3) and one with some variation, also referred to as “wiggles” by other authors (Fossette et al., 2007; Profile B in Fig. 3). Not all papers present dive profiles with sufficient detail to show these differences; in fact, such distinctions have not been made by all authors, although they may exist in the raw data. The question is when should we recognize these wiggles as indicators of different behavior during the bottom phase (e.g., amplitude, frequency)? It has been suggested that wiggles occur during feeding and feeding related behaviors (searching, seizing, etc.). However, these small scale movements during the bottom phase of a dive might be easily missed if the sensor resolution is not finely tuned, or if the sampling interval is too long. In fact, Hochscheid et al. (1999), using a 15 s sampling interval with a pressure sensor resolution of 0.1 m, recorded U-shaped dives which all looked very much alike, but additional data recorded simultaneously by an activity sensor showed that green turtles were indeed quite active during the bottom phase of some of these dives, while they did not move (i.e., rested) during others.

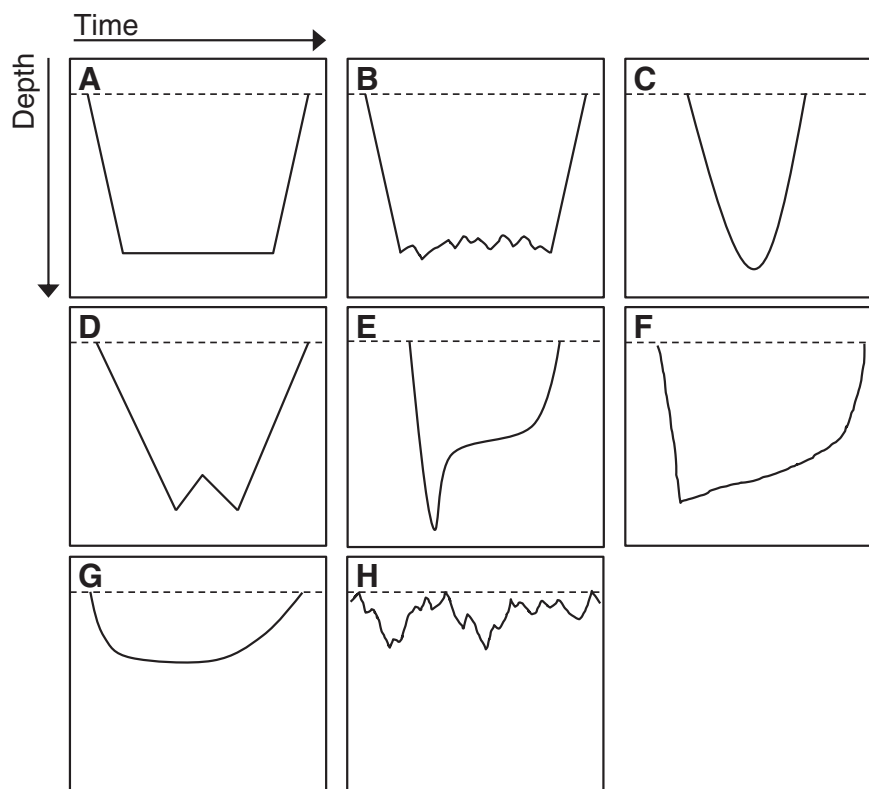
Additional consideration of dive depth and duration, as well as time of day and, if available, location, make researchers today fairly confident in differentiating resting and feeding Profile A dives. Other profiles, such as Profiles C or E (Fig. 3), are less easily associated with common underwater activities, such as exploration, orientation, foraging, and swimming. In particular, Profile E is again another example of multiple functions, being described as mid-water resting, traveling, and foraging dives, which are strategically quite contrasting activities (Table 3). The disagreement among studies in the assignment of activities to distinct dive profiles highlights the shortcomings of TDR data as the only source for behavioral investigations. Of course, multiple behaviors may be exhibited during a single dive, especially if the shape is more complex, as was demonstrated by simultaneous visual observations on a diving hawksbill turtle (cf. Fig. 8 in Blumenthal et al., 2009). Thus, having identified the characteristic dive profiles performed by marine turtles, one of the next steps in teasing apart the details of their free-living behavior is to gather information from direct observations or additional sensors, because the interpretation of dive profiles is mostly based on speculation and guesswork.



**Fig. 2.** Average dive duration in relation to body mass for different marine turtle species. Mean dive durations, body masses and references for each species are given in Table 1.

Few studies have made an effort to validate TDR records through synchronization with visual observations (reviewed by Francke et al., 2013); yet, such studies deliver valuable information about specific behavior-related movement patterns, that help us understand to what extent fine-scale changes in behavior may be captured by electronic tags. However, direct observations have obvious limitations (e.g., visibility, habitat type, and animal disturbance), and are certainly not applicable in most situations that require remote telemetry techniques

in the first place. In this respect, underwater cameras linked to TDRs represent a practical solution to mitigate some of the constraints of direct observation (Marshall, 1998). Swimming, breathing and feeding could be captured either as snapshot photos or short videos, thus allowing these behaviors to be directly linked with specific dive profiles (Fuller et al., 2009; Hays et al., 2007; Heithaus et al., 2002; Reina et al., 2005; Seminoff et al., 2006). Some studies even revealed hitherto unknown aspects of turtle biology, such as, for example,



**Fig. 3.** Generalized drawings of dive profiles that have been described for sea turtles. The depth and time arrows merely indicate the axis variables, but the figure does not represent true proportions of depths and durations for the various profiles, with exception of drawings shown in panel G and H, which have only been described for shallow dives (<5 m). Names and activities that have been associated with these profiles are listed in Table 3 with the corresponding references.

**Table 3**

Activities that have been associated with the different dive types presented in Fig. 3. Dive profile descriptors refer to panel numbers A–H in Fig. 3, while profile names were given by the authors in the respective publication.

Dive profile <sup>a</sup>	Described by	Species	Profile name	Scope	Notes
A	Sakamoto et al. (1993)	<i>Caretta caretta</i>	Type 1	Bottom resting	Same name was used for “active dives” which resemble more Profile F
	Minamikawa et al. (1997)	<i>C. caretta</i>	Type 1	Bottom resting	
	Hochscheid et al. (1999)	<i>Chelonia mydas</i>	U-dive	Bottom resting + feeding	
	Houghton et al. (2002)	<i>C. caretta</i>	Type 1a	Bottom resting	
	Seminoff et al. (2006)	<i>C. mydas</i>	Type 1	Bottom feeding	
	Rice and Balazs (2008)	<i>C. mydas</i>	Type 4	Bottom resting	
	Cheng (2009)	<i>C. mydas</i>	U-dive	Bottom resting	
B	Houghton et al. (2002)	<i>C. caretta</i>	Type 1b	Bottom feeding <sup>a</sup>	
C	Minamikawa et al. (1997)	<i>C. caretta</i>	Type 2	Not given	Also of benthic habitats Also compared to dives of Profile E
	Hochscheid et al. (1999)	<i>C. mydas</i>	V-dive	Exploration, orientation	
	Houghton et al. (2002)	<i>C. caretta</i>	Type 2	Not given	
	Seminoff et al. (2006)	<i>C. mydas</i>	Type 2	Exploration	
	Fossette et al. (2007)	<i>Dermochelys coriacea</i>	Type 2	Searching + feeding	
D	Salmon et al. (2004)	<i>D. coriacea</i> , <i>C. mydas</i>	W-dive	Pelagic foraging + feeding	Described also profiles A and C, but did not assign specific activity other than shallow pelagic diving of post-hatchling juveniles
	Seminoff et al. (2006)	<i>C. mydas</i>	Type 6	Benthic exploration	
E	Minamikawa et al. (1997)	<i>C. caretta</i>	Type 4	Mid-water resting	Other activities were discussed, but this seemed the most plausible
	Hochscheid et al. (1999)	<i>C. mydas</i>	S-dive	Traveling by swim and glide	
	Houghton et al. (2002)	<i>C. caretta</i>	Type 4	Mid-water resting	
	Hays et al. (2001)	<i>C. mydas</i>	Type 2	Mid-water resting	
	Rice and Balazs (2008)	<i>C. mydas</i>	Type 3	Pelagic exploration + feeding	
F	Minamikawa et al. (1997)	<i>C. caretta</i>	Type 3	Mid-water resting	Type 3 dives resembled also Profile B  Authors called this “active U-dive” but the profiles presented resembled in shape Profile F
	Hays et al. (2001)	<i>C. mydas</i>	Type 1	Mid-water resting	
	Houghton et al. (2002)	<i>C. caretta</i>	Type 3	Traveling	
	Fossette et al. (2007)	<i>D. coriacea</i>	Type 3 + 4	Foraging	
	Rice and Balazs (2008)	<i>C. mydas</i>	Type 2	Traveling	
	Cheng (2009)	<i>C. mydas</i>	U-dive	Searching, traveling, feeding	
G	Houghton et al. (2002)	<i>C. caretta</i>	Type 5	Traveling	Compared to SSD <sup>b</sup> in Hochscheid et al. (1999) Turtle was also observed feeding on pelagic prey during a dive of this profile
	Seminoff et al. (2006)	<i>C. mydas</i>	Type 5	Orientation, traveling	
	Fossette et al. (2007)	<i>D. coriacea</i>	Type 1	Traveling	
H	Hochscheid et al. (1999)	<i>C. mydas</i>	SSD	Traveling	
	Southwood et al. (2003b)	<i>C. mydas</i>	Shallows	Not given	
	Rice and Balazs (2008)	<i>C. mydas</i>	Type 1	Traveling	

<sup>a</sup> Not specified for this particular dive profile, but suggested as possible “bottom activity”.

<sup>b</sup> SSD = sub-surface dives.

delivering proof that green turtles opportunistically forage for pelagic macroplankton (Heithaus et al., 2002; Seminoff et al., 2006), despite being assumed vegetarian. But, as with direct observations, the deployment of video cameras on turtles also has its limitations, such as being constrained to large animals that are able to carry bulky equipment.

Electronically enhanced tags provided an efficient means of building a better framework for categorizing behaviors on the base of time–depth data. In the following sentences, a few important findings from the use of multi-sensor data loggers are summarized to show how these instruments contributed to our understanding of particular underwater activities. Sensors used to measure swim speed were employed with moderate success, but Minamikawa et al. (1997) were nonetheless able to show that swimming during flat bottom phases (Profile A) and gradual ascent phases (Profiles E and F) ceased or slowed down significantly, lending support to the theory that these parts of the dive cycle serve to minimize energy expenditure. Active swimming versus gliding during these phases was further demonstrated by the application of an IMASU (Integrated Movement Assessing Sensory Unit) that recorded flipper beat frequency during diving in green

turtles (Hays et al., 2004b). An Inter-Mandibular Angle Sensor (IMASEN), a modified version of the IMASU movement sensor system, was developed to measure beak movements instead, revealing several insights in turtle underwater behavior. First, the true “sleeping phases” of Profile A dives were identified as the times at which buccal pumping (a mechanism by which turtles sample the environment for olfactory sensory information [Manton et al., 1972]) ceases (Houghton et al., 2008b). Other studies, focusing on the actual buccal oscillations instead, showed how leatherback turtles sample the water in search for prey during the descent phases of Profile C dives, and during the wiggles at the bottom of Profile A and D dives (Fossette et al., 2008a; Myers and Hays, 2006). Finally, benthic foraging of loggerhead turtles during Profile A dives was quantitatively determined, and even qualitatively assessed (Hochscheid et al., 2013), obtaining an initial estimate of how much time turtles have to spent feeding to sustain other activities. Meanwhile, building on the experience from the 3D compass system used as means to measure the level of activity in free-ranging turtles (Hochscheid and Wilson, 1999; Hochscheid et al., 1999), 2- and 3-axis accelerometers are now being successfully deployed to obtain dynamic



body acceleration (DBA) for various underwater activities (Fossette et al., 2012; Okuyama et al., 2009; Wilson et al., 2008). Besides a series of exciting applications for this methodology (see also Section 8.2), the doubt about which dive profile represents mid-water resting may have been eliminated by showing that average DBA of loggerhead turtles performing Profile F dives is as low as during bottom resting dives (Fossette et al., 2012).

### 5.2. Diel patterns

Many studies have reported diel diving patterns where sea turtles alternate between periods of activity (foraging, traveling, etc.) and inactivity (resting) in correspondence to the light–dark cycle. These patterns are manifested by differences in dive depth, duration, and/or frequency between day and night, and are often related to the habitat and availability of suitable forage. The predominant pattern in neritic foraging and developmental habitats is diurnal activity (e.g., shorter and shallower dives) and nocturnal resting (e.g., longer and deeper dives) (Blumenthal et al., 2009, 2010; Hazel et al., 2009; Makowski et al., 2006; Sasso and Witzell, 2006; Taquet et al., 2006; van Dam and Diez, 1996; Witt et al., 2010), which is often, but not always (Makowski et al., 2006), accompanied by horizontal movements between foraging and resting sites. Foraging activity during daylight often peaks around dawn and late afternoon hours and may be interrupted by bouts of resting dives during the middle of the day (Hochscheid et al., 2013; Makowski et al., 2006). Although chemoreception may play an important role in searching for prey (Hochscheid et al., 2005b; Manton et al., 1972; Myers and Hays, 2006), this foraging activity during daylight hours strongly suggests that turtles rely on visual cues to locate food. Thus, night time foraging is seldom observed in neritic habitats where prey availability is constant, although reversions of this pattern may occur occasionally when night light intensity is high (e.g., on cloudless moon nights; Taquet et al., 2006).

Species that forage on mobile prey synchronize their activity cycles to enhance prey encounters and foraging success. The depth utilization of leatherback turtles, for example, indicates that they forage on gelatinous plankton in the deep scattering layer (DSL), and may follow their prey during vertical movements to some extent (Eckert et al., 1989; Hays et al., 2004c). Since the DSL moves into shallow depths during the night, most foraging is assumed to be nocturnal. In fact, loggerhead and green turtles diving in the oceanic realm have also been shown to adopt deep and long dives at night, and may as well forage on macroplankton when it is within diving reach (Cheng et al., 2013; Hatase et al., 2007; Hochscheid et al., 2010; Rice and Balazs, 2008; Sakamoto et al., 1990a). Yet, again, this nocturnal foraging pattern on vertically migrating plankton is not universal, as was suggested by Fossette et al. (2007) for inter-nesting leatherback turtles that presumably foraged during the day near the continental shelf off French Guiana, where suitable prey is available at shallower depths. Furthermore, the activity of benthic mobile prey may also influence turtle diving behavior, as was recently shown by Hochscheid et al. (2013), who successfully measured feeding on crabs by a loggerhead turtle using a beak movement sensor. In fact, feeding occurred predominantly during early morning and late afternoon, where the nocturnal crabs may still be active and light conditions allow for better hunting.

Although some clear diel patterns are evident, it has also been repeatedly shown that behavioral dichotomy exists at the individual and population level, mostly depending on the temporal use of a habitat and its resources (Eder et al., 2012; Hatase et al., 2010; Hawkes et al., 2006; Mansfield et al., 2009; McClellan et al., 2010; Richardson et al., 2013). Both green turtles nesting in Taiwan and loggerhead turtles nesting in Japan used oceanic and neritic habitats during the inter-nesting period, which was reflected in different diel diving patterns (Cheng et al., 2013; Hatase et al., 2007; Sakamoto et al., 1990a). As a rule of thumb, however, turtles in oceanic habitats and feeding in the DSL dive deeper (mean dive depth  $\geq 50$  m; Houghton et al., 2008a;

Sakamoto et al., 1990a, 1990b; Sale et al., 2006) compared to their conspecifics in coastal habitats (mean dive depth  $\leq 30$  m) (Polovina et al., 2003). These deep dives are also often associated with prolonged dive durations, which may even exceed the cADL of some species (Hochscheid et al., 2010; Houghton et al., 2008a), because foraging in an environment with patchy food distribution may lead turtles to maximize their feeding success by incurring an oxygen debt (Thompson and Fedak, 2001). At any rate, changes in diel diving patterns occur along horizontal migration paths, when resource availability changes and turtles are constrained to adapt different foraging strategies, as shown for leatherback turtles in several studies (James et al., 2006b; Sale et al., 2006).

### 5.3. Seasonal patterns

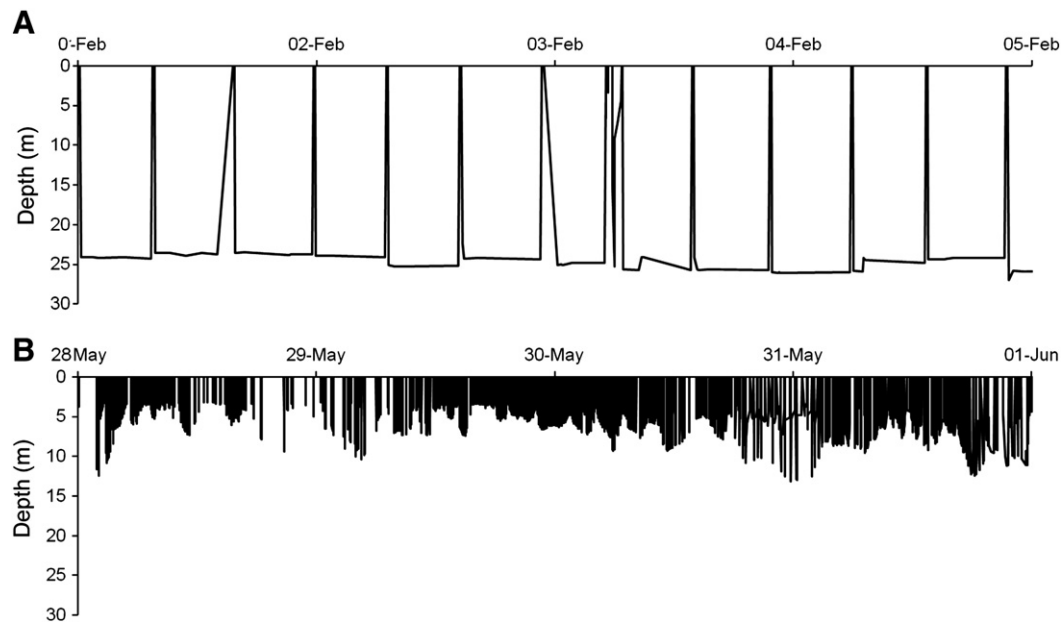
Seasonal variation in environmental conditions and prey availability might also induce changes in dive behavior, as observed for diel cycles. One factor that is likely to change across seasons, at least outside the tropics, is temperature, which is negatively correlated with dive duration, as discussed in Section 4.1.1. Loggerhead and green turtles overwintering in coastal temperate waters show an increase in dive duration when water temperatures drop (Hochscheid et al., 2005a, 2007a), which sometimes coincides with offshore movement into deeper waters (Broderick et al., 2007; Godley et al., 2002). The typical dive pattern is that of long flat-bottomed dives, which is indicative of turtles resting on the sea floor at depths between 10 and 30 m, returning only infrequently to the surface after intervals of several hours (Fig. 4A). During spring, the turtles become more active, and return to shallow inshore feeding areas where they dive more frequently, and dive durations decrease drastically. Seasonal offshore movements may be, as in this case, as short as a few kilometers (Broderick et al., 2007), or as far as 100 km, as reported for loggerhead turtles overwintering off the north eastern coast of America at the edge of the Gulf Stream, thus avoiding colder inshore waters (Hawkes et al., 2007). The general winter dive pattern of the North American turtles was similar to that of the North African turtles, albeit at slightly deeper depths (median 30 to 70 m); however, the reason for the offshore overwintering may be driven more by temperature rather than the presence of favorable resting depths.

Regional or population differences in overwintering behavior were first identified by Felger et al. (1976), who reported on green turtles hibernating in the Gulf of California; however, Hatase et al. (2007) were the first to show mid-water dormancy of  $>5$  h at 18 °C by loggerhead turtles in the Northwest Pacific Ocean. This peculiar behavior, previously also only reported for loggerheads in Japanese waters (Minamikawa et al., 2000), was shown by dive depths to  $<25$  m at a sea floor depths of  $>100$  m. This phenomenon is yet another example of behavioral plasticity in these marine reptiles, which may undertake long quiescent winter dives even in the absence of suitable bottom resting places, although this “hovering” and buoyancy dependent resting may be more costly energetically.

In comparison to the low activity dive patterns during the cold season, the warm summer months are generally associated with peak activities and overall short dive durations (Arendt et al., 2012; Godley et al., 2003; Hochscheid et al., 2007a; Storch et al., 2005) (Fig. 4B). Even in regions with less pronounced temperature differences (mean summer versus mean winter = 26.2–21.3 °C), seasonal variation in dive behavior has also been recorded for juvenile green turtles residing in sub-tropical waters off east Australia (Southwood et al., 2003b). These juveniles preferred inhabiting shallower depths in winter ( $<1$  m) compared to summer, during which they doubled their average dive duration (24 min) and tripled surface intervals (mean 1.8 min).

For species residing in oceanic regions year-round, such as leatherback turtles (James et al., 2005), seasonal changes in dive behavior may be driven by variations in prey distribution (Hays et al., 2006; James et al., 2006b). In the North Atlantic, leatherback turtles undergo





**Fig. 4.** Seasonal dive patterns for a juvenile loggerhead turtle in a neritic foraging and overwintering ground. A) long flat-bottomed winter resting dives, modified from Hochscheid et al. (2008), B) short summer foraging dives (from same dataset as in panel A, but not published).

round-trip migrations, visiting lower latitudes during the winter months and higher latitudes in summer, whereby these southern and northern migrations are characteristic of marked changes in diel dive patterns (see also Section 5.2). However, the changes in turtle dive behavior appear to be regionally specific, and may be broadly distinguished between short and shallow northern diving, where prey is readily available in surface waters, and pronounced diel patterns in southern regions, where the diel vertical migration of prey is more expressed (Hays et al., 2006). Nonetheless, an overall increase of average dive duration and dive depth also occurred in relation to the Northern Hemisphere winter period (Hays et al., 2006), indicating that even leatherback seasonal cycles are shaped by temperature conditions to some degree.

#### 5.4. Depth utilization during migration

Geographically related differences in diving behavior have been clearly demonstrated (see Sections 4.1.3, 5.2, 5.3); hence, it may be expected that turtles temporarily using different habitats during breeding migrations also display different behaviors. It has been shown that leatherback turtles invest in longer and deeper dives during transit compared to foraging (Jonsen et al., 2006). However, leatherbacks tend to move continuously within their oceanic life style, and do not periodically shuttle between coastal feeding and breeding areas, as other turtle species. This latter group presents a great opportunity to study behavioral changes during relatively predictable short-term habitat shifts, with a number of investigations focusing on the migrations of green turtles to and from their breeding grounds.

One indisputable common feature of directed migrations is that turtles travel towards a “known” destination, which involves covering horizontal distance by active swimming, at least during parts of the transit. Corresponding to the theory of drag minimization by swimming at near-surface depths (i.e. 2.5–3 times body thickness [Hertel, 1966]), it has been repeatedly shown that turtles make predominant use of shallow waters (e.g. 0.9 to 1.5 m depth) during migration (Godley et al., 2002; Hays et al., 2001; Rice and Balazs, 2008). Hays et al. (1999) also noted a clear and significant diel pattern in submergence duration during migration from Ascension Island towards Brazil,

with longer submergences at night and shorter submergences during the daytime, with submergences generally being much shorter compared to during the inter-nesting interval. This bimodality in dive duration was also confirmed for green turtles migrating from Cyprus to the North African coast, but no associated diel rhythms were presented (Godley et al., 2002). It is possible that migrating turtles alternate between active short swimming dives and longer resting dives. It has been suggested that in the absence of suitable food in the open ocean for herbivorous green turtles, the best strategy is to swim directly towards the goal (Godley et al., 2002). Yet, opportunistic feeding en-route during coastal migratory phases may have occurred as indicated by changes in the depth utilization (generally deeper dives).

Further insights about turtle behavior during oceanic migratory phases were provided by the collection of TDR data for both males and female turtles (Hays et al., 2001; Rice and Balazs, 2008). The biphasic diving behavior of shallow (1–4) and short (1–18 min) daylight diving and longer (35–44 min) and deeper (35–55 m) night time diving might be linked to specific dive profiles (Fig. 5). Short, irregularly-shaped sub-surface dives (max 4 m; see Profile H in Fig. 3) occurred predominantly during the day, and were classified as traveling dives (Hays et al., 2001; Rice and Balazs, 2008). The deeper and longer night dives had a characteristic gradual ascent phase, occupying the largest proportion of the dive duration, which were either directly initiated at depths between 15 and 30 m or were preceded by a deeper short excursion (Fig. 3E and F). Interestingly, the same sort of diving behavior was also recorded for a green turtle in Taiwan that wandered into the open sea during its inter-nesting interval (Cheng et al., 2013). However, there was no general agreement on the purpose of these particularly shaped long deep dives. It was proposed by Hays et al. (2001) that, when the seafloor is out of diving reach, the turtles rested mid-water during the night at depths of between 13 and 21 m, where they presumably still obtain neutral buoyancy. In comparison, Rice and Balazs (2008) did not exclude the possibility that green turtles in the Pacific, which dove even deeper (35 to 55 m), might have exploited the water column for macroplanktonic food to counter-balance the energy expenditure for traveling and deep diving (see also Cheng et al., 2013).

Hopefully, new sensor technology (e.g., acceleration loggers and movement sensors (Fossette et al., 2012; Hochscheid et al., 2013)), which has been successfully deployed in neritic habitats, will soon also reveal more details in connection with dive profiles recorded during oceanic crossing.

## 6. What is missing?

Based on the general overview in Section 4, it clearly emerges that certain species are underrepresented, namely both ridley species and the flatback turtle. This observation implies that there may be yet undiscovered behavioral traits that stem from species-specific life histories. For example, McMahon et al. (2007) recently showed extraordinary performances by olive ridley turtles conducting deep ( $\geq 100$  m) and long (up to 3 h) benthic dives off northern Australia, providing evidence that this species may be fitter than others to exploit a wide range of habitats. Other gaps include underrepresented life stages, such as post-hatchlings and small juveniles, particularly during their “lost years.” The small size of this life stage, and often unknown whereabouts, makes studies a challenge; however, such limitations are expected to be surmounted with new technological developments. Exemplary for the difficulty in studying turtles in the oceanic realm, is the lack of dive data on juvenile stages of leatherbacks, for which data were obtained, with few exceptions, from adult females only. Also missing for leatherback turtles, and for most other species, are information about the dive behavior of male turtles. In addition, difficulties in sexing immature turtles prevents the sex ratios of the studied animals from being determined for non-adult life stages.

Marked differences in dive behavior were noted in relation to habitat type and geography, highlighting the need for further dive data about migratory paths, as well as overwintering grounds, both of which are areas of conservation interest, where turtles occur frequently and repeatedly, and may also be more vulnerable (e.g., dormant turtles are more prone to capture in bottom trawls (Carr et al., 1980)). While preliminary dive profiles for winter dormant turtles did not confirm that sea turtles do indeed hibernate, the true behavior of the apparently hibernating turtle populations (Cape Canaveral loggerhead turtles (Carr et al., 1980) and Gulf of California green turtles (Felger et al., 1976)) remains merely a myth. By and by, methodological solutions will be available to facilitate diving studies in remote areas, such as the oceanic developmental habitats and foraging grounds, to help improve our understanding about the role of sea turtles in complex dynamic marine systems. In this area, an important objective, certainly for mid-water foragers, is to simultaneously record the vertical movements of turtles

as well as the vertical distribution of their prey. Optimum prey search can be investigated through the mathematical properties of sequential dive depths (see Sims et al., 2008).

This review was focused on diving behavior, because that is what turtles do for 95% of their time. Yet, turtles also spend occasionally extended periods of time at the sea surface, as demonstrated by Hochscheid et al. (2010), who documented the frequency and occurrence of extended surface times in free-ranging loggerhead turtles, and attempted to investigate the reasons for remaining at the surface. Even though this behavior is not diving per se (Section 2), it seems nonetheless correlated to the preceding dive behavior, and deserves more attention in follow up studies. It is also true that surface time has typically been treated as part of the diving cycle (Kramer, 1988), because this is when animals gain access to oxygen to again dive below the surface.

Without the use of telemetry devices, we would not have the current knowledge about sea turtle diving behavior; hence, little can be done to circumvent attaching electronic equipment, well embedded in sea water resistant casts, to body parts of the turtles. Yet, surprisingly, there has been limited focus about the potential effects of these devices on the behavior that we intend to investigate. Watson and Granger (1998) performed wind tunnel tests to show that drag increases due to satellite transmitter attachments, potentially reducing green turtle swim speeds by as much as 11%. More recently, Jones et al. (2011) intensified experimental drag studies involving a series of attachment scenarios and tag shapes, clearly demonstrating that anything mounted on a turtle will not go unnoticed, whereby tag type and attachment procedures have profound effects on increasing drag. The alarming outcome of these evaluations call for further studies in which variations in turtle dive behavior may be linked to the added equipment. It must be acknowledged that these studies are logistically difficult to conduct; however, without direct comparison of the behavior of equipped versus “tag-free” turtles by some standards (e.g., breathing frequency and time at surface), the true behavior of turtles may yet remain undisclosed. One telltale example are the investigations on buoyancy regulation, where sea turtles with externally added weights used shallower depths compared to those without weights (Minamikawa et al., 2000); (Hays et al., 2004a). Therefore, in addition to the evident drag effects, biotelemetry devices (including the attachment material) alter the specific gravity of turtles and, hence, impact their state of buoyancy.

## 7. A plea for standardization

Some difficulties in compiling review derived from the variety in which authors designed their studies, configured electronic tags, analyzed, and presented their data. This meant that some results could not be compared or summarized (e.g., comparing mean and median dive parameters), and some basic information was missing, which would have been useful to present clearer overall pictures about dive relationships with other factors (e.g., scaling factors of diving parameters cannot be elucidated when turtle sizes are not given). Thus, it would be common good practice to provide always a minimum suite of extra information along with the dive data, which should always include body mass and dimensions of the turtles, sex (if known), and ambient temperature to which turtles were subject during study period (see Supplementary material).

Before we even start to record and analyze data, we should carefully consider how electronic tags are going to be configured. Depending on the duration of study period (and ultimately battery lifetime), and maximum storage capacity (or message size for data relayed via satellite, respectively), the sensors should be sampled at sufficiently high frequencies and resolutions. This would enhance data quality and the probability to detect finely tuned behavioral changes. If the study duration is supposed to be extended by duty cycles or sampling seasons, then these parameters should be synchronized as much as possible with already known diurnal or seasonal patterns. Generally, building on what

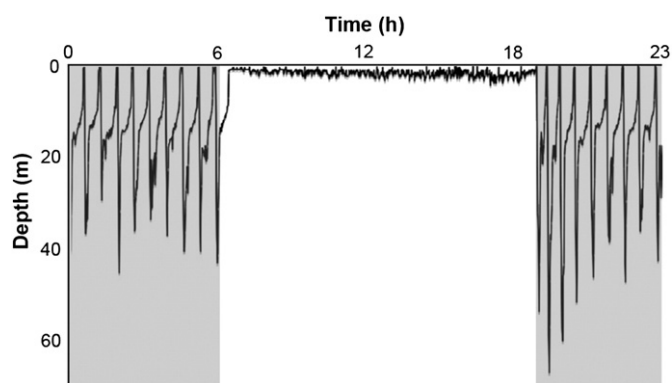


Fig. 5. Dive profiles for a female green turtle during oceanic migration showing a typical diel pattern of shallow diurnal dives and deeper, longer nocturnal dives (gray shaded areas).

Modified from Rice and Balazs (2008).

we know already, sampling regimes (i.e., periods over which dive data are collected and summarized) should correspond to natural behavioral (diel or seasonal) cycles (e.g., less frequent sensor sampling is necessary in quiescent turtles during the winter months).

When it comes to attaching instruments on turtles, the 3-fold minimization rule should govern: (1) minimize handling time – the less the animal is stressed, the more “normal” behavior data will be recorded, and the more ethical guidelines will be respected; (2) minimize drag, because it affects the turtles swimming capacities and we do not even know yet to which extent; and (3) minimize changes to the specific gravity of turtles, including any material used for the attachment, because adding weight changes the turtles' depth utilization (see Section 6), as may floats (e.g., for pop-up recovery). For as long as researchers have been attaching electronic instruments to turtles, there has been development in the attachment methods and materials and there is now a wealth of species and life stage-specific recommendations available that can be applied as good practice (see, for example, Fossette et al., 2008b; Mansfield et al., 2012; Seney et al., 2010). Certainly, once device effects on turtle behavior have been assessed quantitatively and qualitatively, standard attachment procedures are required to make datasets widely comparable.

Finally, some standard terminology and descriptive parameters would aid in the process of putting the effort of many decades worth of research together, and improving the overall picture that emerged from this review. For example, multiple naming of the same observed (and already described) phenomena should be avoided (see Section 5.1 and Table 3). Along with the statistical results of your analysis, provide also mean  $\pm$  SD values for dive performance, even if they are not the correct statistical descriptors for a given dataset, because they are the most widely used in current literature; and provide always maximum dive duration and dive depth to allow more accurate future assessments of diving capacities. In this regard, it may perhaps be worth mentioning that data-archiving would be really useful for allowing published datasets to be available to the wider community. This feature may emerge as academic journals increasingly ask that datasets are placed in a publically accessible data-base (e.g., Dryad) as part of the publication process.

## 8. Concluding remarks

### 8.1. Why we mind turtles' underwater business

It would be misleading to claim that all the investments by diving behavior studies on sea turtles were serving the greater goal of conservation; although, this should be the only ethical justification for thus disturbing and impeding already vulnerable species (e.g. all species of sea turtles, except the flatback turtle which is data deficient, are listed in the IUCN Red List of Threatened Species with various statuses, IUCN, 2013). However, sea turtles are fascinating animals that captured the interest of scientists and the public long before the first questions about their dive depth and duration were raised. Among the air-breathing animals that have made the oceans their home through a series of specialized adaptations, sea turtles are the undefeated record holders for breath-hold diving, and the leatherback turtle is among the top three deep diving species only exceed by northern elephant seals *Mirounga angustirostris* (1500 m) and sperm whales *Physeter macrocephalus* (>2000 m) (Kooyman and Ponganis, 1997). It lies in the nature of scientists to be intrigued by how sea turtles face challenges during their lifespan, and wanting to elucidate the underlying biological mechanisms. Fortunately, this curiosity has laid the groundwork towards understanding the constraints of sea turtle behavior and towards applying this knowledge in establishing objective protection measures.

Therefore, basic knowledge about dive depth, duration, and temporal patterns of diving for a given species and region is required to design regulations aiming to avoid overlap between peak activities

of fisheries and turtles, and hence reduce by-catch rates (e.g. Polovina et al., 2003). Another important feature that has emerged over the years is the behavioral plasticity of sea turtles, which will ultimately reflect how this group of marine vertebrates responds to environmental variations, particularly climate change (see, for example, Hawkes et al., 2009; McMahon and Hays, 2006). In this respect, behavior orientated studies deliver useful information for the mitigation of these threats, that are recognized as major perils worldwide (Wallace et al., 2011), and are well integrated with the priority research categories that have been identified to assist sea turtle conservation (Hamann et al., 2010).

### 8.2. What does the future bring?

Having clarified the current state of knowledge about sea turtle diving behavior, we must now fill the remaining gaps, by keeping track of technological progress and making the best use of it. A recent breakthrough in biologging science made it possible to follow the first movements of neonate loggerhead sea turtles after entering the sea using solar-powered miniature satellite tags (Mansfield, 2013). Thus, this drastic miniaturization of satellite tags (through removing the need for heavyweight batteries) opens new avenues in the behavioral research of the juvenile stages of sea turtles. Similarly promising preliminary results were obtained for low-cost data retrieval either by, for example, relying on members of the public to find and return washed up archival tags (Righton et al., 2012), or by sending recorded data as text messages through the international GSM mobile phone network (<http://www.smru.st-and.ac.uk/Instrumentation/GPSPHONEtag/>). Such applications may facilitate the study of turtles that cannot be recaptured in inaccessible foraging grounds and overwintering areas. Finally, the use of additional sensors to record animal movement and behavior-linked parameters has already taken root in telemetry studies on marine animals, not to mention accelerometry, which has just begun to reveal exciting new data. This technique has the potential of an all-round non-invasive tool and proxy for overall dive performance, activity level, cost of diving, and energy expenditure (Fossette et al., 2012; Okuyama et al., 2012), thus opening new avenues of behavioral investigations which is particularly attractive for research on endangered species.

In conclusion, I have explored a selection of factors that explain some of the variability in diving behavior observed in marine turtles; however, as I have also shown, there is scope for improvement. It may be idealistic to aim to identify universal relationships between diving behavior and underlying biological mechanisms, yet a solid groundwork has been laid both through laboratory research in controlled conditions, and elaborately designed field experiments. The efforts made in behavioral studies have greatly contributed to catapulting sea turtles to the top of applied science in conservation biology. Currently remaining gaps in the knowledge of factors that impact sea turtle diving should, therefore, only encourage further work along this line to help understand the extent of behavioral plasticity and adaptability of sea turtles to environmental change.

## Acknowledgments

I am grateful to Graeme Hays and Gail Schofield for providing valuable comments on earlier versions of this paper. I would also like to thank Fulvio Maffucci and Raffaella Bova for helping me finalize the manuscript just on time. [SS]

## Appendix 1. References for diving behavior data presented in Table 1

1. Bell, I.P., Parmenter, C.J., 2008. The diving behaviour of inter-nesting hawksbill turtles, *Eretmochelys imbricata* (Linnaeus 1766) on Milman Island Reef, Queensland, Australia. *Herpetol. Conserv. Biol.* 3(2), 254–263.
2. Blumenthal, J.M., Austin, T.J., Bothwell, J.B., Broderick, A.C., Ebanks-Petrie, G., Olynik, J.R., Orr, M.F., Solomon, J.L., Witt, M.J., Godley,



- B.J., 2009. Diving behavior and movements of juvenile hawksbill turtles *Eretmochelys imbricata* on a Caribbean coral reef. *Coral Reefs* 28, 55–65.
3. Blumenthal, J.M., Austin, T.J., Bothwell, J.B., Broderick, A.C., Ebanks-Petrie, G., Olynik, J.R., Orr, M.F., Solomon, J.L., Witt, M.J., Godley, B.J., 2010. Life in (and out of) the lagoon: fine-scale movements of green turtles tracked using time–depth recorders. *Aquat. Biol.* 9 (2), 113–121.
4. Broderick, A.C., Coyne, M.S., Fuller, W.J., Glen, F., Godley, B.J., 2007. Fidelity and over-wintering of sea turtles. *Proceedings of the Royal Society B* 274, 1533–1538.
5. Cheng, I.J., Bentivegna, F., Hochscheid, S., 2013. The behavioural choices of green turtles nesting at two environmentally different islands in Taiwan. *J. Exp. Mar. Biol. Ecol.* 440, 141–148.
6. Eckert, S.A., Nellis, D.W., Eckert, K.L., Kooyman, G.L., 1986. Diving patterns of two leatherback sea turtles (*Dermochelys coriacea*) during interesting intervals at Sandy Point, St. Croix, U. S. Virgin Islands. *Herpetologica* 42 (3), 381–388.
7. Eckert, S.A., Eckert, K.L., Ponganis, P., Kooyman, G.L., 1989. Diving and foraging behavior of leatherback sea turtles (*Dermochelys coriacea*). *Can. J. Zool.* 67, 2834–2840.
8. Eckert, S.A., Liew, H.-C., Eckert, K.L., Chan, E.-H., 1996. Shallow water diving by leatherback turtles in the South China Sea. *Chelonian Conserv. Biol.* 2 (2), 237–243.
9. Eguchi, T., Seminoff, J.A., Garner, S.A., Alexander-Garner, J., Dutton, P.H., 2006. Flipper taggin with archival data recorders for short-term assessment of diving in nesting female turtles. *Endanger. Species Res.* 1 (2), 7–13.
10. Fossette, S., Gaspar, P., Handrich, Y., Le Maho, Y., Georges, J.Y., 2008. Dive and beak movement patterns in leatherback turtles *Dermochelys coriacea* during interesting intervals in French Guiana. *J. Anim. Ecol.* 77 (2), 236–246.
11. Fossette, S., Ferraroli, S., Tanaka, H., Ropert-Coudert, Y., Arai, N., Sato, K., Naito, Y., Le Maho, Y., Georges, J.Y., 2007. Dispersal and dive patterns in gravid leatherback turtles during the nesting season in French Guiana. *Mar. Ecol. Prog. Ser.* 338, 233–247.
12. Fossette, S., Gleiss, A.C., Myers, A.E., Garner, S., Liebsch, N., Whitney, N.M., Hays, G.C., Wilson, R.P., Lutcavage, M.E., 2010. Behaviour and buoyancy regulation in the deepest-diving reptile: the leatherback turtle. *J. Exp. Biol.* 213, 4074–4083.
13. Francke, D.L., Hargrove, S.A., Vetter, E.W., Winn, C.D., Balazs, G.H., Hyrenbach, K.D., 2013. Behavior of juvenile green turtles in a coastal neritic habitat: Validating time–depth–temperature records using visual observations. *J. Exp. Mar. Biol. Ecol.* 444, 55–65.
14. Fuller, W.J., Broderick, A.C., Hooker, S.K., Witt, M.J., Godley, B.J., 2009. Insights into habitat utilization by green turtles (*Chelonia mydas*) during the inter-nesting period using animal-borne digital cameras. *Mar. Technol. Soc. J.* 43 (3), 1–9.
15. Glen, F., Broderick, A.C., Godley, B.J., Metcalfe, J.D., Hays, G.C., 2001. Dive angles for a green turtle (*Chelonia mydas*). *J. Mar. Biol. Assoc. U.K.* 81, 683–686.
16. Hatase, H., Omuta, K., Tsukamoto, K., 2007. Bottom or midwater: alternative foraging behaviours in adult female loggerhead sea turtles. *J. Zool.* 273, 46–55.
17. Hays, G.C., Metcalfe, J.D., Walne, A.W., 2004. The implications of lung regulated buoyancy control for dive depth and duration. *Ecology* 85 (4), 1137–1145.
18. Hays, G.C., Marshall, G.J., Seminoff, J.A., 2007. Flipper beat frequency and amplitude changes in diving green turtles, *Chelonia mydas*. *Mar. Biol.* 150, 1003–1009.
19. Hays, G.C., Houghton, J.D.R., Isaacs, C., King, R.S., Lloyd, C., Lovell, P., 2004. First records of oceanic dive profiles for leatherback turtles, *Dermochelys coriacea*, indicate behavioural plasticity associated with long distance migration. *Anim. Behav.* 67, 733–743.
20. Hays, G.C., Adams, C.R., Broderick, A.C., Godley, B.J., Lucas, D.J., Metcalfe, J.D., Prior, A.A., 2000. The diving behaviour of green turtles at Ascension Island. *Anim. Behav.* 59, 577–586.
21. Hays, G.C., Akesson, S., Broderick, A.C., Glen, F., Godley, B.J., Luschi, P., Martin, C., Metcalfe, J.D., Papi, F., 2001. The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution. *J. Exp. Biol.* 204 (23), 4093–4098.
22. Hazel, J., Lawler, I.R., Hamann, M., 2009. Diving at the shallow end: Green turtle behaviour in near-shore foraging habitat. *J. Exp. Mar. Biol. Ecol.* 371, 84–92.
23. Hochscheid, S., Bentivegna, F., Hays, G.C., 2005. First records of dive durations for a hibernating sea turtle. *Biol. Lett.* 1, 82–86.
24. Hochscheid, S., Godley, B.J., Broderick, A.C., Wilson, R.P., 1999. Reptilian diving: Highly variable dive patterns in the green turtle, *Chelonia mydas*. *Mar. Ecol. Prog. Ser.* 185, 101–112.
25. Houghton, J.D.R., Woolmer, A., Hays, G.C., 2000. Sea turtle diving and foraging behaviour around the Greek Island of Kefalonia. *J. Mar. Biol. Assoc. U.K.* 80 (4), 761–762.
26. Houghton, J.D.R., Callow, M.J., Hays, G.C., 2003. Habitat utilization by juvenile hawksbill turtles (*Eretmochelys imbricata*, Linnaeus, 1766) around a shallow water coral reef. *J. Nat. Hist.* 37(10), 1269–1280.
27. Houghton, J.D.R., Broderick, A.C., Godley, B.J., Metcalfe, J.D., Hays, G.C., 2002. Diving behaviour during the interesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. *Mar. Ecol. Prog. Ser.* 227, 63–70.
28. Houghton, J.D.R., Doyle, T., Davenport, J., Wilson, R.P., Hays, G.C., 2008. The role of infrequent and extraordinary deep dives in leatherback turtles (*Dermochelys coriacea*). *J. Exp. Biol.* 211, 2566–2575.
29. Houghton, J.D.R., Cedras, A., Myers, A.E., Liebsch, N., Metcalfe, J.D., Mortimer, J.A., Hays, G.C., 2008. Measuring the state of consciousness in a free-living diving sea turtle. *J. Exp. Mar. Biol. Ecol.* 356, 115–120.
30. James, M.C., Davenport, J., Hays, G.C., 2006. Expanded thermal niche for a diving vertebrate: A leatherback turtle diving into near-freezing water. *J. Exp. Mar. Biol. Ecol.* 335, 221–226.
31. Makowski, C., Seminoff, J.A., Salmon, M., 2006. Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. *Mar. Biol.* 148, 1167–1179.
32. McMahon, C.R., Bradshaw, C.J.A., Hays, G.C., 2007. Satellite tracking reveals unusual diving characteristics for a marine reptile, the olive ridley turtle *Lepidochelys olivacea*. *Mar. Ecol. Prog. Ser.* 329, 239–252.
33. Minamikawa, S., Naito, Y., Uchida, I., 1997. Buoyancy control in diving behaviour of the loggerhead turtle, *Caretta caretta*. *J. Ethol.* 15, 109–118.
34. Minamikawa, S., Naito, Y., Sato, K., Matsuzawa, Y., Bando, T., Sakamoto, W., 2000. Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *J. Exp. Biol.* 203, 2967–2975.
35. Okuyama, J., Kataoka, K., Kobayashi, M., Abe, O., Yoseda, K., Arai, N., 2012. The regularity of dive performance in sea turtles: a new perspective from precise activity data. *Anim. Behav.* 84 (2), 349–359.
36. Polovina, J.J., Howell, E., Parker, D.M., Balazs, G.H., 2003. Dive-depth distribution of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific: Might deep longline sets catch fewer turtles? *Fish. Bull.* 101 (1), 189–193.
37. Reina, R., Abernathy, K.J., Marshall, G.J., Spotila, J.R., 2005. Respiratory frequency, dive behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. *J. Exp. Mar. Biol. Ecol.* 316, 1–16.
38. Rice, M.R., Balazs, G.H., 2008. Diving behavior of the Hawaiian green turtle (*Chelonia mydas*) during oceanic migrations. *J. Exp. Mar. Biol. Ecol.* 356 (1–2), 121–127.

39. Sakamoto, W., Naito, Y., Uchida, I., Kureha, K., 1990. Circadian rhythm on diving motion of the loggerhead turtle *Caretta caretta* during inter-nesting and its fluctuations induced by the oceanic environmental events. *Nippon Suisan Gakkaishi* 56 (2), 263–272.
40. Sakamoto, W., Sato, K., Tanaka, I., Naito, Y., 1993. Diving pattern and swimming environment of two loggerhead turtles during inter-nesting. *Nippon Suisan Gakkaishi* 50 (7), 1129–1137.
41. Sakamoto, W., Uchida, I., Naito, Y., Kureha, K., Tujimura, M., Sato, K., 1990. Deep diving behavior of the loggerhead turtle near the frontal zone. *Nippon Suisan Gakkaishi* 56 (9), 1435–1443.
42. Sale, A., Luschi, P., Mencacci, R., Lambardi, P., Hughes, G.R., Hays, G.C., Benvenuti, S., Papi, F., 2006. Long-term monitoring of leatherback turtle diving behaviour during oceanic movements. *J. Exp. Mar. Biol. Ecol.* 328 (2), 197–210.
43. Salmon, M., Jones, T.T., Horsch, K.W., 2004. Ontogeny of diving and feeding behavior in juvenile seaturtles: leatherback seaturtles (*Dermochelys coriacea* L) and green seaturtles (*Chelonia mydas* L) in the Florida Current. *J. Herpetol.* 38 (1), 36–43.
44. Salmon, M., Hamann, M., Wyneken, J., 2010. The Development of Early Diving Behavior by Juvenile Flatback Sea Turtles (*Natator depressus*). *Chelonian Conserv. Biol.* 9 (1), 8–17.
45. Sasso, C.R., Witzell, W.N., 2006. Diving behaviour of an immature Kemp's ridley turtle (*Lepidochelys kempii*) from Gullivan Bay, Ten Thousand Islands, south-west Florida. *J. Mar. Biol. Assoc. U.K.* 86, 919–925.
46. Seminoff, J.A., Jones, T.T., Marshall, G.J., 2006. Underwater behaviour of green turtles monitored with video–time–depth recorders: what's missing from dive profiles? *Mar. Ecol. Prog. Ser.* 322, 269–280.
47. Southwood, A.L., Reina, R.D., Jones, V.S., Jones, D.R., 2003. Seasonal diving patterns and body temperatures of juvenile green turtles at Heron Island, Australia. *Can. J. Zool.* 81, 1014–1024.
48. Southwood, A.L., Andrews, R.D., Paladino, F.V., Jones, D.R., 2005. Effects of diving and swimming behavior on body temperatures of Pacific leatherback turtles in tropical seas. *Physiol. Biochem. Zool.* 78 (2), 285–297.
49. Southwood, A.L., Andrews, R.D., Lutcavage, M.E., Paladino, F.V., West, N.H., George, R.H., Jones, D.R., 1999. Heart rates and diving behaviour of leatherback sea turtles in the Eastern Pacific Ocean. *J. Exp. Biol.* 202, 1115–1125.
50. Storch, S., Wilson, R.P., Hillis-Starr, Z.M., Adelung, D., 2005. Cold-blooded divers: temperature-dependent dive performance in the wild hawksbill turtle *Eretmochelys imbricata*. *Mar. Ecol. Prog. Ser.* 293, 263–271.
51. Swimmer, Y., Arauz, R., McCracken, M., McNaughton, L., Ballestero, J., Musyl, M., Bigelow, K., Brill, R., 2006. Diving behavior and delayed mortality of olive ridley sea turtles *Lepidochelys olivacea* after their release from longline fishing gear. *Mar. Ecol. Prog. Ser.* 323, 253–261.
52. Thomson, J.A., Heithaus, M.R., Dill, L.M., 2011. Informing the interpretation of dive profiles using animal-borne video: A marine turtle case study. *J. Exp. Mar. Biol. Ecol.* 410, 12–20.
53. van Dam, R.P., Diez, C.E., 1996. Diving behaviour of immature hawksbills (*Eretmochelys imbricata*) in a Caribbean cliff-wall habitat. *Mar. Biol.* 127, 171–178.
54. von Brandis, R.G., Mortimer, J.A., Reilly, B.K., 2010. In-Water Observations of the Diving Behaviour of Immature Hawksbill Turtles, *Eretmochelys imbricata*, on a Coral Reef at D'Arros Island, Republic of Seychelles. *Chelonian Conserv. Biol.* 9(1), 26–32.
55. Wallace, B.P., Williams, C.L., Paladino, F.V., Morreale, S.J., Lindstrom, R.T., Spotila, J.R., 2005. Bioenergetics and diving activity of inter-nesting leatherback turtles *Dermochelys coriacea* at Parque Nacional Marino Las Baulas, Costa Rica. *J. Exp. Biol.* 208, 3873–3884.
56. Witt, M.J., McGowan, A., Blumenthal, J.M., Broderick, A.C., Gore, S., Wheatley, D., White, J., Godley, B.J., 2010. Inferring vertical and horizontal movements of juvenile marine turtles from time–depth-recorders. *Aquat. Biol.* 8, 169–177.
57. Yasuda, T., Arai, N., 2009. Changes in flipper beat frequency, body angle and swimming speed of female green turtles *Chelonia mydas*. *Mar. Ecol. Prog. Ser.* 386, 275–286.

## Appendix 2. Supplementary data

A graphical summary of the key information that is required from future studies on the dive behaviour of sea turtles to enable comprehensive overview. Highlighted are the various phases of a such a study with a corresponding checklist of the required data. Additional information on the nature and importance of the data are also given. Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jembe.2013.10.016>.

## References

- Arendt, M.D., Segars, A.L., Byrd, J.L., Boynton, J., Schwenter, J.A., Whitaker, J.D., Parker, L., 2012. Migration, distribution, and diving behavior of adult male loggerhead sea turtles (*Caretta caretta*) following dispersal from a major breeding aggregation in the Western North Atlantic. *Mar. Biol.* 159 (1), 113–125.
- Bentivegna, F., Hochscheid, S., Minucci, C., 2003. Seasonal variability in voluntary dive duration of the Mediterranean loggerhead turtle, *Caretta caretta*. *Sci. Mar.* 67 (3), 371–375.
- Blumenthal, J.M., Austin, T.J., Bothwell, J.B., Broderick, A.C., Ebanks-Petrie, G., Olynyk, J.R., Orr, M.F., Solomon, J.L., Witt, M.J., Godley, B.J., 2009. Diving behavior and movements of juvenile hawksbill turtles *Eretmochelys imbricata* on a Caribbean coral reef. *Coral Reefs* 28, 55–65.
- Blumenthal, J.M., Austin, T.J., Bothwell, J.B., Broderick, A.C., Ebanks-Petrie, G., Olynyk, J.R., Orr, M.F., Solomon, J.L., Witt, M.J., Godley, B.J., 2010. Life in (and out of) the lagoon: fine-scale movements of green turtles tracked using time–depth recorders. *Aquat. Biol.* 9 (2), 113–121.
- Broderick, A.C., Coyne, M.S., Fuller, W.J., Glen, F., Godley, B.J., 2007. Fidelity and over-wintering of sea turtles. *Proc. R. Soc. B* 274, 1533–1538.
- Carr, A., Ogren, L., McVea Jr., C., 1980. Apparent hibernation by the Atlantic loggerhead turtle off Cape Canaveral, Florida. *Biol. Conserv.* 19, 7–14.
- Cheng, I.J., 2009. Changes in diving behaviour during the inter-nesting period by green turtles. *J. Exp. Mar. Biol. Ecol.* 381, 18–24.
- Cheng, I.J., Bentivegna, F., Hochscheid, S., 2013. The behavioural choices of green turtles nesting at two environmentally different islands in Taiwan. *J. Exp. Mar. Biol. Ecol.* 440, 141–148.
- Davenport, J., Ingle, G., Hughes, A.K., 1982. Oxygen uptake and heart rate in young green turtles (*Chelonia mydas*). *J. Zool. (Lond.)* 198, 399–412.
- Doyle, T., Houghton, J.D.R., O'Suilleabhain, P.F., Hobson, V.J., Marnell, F., Davenport, J., Hays, G.C., 2008. Leatherback turtles satellite-tagged in European waters. *Endanger. Species Res.* 4, 23–31.
- Eckert, S.A., Nellis, D.W., Eckert, K.L., Kooyman, G.L., 1986. Diving patterns of two leatherback sea turtles (*Dermochelys coriacea*) during inter-nesting intervals at Sandy Point, St. Croix, U. S. Virgin Islands. *Herpetologica* 42 (3), 381–388.
- Eckert, S.A., Eckert, K.L., Ponganis, P., Kooyman, G.L., 1989. Diving and foraging behavior of leatherback sea turtles (*Dermochelys coriacea*). *Can. J. Zool.* 67, 2834–2840.
- Eckert, S.A., Liew, H.-C., Eckert, K.L., Chan, E.-H., 1996. Shallow water diving by leatherback turtles in the South China Sea. *Chelonian Conserv. Biol.* 2 (2), 237–243.
- Eder, E., Ceballos, A., Martins, S., Pérez-García, H., Marín, I., Marco, A., Cardona, L., 2012. Foraging dichotomy in loggerhead sea turtles *Caretta caretta* off northwestern Africa. *Mar. Ecol. Prog. Ser.* 470, 113–122.
- Fedak, M.A., Thompson, D., 1993. Behavioural and physiological options in diving seals. *Symp. Zool. Soc. Lond.* 66, 333–348.
- Felger, R.S., Clifton, K., Regal, P.J., 1976. Winter dormancy in sea turtles: independent discovery and exploitation in the Gulf of California by two local cultures. *Science* 191, 283–285.
- Fossette, S., Ferraroli, S., Tanaka, H., Ropert-Coudert, Y., Arai, N., Sato, K., Naito, Y., Le Maho, Y., Georges, J.Y., 2007. Dispersal and dive patterns in gravid leatherback turtles during the nesting season in French Guiana. *Mar. Ecol. Prog. Ser.* 338, 233–247.
- Fossette, S., Gaspar, P., Handrich, Y., Le Maho, Y., Georges, J.Y., 2008a. Dive and beak movement patterns in leatherback turtles *Dermochelys coriacea* during inter-nesting intervals in French Guiana. *J. Anim. Ecol.* 77 (2), 236–246.
- Fossette, S., Corbel, H., Gaspar, P., Le Maho, Y., Georges, J.Y., 2008b. An alternative technique for the long-term satellite tracking of leatherback turtles. *Endanger. Species Res.* 4, 33–41.
- Fossette, S., Schofield, G., Lilley, M.K.S., Gleiss, A.C., Hays, G.C., 2012. Acceleration data reveal the energy management strategy of a marine ectotherm during reproduction. *Funct. Ecol.* 26, 324–333.
- Francke, D.L., Hargrove, S.A., Vetter, E.W., Winn, C.D., Balazs, G.H., Hyrenbach, K.D., 2013. Behavior of juvenile green turtles in a coastal neritic habitat: validating time–depth–temperature records using visual observations. *J. Exp. Mar. Biol. Ecol.* 444, 55–65.
- Fuller, W.J., Broderick, A.C., Hooker, S.K., Witt, M.J., Godley, B.J., 2009. Insights into habitat utilization by green turtles (*Chelonia mydas*) during the inter-nesting period using animal-borne digital cameras. *Mar. Technol. Soc. J.* 43 (3), 1–9.



- Galli, S., Gaspar, P., Fossette, S., Calmettes, B., Hays, G.C., Lutjeharms, J.R.E., Luschi, P., 2012. Orientation of migrating leatherback turtles in relation to ocean currents. *Anim. Behav.* 84, 1491–1500.
- Girard, C., Tucker, A.D., Calmettes, B., 2009. Post-nesting migrations of loggerhead sea turtles in the Gulf of Mexico: dispersal in highly dynamic conditions. *Mar. Biol.* 156, 1827–1839.
- Gitschlag, G.R., 1996. Migration and diving behavior of Kemp's ridley (Garman) sea turtles along the U.S. southeastern Atlantic coast. *J. Exp. Mar. Biol. Ecol.* 205, 115–135.
- Godley, B.J., Richardson, S., Broderick, A.C., Coyne, M.S., Glen, F., Hays, G.C., 2002. Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. *Ecography* 25, 352–362.
- Godley, B.J., Broderick, A.C., Glen, F., Hays, G.C., 2003. Post-nesting movements and submergence patterns of loggerhead marine turtles in the Mediterranean assessed by satellite tracking. *J. Exp. Mar. Biol. Ecol.* 287, 119–134.
- Hamann, M., Godfrey, M.H., Seminoff, J.A., Arthur, K.E., Barata, P.C.R., Bjørndal, K.A., Bolten, A.B., Broderick, A.C., Campbell, L.M., Carreras, C., Casale, P., Chaloupka, M., Chan, S.K.F., Coyne, M.S., Crowder, L.B., Diez, C.E., Dutton, P.H., Epperly, S.P., FitzSimmons, N.N.K., Formia, A., Girondot, M., Hays, G.C., Cheng, I.J., Kaska, Y., Lewison, R., Mortimer, J.A., Nichols, W.J., Reina, R.D., Shanker, K., Spotila, J.R., Tomas, J., Wallace, B.P., Work, T.M., Zbinden, J., Godley, B.J., 2010. Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endanger. Species Res.* 11, 245–269.
- Hatase, H., Takai, N., Matsuzawa, Y., Sakamoto, W., Omuta, K., Goto, K., Arai, N., Fujiwara, T., 2002. Size-related differences in feeding habitat use of adult female loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. *Mar. Ecol. Prog. Ser.* 233, 273–281.
- Hatase, H., Omuta, K., Tsukamoto, K., 2007. Bottom or midwater: alternative foraging behaviours in adult female loggerhead sea turtles. *J. Zool.* 273, 46–55.
- Hatase, H., Omuta, K., Tsukamoto, K., 2010. Oceanic residents, neritic migrants: a possible mechanism underlying foraging dichotomy in adult female loggerhead turtles (*Caretta caretta*). *Mar. Biol.* 157, 1337–1342.
- Hawkes, L.A., Broderick, A.C., Coyne, M.S., Godfrey, M.H., Lopez-Jurado, L.-F., Lopez-Suarez, P., Merino, S.E., Varo-Cruz, N., Godley, B.J., 2006. Phenotypically linked dichotomy in sea turtle foraging requires multiple conservation approaches. *Curr. Biol.* 16, 990–995.
- Hawkes, L.A., Broderick, A.C., Coyne, M.S., Godfrey, M.H., Godley, B.J., 2007. Only some like it hot – quantifying the environmental niche of the loggerhead sea turtles. *Divers. Distrib.* 13, 447–457.
- Hawkes, L.A., Broderick, A.C., Godfrey, M.H., Godley, B.J., 2009. Climate change and marine turtles. *Endanger. Species Res.* 7, 137–154.
- Hays, G.C., Luschi, P., Papi, F., del Seppia, C., Marsh, R., 1999. Changes in behaviour during the inter-nesting period and post-nesting migration for Ascension Island green turtles. *Mar. Ecol. Prog. Ser.* 189, 263–273.
- Hays, G.C., Akesson, S., Broderick, A.C., Glen, F., Godley, B.J., Luschi, P., Martin, C., Metcalfe, J.D., Papi, F., 2001. The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution. *J. Exp. Biol.* 204 (23), 4093–4098.
- Hays, G.C., Metcalfe, J.D., Walne, A.W., 2004a. The implications of lung regulated buoyancy control for dive depth and duration. *Ecology* 85 (4), 1137–1145.
- Hays, G.C., Metcalfe, J.D., Walne, A.W., Wilson, R.P., 2004b. First records of flipper beat frequency during sea turtle diving. *J. Exp. Mar. Biol. Ecol.* 303, 243–260.
- Hays, G.C., Houghton, J.D.R., Isaacs, C., King, R.S., Lloyd, C., Lovell, P., 2004c. First records of oceanic dive profiles for leatherback turtles, *Dermochelys coriacea*, indicate behavioural plasticity associated with long distance migration. *Anim. Behav.* 67, 733–743.
- Hays, G.C., Hobson, V.J., Metcalfe, J.D., Righton, D., Sims, D.W., 2006. Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology* 87 (10), 2647–2656.
- Hays, G.C., Marshall, G.J., Seminoff, J.A., 2007. Flipper beat frequency and amplitude changes in diving green turtles, *Chelonia mydas*. *Mar. Biol.* 150, 1003–1009.
- Hays, G.C., Fossette, S., Katselidis, K.A., Mariani, P., Schofield, G., 2010. Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. *J. R. Soc. Interface* 7, 1319–1327.
- Hazel, J., Lawler, I.R., Hamann, M., 2009. Diving at the shallow end: green turtle behaviour in near-shore foraging habitat. *J. Exp. Mar. Biol. Ecol.* 371, 84–92.
- Heithaus, M.R., McLash, J.J., Frid, A., Dill, L.M., Marshall, G.J., 2002. Novel insights into green sea turtle behaviour using animal-borne video cameras. *J. Mar. Biol. Assoc. U. K.* 82 (6), 1049–1050.
- Hertel, H., 1966. Structure, Form, Movement. Reinhold, New York.
- Heupel, M.R., Simpfendorfer, C.A., Hueter, R.E., 2003. Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. *J. Fish Biol.* 63, 1357–1363.
- Hochscheid, S., Wilson, R.P., 1999. A new method for the determination of at-sea activity in sea turtles. *Mar. Ecol. Prog. Ser.* 185, 293–296.
- Hochscheid, S., Godley, B.J., Broderick, A.C., Wilson, R.P., 1999. Reptilian diving: highly variable dive patterns in the green turtle, *Chelonia mydas*. *Mar. Ecol. Prog. Ser.* 185, 101–112.
- Hochscheid, S., Bentivegna, F., Speakman, J.R., 2002. Regional blood flow in sea turtles: implications for heat exchange in an aquatic ectotherm. *Physiol. Biochem. Zool.* 75 (1), 66–76.
- Hochscheid, S., Bentivegna, F., Speakman, J.R., 2004. Long-term cold acclimation leads to high Q10 effects on oxygen consumption of loggerhead sea turtles, *Caretta caretta*. *Physiol. Biochem. Zool.* 77 (2), 209–222.
- Hochscheid, S., Bentivegna, F., Hays, G.C., 2005a. First records of dive durations for a hibernating sea turtle. *Biol. Lett.* 1, 82–86.
- Hochscheid, S., Maffucci, F., Bentivegna, F., Wilson, R.P., 2005b. Gulps, wheezes, and sniffs: how measurement of beak movement in sea turtles can elucidate their behaviour and ecology. *J. Exp. Mar. Biol. Ecol.* 316, 45–53.
- Hochscheid, S., Bentivegna, F., Bradai, M.N., Hays, G.C., 2007a. Overwintering behaviour in sea turtles: dormancy is optional. *Mar. Ecol. Prog. Ser.* 340, 287–298.
- Hochscheid, S., McMahon, C.R., Bradshaw, C.J.A., Maffucci, F., Bentivegna, F., Hays, G.C., 2007b. Allometric scaling of lung volume and its consequences for marine turtle diving performance. *Comp. Biochem. Physiol. A* 148, 360–367.
- Hochscheid, S., Bentivegna, F., Hays, G.C., 2008. Winter ecology and physiology of sea turtles. In: Lovegrove, B.G., McKechnie, A.E. (Eds.), *Hypometabolism in Animals: Hibernation, Torpor and Cryobiology*. University of KwaZulu-Natal, Pietermaritzburg.
- Hochscheid, S., Bentivegna, F., Hamza, A., Hays, G.C., 2010. When surfacers do not dive: multiple significance of extended surface times in marine turtles. *J. Exp. Biol.* 213, 1328–1337.
- Hochscheid, S., Travaglini, A., Maffucci, F., Hays, G.C., Bentivegna, F., 2013. Since turtles cannot talk: what beak movement sensors can tell us about the feeding ecology of neritic loggerhead turtles, *Caretta caretta*. *Mar. Ecol.* 34, 321–333.
- Hooker, S.K., Biuw, M., McConnell, B.J., Miller, P.J., Sparling, C.E., 2007. Biologging science: logging and relaying physical and biological data using animal-attached tags. *Deep-Sea Res. II* 54, 177–182.
- Houghton, J.D.R., Broderick, A.C., Godley, B.J., Metcalfe, J.D., Hays, G.C., 2002. Diving behaviour during the internesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. *Mar. Ecol. Prog. Ser.* 227, 63–70.
- Houghton, J.D.R., Doyle, T., Davenport, J., Wilson, R.P., Hays, G.C., 2008a. The role of infrequent and extraordinary deep dives in leatherback turtles (*Dermochelys coriacea*). *J. Exp. Biol.* 211, 2566–2575.
- Houghton, J.D.R., Cedras, A., Myers, A.E., Liebsch, N., Metcalfe, J.D., Mortimer, J.A., Hays, G.C., 2008b. Measuring the state of consciousness in a free-living diving sea turtle. *J. Exp. Mar. Biol. Ecol.* 356, 115–120.
- Howell, E.A., Dutton, P.H., Polovina, J.J., Bailey, H., Parker, D.M., Balazs, G.H., 2010. Oceanographic influences on the dive behaviour of juvenile loggerhead turtles (*Caretta caretta*) in the North Pacific Ocean. *Mar. Biol.* 157 (5), 1011–1026.
- IUCN, 2013. IUCN Red List of Threatened Species. Version 2013.1. [www.iucnredlist.org](http://www.iucnredlist.org) (Downloaded on 26 September 2013).
- James, M.C., Ottensmeyer, C.A., Myers, R.A., 2005. Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol. Lett.* 8, 195–201.
- James, M.C., Davenport, J., Hays, G.C., 2006a. Expanded thermal niche for a diving vertebrate: a leatherback turtle diving into near-freezing water. *J. Exp. Mar. Biol. Ecol.* 335, 221–226.
- James, M.C., Ottensmeyer, C.A., Eckert, S.A., Myers, A.E., 2006b. Changes in diel diving patterns accompany shifts between northern foraging and southward migration in leatherback turtles. *Can. J. Zool.* 84 (5), 754–765.
- Jones, T.T., Bostrom, B.L., Carey, M., Imlach, B., Mikkelsen, J., Ostafichuk, P., Eckert, S., Opat, P., Swimmer, Y., Seminoff, J.A., Jones, D.R., 2011. Determining transmitter drag and best practice attachment procedures for sea turtle biotelemetry studies. NOAA Technical Memorandum NMFS-SWFSC-480.
- Jonsen, I.D., Myers, R.A., James, M.C., 2006. Robust hierarchical state-space models reveal diel variation in travel rates of migrating leatherback turtles. *J. Anim. Ecol.* 75 (5), 1046–1057.
- Kobayashi, D.R., Cheng, I.J., Parker, D.M., Polovina, J.J., Kamezaki, N., Balazs, G.H., 2011. Loggerhead turtle (*Caretta caretta*) movement off the coast of Taiwan: characterization of a hotspot in the East China Sea and investigation of mesoscale eddies. *ICES J. Mar. Sci.* 12 (published online).
- Kooyman, G.L., 1989. *Diverse Divers*. Springer-Verlag, Berlin (200 pp.).
- Kooyman, G.L., 2004. Genesis and evolution of bio-logging devices: 1963–2002. *Mem. Natl. Inst. Polar Res. Spec. Issue* 58, 15–22.
- Kooyman, G.L., Ponganis, P.J., 1997. The challenges of diving to depth. *Am. Sci.* 85, 530–539.
- Kramer, D.L., 1988. The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.* 66, 89–94.
- Kraus, D.R., Jackson, D.C., 1980. Temperature effects on ventilation and acid–base balance of the green turtle. *Am. J. Physiol.* 239, R254–R258.
- Lambardi, P., Lutjeharms, J.R.E., Mencacci, R., Hays, G.C., Luschi, P., 2008. Influence of ocean currents on long-distance movement of leatherback sea turtles in the Southwest Indian Ocean. *Mar. Ecol. Prog. Ser.* 353, 289–301.
- López-Mendilaharsu, M., Rocha, C.F.D., Miller, P., Domingo, A., Prodocimi, L., 2009. Insights on leatherback turtle movements and high use areas in the Southwest Atlantic Ocean. *J. Exp. Mar. Biol. Ecol.* 378 (1–2), 31–39.
- Luschi, P., Hays, G.C., Papi, F., 2003. A review of long-distance movements by marine turtles, and the possible role of ocean currents. *Oikos* 103, 293–302.
- Lutcavage, M.E., Lutz, P.L., 1997. Diving physiology. In: Lutz, P.L., Musick, J.A. (Eds.), *The Biology of Sea Turtles*. CRC Press, Boca Raton, pp. 277–296.
- Lutz, P.L., Bergery, A., Bergery, M., 1989. Effects of temperature on gas exchange and acid–base balance in the sea turtle *Caretta caretta* at rest and during routine activity. *J. Exp. Biol.* 144, 155–169.
- Makowski, C., Seminoff, J.A., Salmon, M., 2006. Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. *Mar. Biol.* 148, 1167–1179.
- Mansfield, K.L., 2013. Oceanic habits and habitats. In: Wyneken, J., Lohman, K.J., Musick, J.A. (Eds.), *Biology of Sea Turtles*. CRC Press, Boca Raton, pp. 189–210.
- Mansfield, K.L., Saba, V.S., Keinath, J.A., Musick, J.A., 2009. Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the northwest Atlantic. *Mar. Biol.* 156, 2555–2570.
- Mansfield, K.L., Wyneken, J., Rittschoff, D., Walsh, M., Lim, C.W., Richards, P., 2012. Satellite tag attachment methods for tracking neonate sea turtles. *Mar. Ecol. Prog. Ser.* 457, 181–192.
- Manton, M., Karr, A., Ehrenfeld, D.W., 1972. Chemoreception in the migratory sea turtle, *Chelonia mydas*. *Biol. Bull.* 143, 184–195.

- Marshall, G.J., 1998. Crittercam: an animal-borne imaging and data logging system. *Mar. Technol. Soc. J.* 32 (1), 11–17.
- McClellan, C.M., Braun-McNeill, J., Avens, L., Wallace, B.P., Read, A.J., 2010. Stable isotopes confirm a dichotomy in juvenile loggerhead sea turtles. *J. Exp. Mar. Biol. Ecol.* 387 (1–2), 44–51.
- McMahon, C.R., Hays, G.C., 2006. Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Glob. Chang. Biol.* 12, 1330–1338.
- McMahon, C.R., Bradshaw, C.J.A., Hays, G.C., 2007. Satellite tracking reveals unusual diving characteristics for a marine reptile, the olive ridley turtle *Lepidochelys olivacea*. *Mar. Ecol. Prog. Ser.* 329, 239–252.
- Minamikawa, S., Naito, Y., Uchida, I., 1997. Buoyancy control in diving behaviour of the loggerhead turtle, *Caretta caretta*. *J. Ethol.* 15, 109–118.
- Minamikawa, S., Naito, Y., Sato, K., Matsuzawa, Y., Bando, T., Sakamoto, W., 2000. Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *J. Exp. Biol.* 203, 2967–2975.
- Monzón-Argüello, C., Dell'Amico, F., Morinière, P., Marco, A., López-Jurado, L.F., Hays, G.C., Scott, R., Marsh, R., Lee, P.M., 2012. Lost at sea: genetic, oceanographic and meteorological evidence for storm-forced dispersal. *J. R. Soc. Interface.* 9, 1725–1732.
- Moon, D.-Y., MacKenzie, D.S., Owens, D.W.M., 1997. Simulated hibernation of sea turtles in the laboratory: I. Feeding, breathing frequency, blood pH, and blood gases. *J. Exp. Zool.* 278, 372–380.
- Myers, A.E., Hays, G.C., 2006. Do leatherback turtles *Dermochelys coriacea* forage during the breeding season? A combination of data-logging devices provide new insights. *Mar. Ecol. Prog. Ser.* 322, 259–267.
- Okuyama, J., Kawabata, Y., Naito, Y., Arai, N., Kobayashi, M., 2009. Monitoring beak movements with an acceleration datalogger: a useful technique for assessing the feeding and breathing behaviors of sea turtles. *Endanger. Species Res.* 10, 39–45.
- Okuyama, J., Kataoka, K., Kobayashi, M., Abe, O., Yoseda, K., Arai, N., 2012. The regularity of dive performance in sea turtles: a new perspective from precise activity data. *Anim. Behav.* 84 (2), 349–359.
- Paladino, F.V., O'Connor, M.P., Spotila, J.R., 1990. Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* 344, 858–860.
- Penick, D.N., Paladino, F.V., Steyermark, A.C., Spotila, J.R., 1996. Thermal dependence of tissue metabolism in the green turtle, *Chelonia mydas*. *Comp. Biochem. Physiol.* 113A (3), 293–296.
- Plotkin, P.T., 2010. Nomadic behaviour of the highly migratory olive ridley sea turtle *Lepidochelys olivacea* in the eastern tropical Pacific Ocean. *Endanger. Species Res.* 13, 33–40.
- Polovina, J.J., Kobayashi, D.R., Parker, D.M., Seki, M.P., Balazs, G.H., 2000. Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997–1998. *Fish. Oceanogr.* 9 (1), 71–82.
- Polovina, J.J., Howell, E., Parker, D.M., Balazs, G.H., 2003. Dive-depth distribution of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific: might deep longline sets catch fewer turtles? *Fish. Bull.* 101 (1), 189–193.
- Prange, H.D., Jackson, D.C., 1976. Ventilation, gas exchange and metabolic scaling of a sea turtle. *Respir. Physiol.* 27, 369–377.
- Rees, A., Al Saady, S., Broderick, A.C., Coyne, M.S., Papatanasopoulou, N., Godley, B.J., 2010. Behavioural polymorphism in one of the world's largest populations of loggerhead sea turtles *Caretta caretta*. *Mar. Ecol. Prog. Ser.* 418, 201–212.
- Reina, R., Abernathy, K.J., Marshall, G.J., Spotila, J.R., 2005. Respiratory frequency, dive behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. *J. Exp. Mar. Biol. Ecol.* 316, 1–16.
- Rice, M.R., Balazs, G.H., 2008. Diving behavior of the Hawaiian green turtle (*Chelonia mydas*) during oceanic migrations. *J. Exp. Mar. Biol. Ecol.* 356 (1–2), 121–127.
- Richardson, P.B., Broderick, A.C., Coyne, M.S., Ekanayake, L., Kapurusinghe, T., Premakumara, C., Ranger, S., Saman, M.M., Witt, M.J., Godley, B.J., 2013. Satellite telemetry reveals behavioural plasticity in a green turtle population nesting in Sri Lanka. *Mar. Biol.* 160 (6), 1415–1426.
- Righton, D., Bendall, V.A., Ellis, J.R., McCully, S.R., Silva, J.F., Hetherington, S.J., Metcalfe, J., 2012. Assessing the survivability of bycaught porbeagle and spurdog and furthering our understanding of their movement patterns in UK marine waters. Defra final report for contract M5201 (2009–2012) (81 pp.).
- Rupert-Coudert, Y., Beaulieu, M., Hanuise, N., Kato, A., 2009. Diving into the world of biologging. *Endanger. Species Res.* 10, 21–27.
- Rutz, C., Hays, G.C., 2009. New frontiers in biologging science. *Biol. Lett.* 5, 289–292.
- Sakamoto, W., Naito, Y., Uchida, I., Kureha, K., 1990a. Circadian rhythm on diving motion of the loggerhead turtle *Caretta caretta* during inter-nesting and its fluctuations induced by the oceanic environmental events. *Nippon Suisan Gakkaishi* 56 (2), 263–272.
- Sakamoto, W., Uchida, I., Naito, Y., Kureha, K., Tujimura, M., Sato, K., 1990b. Deep diving behavior of the loggerhead turtle near the frontal zone. *Nippon Suisan Gakkaishi* 56 (9), 1435–1443.
- Sakamoto, W., Sato, K., Tanaka, I., Naito, Y., 1993. Diving pattern and swimming environment of two loggerhead turtles during internesting. *Nippon Suisan Gakkaishi* 50 (7), 1129–1137.
- Sale, A., Luschi, P., Mencacci, R., Lambardi, P., Hughes, G.R., Hays, G.C., Benvenuti, S., Papi, F., 2006. Long-term monitoring of leatherback turtle diving behaviour during oceanic movements. *J. Exp. Mar. Biol. Ecol.* 328 (2), 197–210.
- Salmon, M., Jones, T.T., Horch, K.W., 2004. Ontogeny of diving and feeding behavior in juvenile sea turtles: leatherback sea turtles (*Dermochelys coriacea* L) and green sea turtles (*Chelonia mydas* L) in the Florida Current. *J. Herpetol.* 38 (1), 36–43.
- Salmon, M., Hamann, M., Wyneken, J., 2010. The development of early diving behavior by juvenile flatback sea turtles (*Natator depressus*). *Chelonian Conserv. Biol.* 9 (1), 8–17.
- Sasso, C.R., Witzell, W.N., 2006. Diving behaviour of an immature Kemp's ridley turtle (*Lepidochelys kempii*) from Gullivan Bay, Ten Thousand Islands, south-west Florida. *J. Mar. Biol. Assoc. U. K.* 86, 919–925.
- Sato, K., Sakamoto, W., Matsuzawa, Y., Tanaka, H., Minamikawa, S., Naito, Y., 1995. Body temperature independence of solar radiation in free-ranging loggerhead turtles, *Caretta caretta*, during internesting periods. *Mar. Biol.* 123, 197–205.
- Sato, K., Matsuzawa, Y., Tanaka, H., Bando, T., Minamikawa, S., Sakamoto, W., Naito, Y., 1998. Interntesting intervals for loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, are effected by temperature. *Can. J. Zool.* 76, 1651–1662.
- Schmidt-Nielsen, K., 1984. Scaling — Why Is Animals Size So Important? Cambridge University Press, Cambridge (241 pp.).
- Schofield, G., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., Hays, G.C., 2007. Behaviour analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation. *Endanger. Species Res.* 3, 71–79.
- Schofield, G., Bishop, C.M., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., Hays, G.C., 2009. Microhabitat selection by sea turtles in a dynamic thermal marine environment. *J. Anim. Ecol.* 78, 14–21.
- Schofield, G., Dimadi, A., Fossette, S., Katselidis, A., Koutsoubas, D., Lilley, M.K.S., Luckman, A., Pantis, J.D., Karagouni, A.D., Hays, G.C., 2013. Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. *Divers. Distrib.* 19 (7), 834–844.
- Schreer, J.F., Kovacs, K.M., 1997. Allometry of diving capacity in air-breathing vertebrates. *Can. J. Zool.* 75, 339–358.
- Seminoff, J.A., Jones, T.T., Marshall, G.J., 2006. Underwater behaviour of green turtles monitored with video-time-depth recorders: what's missing from dive profiles? *Mar. Ecol. Prog. Ser.* 322, 269–280.
- Seney, E.E., Higgins, B.M., Landry, A.M.J., 2010. Satellite transmitter attachment techniques for small juvenile sea turtles. *J. Exp. Mar. Biol. Ecol.* 384 (1–2), 61–67.
- Shillinger, G.L., Swithenbank, A.M., Bailey, H., Bograd, S.J., Castleton, M.R., Wallace, B.P., Spotila, J.R., Paladino, F.V., Piedra, R., Block, B.A., 2011. Vertical and horizontal habitat preferences of post-nesting leatherback turtles in the South Pacific Ocean. *Mar. Ecol. Prog. Ser.* 422, 275–289.
- Shillinger, G.L., Di Lorenzo, E., Luo, H., Bograd, S., Hazen, E., Bailey, H., Spotila, J.R., 2012. On the dispersal of leatherback hatchlings from Mesoamerican nesting beaches. *Proc. R. Soc. Lond. B Biol. Sci.* 279, 2391–2395.
- Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W., James, A., Ahmed, M.Z., Brierley, A.S., Hindell, M.A., Morritt, D., Musyl, M.K., Righton, D., Shepard, E.L.C., Wearmouth, V.J., Wilson, R.P., Witt, M.J., Metcalfe, J.D., 2008. Scaling laws of marine predator search behaviour. *Nature* 451, 1098–1102.
- Southwood, A.L., Darveau, C.A., Jones, D.R., 2003a. Metabolic and cardiovascular adjustments of juvenile green turtles to seasonal changes in temperature and photoperiod. *J. Exp. Biol.* 206, 4521–4531.
- Southwood, A.L., Reina, R.D., Jones, V.S., Jones, D.R., 2003b. Seasonal diving patterns and body temperatures of juvenile green turtles at Heron Island, Australia. *Can. J. Zool.* 81, 1014–1024.
- Southwood, A.L., Andrews, R.D., Paladino, F.V., Jones, D.R., 2005. Effects of diving and swimming behavior on body temperatures of Pacific leatherback turtles in tropical seas. *Physiol. Biochem. Zool.* 78 (2), 285–297.
- Southwood, A.L., Reina, R.D., Jones, V.S., Speakman, J.R., Jones, D.R., 2006. Seasonal metabolism of juvenile green turtles (*Chelonia mydas*) at Heron Island, Australia. *Can. J. Zool.* 84, 125–135.
- Spotila, J.R., Standora, E.A., 1985. Environmental constraints on the thermal energetics of sea turtles. *Copeia* 1985 (3), 694–702.
- Storch, S., Wilson, R.P., Hillis-Starr, Z.M., Adelung, D., 2005. Cold-blooded divers: temperature-dependent dive performance in the wild hawksbill turtle *Eretmochelys imbricata*. *Mar. Ecol. Prog. Ser.* 293, 263–271.
- Storch, S., Hays, G.C., Hillis-Starr, Z., Wilson, R.P., 2006. The behaviour of a hawksbill turtle data-logged during the passage of hurricane Georges through the Caribbean. *Mar. Freshw. Behav. Physiol.* 39 (4), 307–313.
- Swimmer, Y., Arauz, R., McCracken, M., McNaughton, L., Ballesterio, J., Musyl, M., Bigelow, K., Brill, R., 2006. Diving behavior and delayed mortality of olive ridley sea turtles *Lepidochelys olivacea* after their release from longline fishing gear. *Mar. Ecol. Prog. Ser.* 323, 253–261.
- Taquet, C., Taquet, M., Dempster, T., Soria, M., Ciccione, S., Roos, D., Dagorn, L., 2006. Foraging of the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean), determined by acoustic transmitters. *Mar. Ecol. Prog. Ser.* 306, 295–302.
- Thompson, D., Fedak, M.A., 2001. How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Anim. Behav.* 61, 287–296.
- Thomson, J.A., Cooper, A.B., Burkholder, D.A., Heithaus, M.R., Dill, L.M., 2012. Heterogeneous patterns of availability for detection during visual surveys: spatiotemporal variation in sea turtle dive-surfacing behaviour on a feeding ground. *Methods Ecol. Evol.* 3 (2), 378–387.
- Ultsch, G.R., 1989. Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. *Biol. Rev.* 64, 435–516.
- van Dam, R.P., Diez, C.E., 1996. Diving behaviour of immature hawksbills (*Eretmochelys imbricata*) in a Caribbean cliff-wall habitat. *Mar. Biol.* 127, 171–178.
- Wallace, B.P., Jones, T.T., 2008. What makes sea turtles go: metabolism and its consequences. *J. Exp. Mar. Biol. Ecol.* 356 (1–2), 8–24.
- Wallace, B.P., DiMatteo, A.D., Bolten, A.B., Chaloupka, M.Y., Hutchinson, B.J., Abreu-Grobois, F.A., Mortimer, J.A., Seminoff, J.A., Amoroso, D., Bjorndal, K.A., Bourjain, J., Bowen, B.W., Briseño Dueñas, R., Casale, P., Choudhury, B.C., Costa, A., Dutton, P.H., Fallabrino, A., Finkbeiner, E.M., Girard, A., Girondot, M., Hamann, M., Hurley, B.J., López-Mendilaharsu, M., Marcovaldi, M.A., Musick, J.A., Nel, R., Pilcher, N.J., Tröeng, S., Witherington, B.E., Mast, R.B., 2011. Global conservation priorities for marine turtles. *PLoS ONE* 6 (9), e24510.

- Watson, K.P., Granger, R.A., 1998. Hydrodynamic effect of a satellite transmitter on a juvenile green turtle (*Chelonia mydas*). J. Exp. Biol. 201 (17), 2497–2505.
- Wilson, R.P., Culik, B.M., Peters, G., Bannasch, R., 1996. Diving behaviour of Gentoo penguins, *Pygoscelis papua*; factors keeping dive profiles in shape. Mar. Biol. 126, 153–162.
- Wilson, R.P., Shepard, E.L.C., Liebsch, N., 2008. Prying into the intimate details of animal lives: use of a daily diary on animals. Endanger. Species Res. 4 (1–2), 123–137.
- Witt, M.J., Broderick, A.C., Johns, D.J., Martin, C., Penrose, R., Hoogmoed, M.S., Godley, B.J., 2007. Prey landscapes help identify potential foraging habitats for leatherback turtles in the NE Atlantic. Mar. Ecol. Prog. Ser. 337, 231–243.
- Witt, M.J., McGowan, A., Blumenthal, J.M., Broderick, A.C., Gore, S., Wheatley, D., White, J., Godley, B.J., 2010. Inferring vertical and horizontal movements of juvenile marine turtles from time–depth–recorders. Aquat. Biol. 8, 169–177.