HIGH-RESOLUTION SATELLITE AND ARCHIVAL TRACKING OF LEATHERBACK SEA TURTLES

Submitted by Jack Boyle to the University of Exeter as a thesis for the degree of Masters by Research in Biological Sciences in March 2017.

This thesis is available for Library use on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Student signature:…………………………………….............

ABSTRACT

Use of marine biologging devices enables the insight into the cryptic lives of marine fauna and the complex environment they inhabit. Using tracking and acoustic monitoring technologies deployed in tandem, we collected fine-scale data on the behaviour and acoustic environment of the leatherback turtle (*Dermochelys coriacea*), nesting in Gabon, Central Africa; a country which supports the largest leatherback nesting population in the world and 60% of all nesting leatherbacks in the Atlantic. A SPLASH10-AF satellite transmitter (Argos tracking), DSG-OpenTag (acoustic and movement) and VHF transmitter (for relocating individuals) were attached to four female turtles using direct carapacial attachment. Data were gathered throughout an entire internesting interval on depth-use, sound, location, and body movement. Here we combine spatial and sound datasets to define the marine soundscape of the nesting leatherback turtle (Chapter 1), whilst combining sound and movement datasets to investigate the effects of ambient acoustic environment on leatherback Vectoral Dynamic Body Acceleration (VeDBA; Chapter 2). Turtles encountered anthrophony (source: shipping activity; occurrence in acoustic files: mean ± SD = 74.7 ± 14.7%, n = 4 turtles; intensity: median = 128.2 dB re 1 µPa, n = 4202), loud noise events (events exceeding the 90th percentile, >135.5 dB re 1 µPa, n = 426), and biophony (source: humpback whale *Megaptera novaeangliae* vocalisations; occurrence in acoustic files: median = 114 vocalisations, n = 4) in the marine soundscape. VeDBA ranged from 0.005 – 0.171g and was significantly affected by depth and broadband sound energy (GLMM: $\chi^2_{1,6}$ = 8.62, p = <0.05) with individual turtle VeDBA influenced by different sound frequencies within the turtle hearing range. We discuss the potential effects of anthropogenic sound sources on this species and potential application of our methodologies. Our findings provide one of the first examples of animal-borne soundscape monitoring over extended periods (9 – 10 days; n = 4) a novel methodology for investigating the effects of marine acoustics on wild animal movement.

ACKNOWLEDGEMENTS

LIST OF CONTENTS

LIST OF FIGURES AND TABLES

5

AUTHOR'S DECLARTION

6

Jack A. Boyle conducted literature searches, data processing and analysis (and associated methodologies for these), manuscript writing and thesis compilation.

Dr Matthew J. Witt and Prof. Brendan J. Godley provided supervision to Jack A. Boyle during data processing, analysis and manuscript writing.

Dr M.J. Witt, Philip D. Doherty, Prof B.J. Godley, Dr A. Formia and Pierre Didier Agamboue coordinated the project under the Memorandum of Understanding between the University of Exeter and the Agence National des Parcs Nationaux.

Dr M.J. Witt, Philip D. Doherty, Pierre Dider Agamboue, Jacob Nzegoe and John Pedro Agamboue conducted the fieldwork (turtle tracking, device attachment and data collection/download).

David A. Mann constructed the DSG-OpenTag (hydrophone-accelerometry device) and assisted with initial data processing.

Lucy A. Hawkes, Sara M. Maxwell, Richard J. Parnell and Guy-Phillipe Sounguet provided academic support throughout the project and writing phases.

GENERAL INTRODUCTION

Understanding the association between an organism and the physical environment is pivotal to ecological studies; important in elucidating behaviour and useful in informing management strategies. Biologging, the use of miniaturised animal-attached tags for logging and/or relaying data on the behaviour and physiology of animals and/or the environments they use (Rutz & Hays, 2009), allows insight into this association. The implementation of biologging instruments in ecological studies and conservation science has generated a boom of data, allowing detailed observations into the secret lives of animals across the globe (Tomkiewicz, 2010).

HISTORY OF MARINE BIOLOGGING

Biologging is a popular and useful methodology in marine ecology (Wilson *et al.*, 2015), due to the vast spatial area animals may cover and the ability of individuals to submerge and evade direct observation (Crossin, 2014). Beginning with an adapted capillary tube to examine diving depth, Scholander (1940) pioneered marine biologging by recording the last dive depth of a harpooned fin whale; an insight into diving behaviour that may have sparked new ingenuity in examining the underwater behaviours of marine animals. However, major advancements in marine biologging took twenty years to arrive via the time depth recorder (TDR). Regarded as 'the device that revolutionised marine organismal biology' (Goldbogen & Meir, 2014) the TDR provided behavioural context to the underwater activity of both Wedell seals (Kooyman, 1966) and Emperor penguins (Kooyman *et al.*, 1971), adding a new layer of complexity and understanding to marine animal movements. Despite the innovative nature of the TDR, it was inhibited by a short time capacity of one hour; Kooyman *et al.* (1976) were able to overcome this limitation by creating a custom biologging instrument (composed of a depth transducer, pressure sensitive paper, spools of wire and an electric motor, housed in an alumni waterproof container) that increased time capacity to multiple days (in this instance every dive for eight days) duration. Gaining detailed insight into the

maximum dive depth and duration of the Wedell seal, Kooyman *et al. (*1976) illuminated the secret underwater life of a marine mammal and expanded biologging research capabilities beyond pure behaviour into physiology. Invention intensified as the power of biologging methods for marine studies were embraced; datalogging durations lengthened enabling longer migration routes to be mapped (>3months; Naito *et al.* 1989) and tag size reduced permitting a wider number of species to be studied, including mammals (Le Boeuf *et al.*, 1986), marine turtles (Eckert *et al.*, 1986), and seabirds (Wilson & Bain, 1984).

With an increase in research capacity, experimentation with biologging instruments led to the incorporation of a vast array of sensors. Implantable sensors logged heart rate and body temperature (Woakes *et al.*, 1995), enabling metabolic rates to be calculated over long ranges; whilst diving behaviour was coupled with jaw movement to reveal the feeding rates of marine vertebrates, inferred daily food intakes of individuals, and interactions between species and human activities (Plötz *et al.*, 2002). Accelerometers enabled the counting of flipper beats and estimates on energy budgets of an individual (van Dam *et al.*, 2002), increasing understanding of energy expenditure during marine movements. The arrival of satellite derived positional data substantially aided animal movement studies (Priede & French, 1991) and has persisted since; revealing the long migrations of multiple marine vertebrate species (Block *et al.*, 2011), identifying movement hotspots (i.e. migratory corridors, foraging grounds, reproductive sites) and informing both local and international marine management strategies (Costa *et al.,* 2012). Technological combinations, such as video attachments allowed scientists to perceive the marine environment from the animal viewpoint, granting verification of feeding strategies and social interactions (Reina *et al.*, 2005; Votier *et al.*, 2013). Continued use, coupled with improved data processing and statistical methods has released the power of biologging studies; accelerometers returned to the forefront able to assess fine-scale movement of the once secret submerged life of animals (McIntyre, 2014), whilst our understanding of the oceans physical properties (temperature, salinity, depth) has been enhanced (Wilmers *et al.*, 2015) – a byproduct of animal-borne sensors. Present day biologging studies carry a level of research

sophistication, harnessing information once unobtainable; a feat of technology, ingenuity and biology.

RESEARCH GAPS

Biologging device size and attachment techniques have created a research bias towards larger marine species and typically adult life stages (Shillinger *et al.*, 2012), excluding earlier developmental stages that may exhibit alternative behaviours and movements within the marine realm. Hazen *et al.* (2012) examined the imbalance of studies across a range of marine species, calling for biologging research within the earlier life stages to address this imbalance; an ever-increasing more realistic feat, as technological advances allow for smaller devices (Fedak, 2002; Wilson *et al.*, 2008; Rutz & Troscianko, 2013) and research ingenuity helps to piece together the lost years of marine species (larval dispersal: Cowen & Sponaugle, 2009; Fischer *et al.*, 2011, and tracking of juveniles: Barbour & Adams, 2012; Scott *et al.*, 2014).

Understanding of fine-scale three-dimensional (3D) movement remains in relative infancy, due to the technical and computing requirements needed to gather and interpret these datasets. Accelerometers collect tri-axial acceleration, gyroscopic and magnetic data; enabling construction of fine-scale tracks (dead reckoning: Wilson & Wilson, 1988; interpolation: Tremblay *et al.*, 2006), calculation of energy proxies (Gleiss *et al.*, 2011; Qasem *et al.*, 2012), and identification of behaviour types (Bidder *et al.,* 2012; Graf *et al.*, 2015). Visualisation solutions for complex multivariate and multi-dimensional datasets are still required to expand research capacity within fine-scale 3D movement. Energy landscapes shape animal movement ecology (Shepard *et al.*, 2013), but energy proxies are still being refined within marine environments (Noda *et al.*, 2012). Quantitative energy proxies can clarify the movement and distribution of foragers (Wilson *et al.*, 2012) and may allow comment on animal fitness, food intake requirements and the evolutionary adaptation of behaviours within and across the marine realm. Comparing energy proxies of animals that inhabit areas of high anthropogenic activity (shipping, seismic activity, tourism) with those in protected areas may highlight the impact of humans and the effectiveness of protection on marine organisms; providing data to inform

mitigation and management strategies (Pichegru *et al.,* 2010). Understanding energy expenditure may further elucidate the capabilities and behaviours of marine organisms.

Environmental monitoring is somewhat a by-product of marine organismal biologging; collected to explain habitat preferences and define niches, the decades of marine biologging studies have sampled a majority of the oceans (Block *et al.*, 2011). As a result, fine-scale sea thermal ocean maps (McMahon *et al.*, 2005), enhanced bathymetry (Padman *et al.*, 2010), improved salinity layers (Lydersen *et al.*, 2002; Hooker & Boyd, 2003) and chlorophyll profiles (Laidre *et al.* 2010; Teo *et al.*, 2009) have been added to the network of remote sensing techniques used to monitor ocean properties. Using species as oceanographic data collectors is encouraged (Boehlert *et al.*, 2001; Charrassin *et al.*, 2002) and adds to the power of the biologging method; promoting an interdisciplinary approach to ecological studies (Fedak, 2004). Despite the array of sensors available oceanographic properties remain under-explored from the animal perspective. For example, marine acoustic environments are not globally mapped to the extent of other oceanographic variables, perhaps due to the difficulty processing and visualising an invisible entity across space and time. Niche acoustic environments have been mapped (McWilliam & Hawkins*,* 2013; Staaterman *et al.*, 2011) and techniques developed for the processing of acoustic habitats have been created (Merchant *et al.,* 2015; Parks *et al.,* 2014; Rako *et al.,* 2013); however published research on specific marine acoustic environments remains sparse, despite the increasing concern of the impacts they have on marine organisms (Clark *et al.*, 2009; Nelms *et al.,* 2016; Tyack, 2008). Showcasing the ability to map acoustic environments and exemplifying how acoustic data can be used in an ecological sense, may aid in our understanding of marine acoustic environment variability and the effect sound has on marine organisms.

In isolation biologging technology provide limited, yet useful, information of animal movement and site residencies. Only when aligning multiple data streams and combining biologging information do we witness the true sophistication of these instruments, which may help to inform marine management strategies for future generations. From oceanographic monitors to

energy expenditure and evolutionary insights, the possibilities of biologging are only inhibited by creativity and technological ingenuity.

BIOLOGGING OF MARINE TURTLES

All seven species of marine turtle have been subject to biologging (green, *Chelonia mydas*: Chambault *et al.*, 2015; leatherback, *Dermochelys coriacea*: Houghton *et al.*, 2008; loggerhead, *Caretta caretta*: Hart *et al.*, 2012; hawksbill, *Ertmochelys imbricata*: Hawkes *et al.*, 2012; Kemp's Ridley, *Lepidochelys kempi*: Shaver *et al.*, 2013; olive ridley, *Lepidochelys olivacea*: Rees *et al.*, 2012; flatback, *Natator depressus*: Whittock *et al.*, 2014). A propensity for terrestrial nesting allows for easier instrument application and retrieval, vulnerable and declining populations justify investment of time and funds, whilst globally distributed populations and movement make marine turtles ideal for biologging studies.

With multiple decades of biologging, turtles have had an array of technology attached to them (Hamann *et al.*, 2010; Hays, 2008) to collect a plethora of information. Turtle movement has been tracked extensively (Godley *et al.*, 2003; Godley *et al.*, 2010; Hays *et al.*, 2004); revealing migration corridors and foraging grounds (Griffin, *et al.*, 2013; Morreale *et al.*, 1996; Stokes *et al.*, 2015). Diving behaviour has revealed physiological capabilities (Fossette *et al.*, 2010), behavioural plasticity (Esteban *et al.*, 2015; Richardson *et al.*, 2013) and habitat preferences within the water column (Hawkes *et al.*, 2007; Shillinger *et al.*, 2011). Accelerometers have begun to reveal the energy expenditure of turtles (Enstipp *et al.,* 2011; Halsey *et al.*, 2011; Wilson *et al.,* 2012), whilst video biologging devices have been used to look at respiratory frequency and unveil social interactions (Reina *et al.*, 2005). The ontogeny bias in tracking is being reduced via innovative miniature biologging devices attached to neonates (Scott *et al.*, 2014); chipping away at the turtle 'lost years'. Details of the underwater lives of turtles are still being discovered, using ever more sophisticated biologging devices to examine fine-scale movement (Wallace *et al.*, 2015; Yasuda & Arai, 2005).

These findings help unravel behavioural and ecological knowledge of marine turtles, but in combination with other data help to inform marine management strategies (Georges *et al.*, 2007; Maxwell *et al.,* 2011), identify potential threats (Witt *et al.*, 2011) and showcase the effectiveness of protected areas (Witt *et al.*, 2008). Despite multiple decades of biologging, nesting populations are still being tagged and efforts are being made to investigate the earlier life history stages (Scott *et al.*, 2014; Scott *et al.*, 2017). Turtle biology and ecology make them an ideal biologging species, providing a platform to test new tags and sampling techniques; helping push biologging methods beyond current capacity and unveiling the secret lives of marine animals.

THIS RESEARCH

To address technological and ecological knowledge gaps in marine turtle acoustic environments and fine-scale 3D behaviour we analyse high-resolution satellite and archival tracking data of the South Atlantic leatherback turtle.

First, we aim to explore the mapping of marine soundscapes and characterisation of acoustic habitats, using the sounds found within the leatherback turtles internesting environment. By combining animal-borne acoustic monitors and satellite tags, we showcase a method to monitor the acoustic environment, how to objectively analyse sound datasets and showcase potential uses of such data.

Continuing to combine data streams from multiple devices we aim to investigate the energetics of leatherback turtles during a nesting season, by analysing accelerometer-derived dynamic body acceleration. Fine-scale movement can be analysed from spatial accelerometry, whilst marine acoustic data will be fed into energy proxy models to elucidate the impact of sound on turtle behaviour.

Marine biologging research is one of experimentation, adaptation and technological advances (Kooyman, 2004); presenting a new type of natural history that offers experimental insights into how animals operate in their natural environment (Ropert-Coudert *et al.,* 2009).

CHAPTER 1

Mapping the marine soundscape using animal-borne sensors

Jack A. Boyle[1], Pierre Didier Agamboue[2], Philip D. Doherty[1], Angela Formia[2], Brendan J. Godley[1], Lucy A. Hawkes[1], David A. Mann[3], Sara M. Maxwell[4], Richard J. Parnell[2,5], Guy-Phillipe Sounguet[2], Matthew J. Witt[1]

[1] University of Exeter, Penryn, Cornwall, UK

[2] Wildlife Conservation Society, Marine Program, Libreville, Gabon, Africa

[3] Loggerhead Instruments, Sarasota, Florida, USA

[4] Department of Biological Sciences, Old Dominion University, Norfolk, VA, USA

[5] For Agence Nationale des Parcs Nationaux, Libreville, Gabon, Africa

ABSTRACT

Awareness of marine noise, and potential associated impacts, is increasing. There is, however, a paucity of research on the acoustic environment from the perspective of the individual. Using tracking and acoustic monitoring technologies deployed in tandem, we collected fine-scale data on the behaviour and acoustic environment of the leatherback turtle (*Dermochelys coriacea*), nesting in Gabon, Central Africa. A SPLASH10-AF satellite transmitter (Argos tracking), DSG-OpenTag (acoustic) and VHF transmitter (for relocating individuals) were attached to four female turtles using direct carapacial attachment. Data were gathered throughout an entire internesting interval (n = 4, mean ± SD = 9.6 ± 0.18days), on depth-use, sound and location. The acoustic environment was sampled for 20 seconds every 10 minutes (n = 5598 files, representing 3.2 GB of data), within an effective frequency range of several Hz to 12.5 kHz; adequately encompassing the range at which leatherback turtles are thought to be sensitive to sound. Acoustic data were filtered and deconstructed to anthrophony (source: shipping activity; occurrence: mean ± SD = 74.7 ± 14.7%, n = 4 turtles; intensity: median = 128.2 dB re 1 µPa, n = 4202), loud noise events (events exceeding the 90th percentile, >135.5 dB re 1 µPa, n = 426), and biophony (source: humpback whale

Megaptera novaeangliae vocalisations; occurrence: median = 114 vocalisations, n = 4), before combining with spatial data to define the marine soundscape. We discuss the spatiotemporal distribution of marine soundscape components and potential uses of this methodology in marine acoustic research. Our findings provide one of the first examples of animal-borne marine soundscape monitoring.

KEYWORDS

acoustic environment; anthropogenic noise; bioacoustics; biologging; marine turtles; whales; shipping

INTRODUCTION

Monitoring of the physical properties of the oceans is important to determine naturally occurring patterns and variation over space and time, allowing us to understand the distributions and activities of the organisms that experience these conditions (Fedak, 2004). Soundscapes are complex phenomena, comprising biological (biophony), geophysical (geophony) and anthropogenic (anthrophony) sounds that emanate from a source and vary over space and time (Pijanowski *et al.*, 2011). A greater understanding of soundscapes enables us to survey animals with known vocalisations (Rodriguez *et al.*, 2014; Towsey *et al.*, 2013), develop acoustic environment baselines (Estabrook *et al.*, 2016; Garrett *et al.*, 2016; Merchant *et al.*, 2016; McWilliam *et al.*, 2013; Pine *et al.*, 2015), and identify potentially impactful anthropogenic activities that may alter acoustic environments (Kuehne *et al.*, 2013), and species behaviour (Dahlheim & Casellote, 2016; Kight & Swaddle, 2011; Tuomainen & Candolin, 2011).

Combining acoustic and landscape ecology, soundscape ecology is a relatively new field of research (Truax & Barrett, 2011). Better documented in terrestrial habitats (Pijanowski, 2016), soundscapes in the marine realm have received comparatively little investigation, perhaps due to the complexities of sound propagation in water (Nedelec *et al.*, 2016) and the challenges of working in marine environments. However, with acoustic datasets being collected at

rapidly increasing rates (Erbe *et al.*, 2016), soundscape research is becoming increasingly widespread.

Commonly sampled via passive acoustic monitoring systems (e.g. static hydrophone arrays; Merchant *et al.*, 2015) it is possible to describe soundscapes (Miksis-Olds, 2016) and features of them, including: anthrophony (e.g. renewable energy: Bailey *et al.*, 2010; shipping: Merchant *et al.*, 2014), biophony (e.g. invertebrate acoustics: Au & Banks, 1998; cetacean vocalisations: Gedamke *et al.*, 2001), and geophony (Martin & Cott, 2015). These broader soundscape descriptions, however, lack the fine-scale insight necessary for sound-induced behavioural research (Frankel *et al.*, 2016); a priority area as awareness of underwater noise pollution and its consequences on the marine environment increases (Simmonds *et al.*, 2014). Animal-borne acoustic recording technology could be used to address this lack of fine-scale information and help to refine our knowledge of marine soundscapes, akin to other animal-borne oceanographic technology (Boehlert *et al.*, 2001; Charrassin *et al.*, 2002).

Marine turtles have a global distribution (Bowen & Karl, 2007) and experience a range of threats (Lascelles *et al.,* 2014), including dangers from shipping routes (Work *et al.*, 2010; MacDonald *et al.*, 2013) and hydrocarbon industry activities (Nelms *et al.*, 2016), artisanal and industrial fishing (Alfaro-Shigueto *et al.*, 2007; Poonian *et al.*, 2008; Wallace *et al.*, 2010). Yet, knowledge of the soundscape marine turtles interact with and the influence of noise pollution on the taxon is largely unknown (Samuel *et al.*, 2005), perhaps due to the unknown role of acoustics in marine turtle ecology (Piniak *et al.*, 2012a) and lack of developed methodologies to investigate this in the wild. Gravid female turtles are large in body size and nest terrestrially, depositing clutches multiple times per season, with an in-water period between each nesting attempt, termed internesting (Lutz *et al.*, 2002); and as such, represent an ideal species for investigating coastal marine soundscapes.

Here we use animal-borne acoustic recording technology to sample the marine soundscape of a near-shore costal environment at a globally important nesting site for leatherback turtles in Gabon, Africa (Witt *et* al., 2009). Providing the first animal-borne acoustic monitored soundscape for marine turtles, we present a

spatio-temporal analysis of fine-scale sound data and highlight opportunities for such techniques to be utilised with other species. Refining our knowledge on soundscapes and individual acoustic exposure will aid an increasing knowledgebase regarding the effects of sound on marine organisms. Further, we highlight how our approach may aid management of anthropogenic noise in habitats supporting acoustically sensitive species (Hatch *et al.*, 2016).

METHODS

Study site and turtle monitoring

Female leatherback turtles were encountered during the early nesting season (October) at Pongara National Park, Gabon, Central Africa (Fig. 1a and 1b; 0.1289° N, 9.6119° E). The Kingere zone within the National Park was surveyed by foot and quad bike to locate nesting leatherback turtles for instrumentation.

Tag specification and attachment procedure

Three devices were attached to the medial ridge of each of six turtles (Fig. 1c; curved carapace length, mean ± 1SD = 152.67 ± 10.4 cm; estimated mass (Georges & Fossette, 2006), mean ± 1SD = 321 ± 54.3 kg). Fitted devices were a Fastloc-GPS enabled Argos-linked satellite tag (SPLASH10-AF; Wildlife Computers, Redmond, Washington, USA), a sound and movement tag (DSG-OpenTag; Loggerhead Instruments, Sarasota, Florida, USA) and a VHF tag (Sirtrack, NZ) (Fig. 1d). The area of tag attachment was cleansed with sterile water and Hibiscrub (Regent Medical Oversea Ltd; Manchester, UK), before narrow channels were made laterally into the medial ridge using individual-use, sterile, veterinary, anti-skid drill bits. Tags were secured to the carapace with nylon coated braided stainless wire loops, closed with a slow degrading ferrule to ensure the later release of tags should the instrumented turtles not be re-encountered for physical device retrieval. A pad of hypoallergenic dental putty (Equinox 35; Smooth-On Inc.; Pennsylvania, US) was inserted between each device and the carapace surface to prevent device movement, reduce friction and improve hydrodynamic flow around each device. Turtles selected for

instrumentation were in good physical condition, had no visible external injuries and exhibited no atypical nesting behaviour. Scientific procedures were subject to ethical review by the University of Exeter (UK) and by Agence National des Parcs Nationaux (Gabon).

Data sampling

Satellite tags collected GPS location data (longitude, latitude; coordinate system World Geodetic System 84) and data on the ambient environment (depth and temperature; 5-second interval sampling). Satellite tags were programmed to gather one valid GPS quality location every hour from up to four attempts. Satellite tags transmitted these data to overpassing satellites (Argos System; www.argos-system.org) when tags were at the sea surface.

The ambient acoustic environments were sampled by the sound and motion tag using an in-built hydrophone for 20 seconds periods at 10 minute intervals at a rate of 50 kHz with a decimation factor of 4; providing an effective frequency range of several Hz to 12.5 kHz. This frequency range encompasses the acoustically sensitive range of marine turtles. Piniak *et al.* (2012b) determined an acoustic range of 50 to 1200 Hz (with a sensitive range of 100 to 400 Hz) based on auditory evoked potentials in leatherback turtles hatchlings, and so for adult leatherback turtles this range is likely smaller due to aging and increased body size, while remaining within these bounds.

Data collection periods for all tags encompassed one internesting period (approx. 10 days). Instrumented turtles were actively relocated during subsequent night patrols. An Argos System hand-held receiver (TSUR-400; Teleonics) detected transmissions made by satellite tags as turtles neared the nesting beach. A VHF receiver and antenna (Ultra; Sirtrack, NZ) were used to detect signals from the VHF tag as turtles emerged onto the beach for nesting. Once instrumented turtles were located, the sound and movement and VHF tags were removed and data downloaded. Depth and temperature data were also downloaded *in-situ* from satellite tags; these tags remained attached for the remainder of the breeding season and into post-nesting migrations.

Data processing

Fastloc-GPS locations (hourly frequency) were interpolated (Tremblay *et al.*, 2006) to provide location data at 10 minute intervals to align with the acoustic data sampling regime. Depth data recorded by each satellite tag were assigned to their respective interpolated locations and acoustic sampling events using time-based matching. Only sub-surface acoustic files were used in subsequent analysis (verified by audible inspection of data and confirmed by assigned depth values; depth ≥ 1 m).

All acoustic files were processed using PAMGuide (Merchant *et al.*, 2015). PAMGuide enables data calibration to instrument specifications, quantification of sound energy within defined acoustic frequency ranges, and visualisation of acoustic data (Fig. 2).

Soundscape characterisation

Anthrophony: Anthropogenic noise in the marine environment is characterised by low frequency sound (Hovem & Korakas, 2014). Energy of low frequency sound was calculated (sound pressure level; dB re 1 µPa) within a one-third-octave band with a centre frequency of 100 Hz (lower band limit = 89.1 Hz, upper band limit = 112 Hz; from here on, referred to as anthrophony). Low frequency sound energy was spatially summarised on a 1 km² hexagonal grid (Whiteaker, 2013) across the sampling area. Each hexagon was assigned the median energy value of all anthrophony data occurring within it. 'Loud' anthropogenic noise events from this data series were also determined, described as those events that exceeded the 90th percentile (> 135.5 dB re 1 µPa) of broadband sound levels across all individuals. Acoustic data were audibly and visually (spectrograms; Fig. 2) inspected for recognisable acoustic signatures of anthrophony (e.g. vessel traffic where propeller and hull noise could be determined above ambient background noise). We investigated variation in anthrophony across space, individuals, and time.

Anthrophony sources: To characterise the spatial distribution of potential anthropogenic sound sources, data on the spatio-temporal, contemporaneous movement of shipping vessels carrying Automated Identification System (AIS) beacons were obtained for the duration of tag deployment. Vessels (>300 GT) and all licenced passenger craft are mandated by the International Maritime Organisation (IMO) to carry beacons transmitting frequent information on at least vessel identification number and position. This information is transmitted by VHF radio signal and can be intercepted by land and space-borne receivers. AIS location data (longitude and latitude; World Geodetic System 1984, exactEarth (Ontario, Canada)) were converted to time-ordered vessel trajectories and projected to the Albers Equal Area Conic coordinate system. Density of vessel trajectories was subsequently estimated (1 km search radius; 250 m grid pixel) and used in analysis.

Biophony: Known biological sounds (e.g. cetacean vocalisations) can be identified from their characteristic acoustic signatures using spectrograms (Appendix B). Unknown biological sounds may be catalogued from spectrograms too, but are challenging to verify without contemporaneous observations of the sound source in wild or captive environments. We therefore quantified only audibly identifiable cetacean vocalisations within each acoustic dataset and examined vocalisation detection rates through space and time and among individuals.

Geophony: Omnipresent within the marine realm, geophysical processes (e.g. wave motion and rain) responsible for this sound source are difficult to extract from the collective soundscape; as such, geophony was not characterised further.

Data manipulation, analysis and mapping were conducted in MATLAB (The MathWorks, R2014b), R v3.0.1 (R Core Team 2013) and ArcGIS (versions 10.1 and 10.2 (ESRI, 2013)) respectively.

RESULTS

Four turtles provided acoustic datasets for analysis; of the six instrumented turtles, one sound and movement tag returned corrupted data, and one turtle nested outside the study region in an inaccessible area preventing retrieval of equipment.

Sound and movement tags gathered 5598 acoustic recordings during the period 25th October to 6th November 2012 (3.2 GB of data; 35.8 cumulative hours; mean ± 1SD = 8.9 ± 0.19 hours per individual). Post-filtering, 4202 sub-surface acoustic recordings were available for analysis (2.4 GB; 26.9 cumulative hours; mean ± 1SD = 6.7 ± 0.14 hours).

The modal internesting duration was 10 days (range: 9 – 10 days; n = 4), with turtles moving a mean (±1SD) minimum straight line distance of 321.2 ± 16.9 km and each occupying a mean (±1SD) area of 572.4 ± 232.7 km^2 (minimum convex polygon). Spatial coverage during the internesting period of the four leatherback turtles overlapped to the west and northwest of Pongara National Park (Fig. 3a). Turtles 1, 3 and 4 had internesting ranges no further than 25 km (radial distance) from the tagging site. Turtle 2 undertook a short foray northward (the only individual to do so), moving ~50 km from the tagging site prior to returning 10 days later to deposit a subsequent nest.

Anthrophony: Identifiable noise signatures of anthropogenic origin occurred in 74.7 ± 14.7% (mean ± SD; n = 4 turtles) of filtered files (3139 of 4202 files) and consisted of sounds generated from shipping activity (i.e. propeller motion, engines). Anthrophony intensities ranged from 88.3 – 148.0 dB re 1 µPa (median = 128.2 dB re 1 µPa; n = 4202) and these noise signatures were distributed towards shallower depths (Shapiro-Wilks normality test: W = 0.8987, n = 4202, p = <0.01; Fig. 4a). Anthrophony intensities differed among turtles (Kruskal-Wallis rank sum test: χ^2_3 = 10.2044, P = <0.01; Fig. 4b), across depths (Kruskal-Wallis rank sum test: χ^2_4 = 27.1394, P = <0.01; Fig. 4c), over sampling days (Kruskal-Wallis rank sum test: χ^2_{11} = 405.4555, P = <0.001) and by time of day (Kruskal-Wallis rank sum test: χ^2_{23} = 47.7316, P = <0.01; Fig. 4d). Median noise levels showed no distinct spatial patterns across the sampling area (Fig.

3c). Shipping density ranged from 0.069 to 17 vessel trajectories per km (Fig. 3b) and formed distinct routes through the turtle internesting area; anthrophony was sampled across the whole shipping density range; leatherback turtle track density (Fig. 3a) indicates the majority of sampling locations occurred with the central shipping density zones (1.1 – 5 vessel trajectories per km). Loud noise events were detected in 426 acoustic datasets and were encountered by all turtles, across the water column and throughout the study period (Fig. 5; median = 80.5, range: 44 – 221 loud noise events). These events were predominantly distributed to the west of Pongara National Park (Fig. 3d).

Biophony: Identifiable events of biophony were detected in 37 ± 9.4% (mean ± SD; n = 4) of depth-filtered recordings and consisted of cetacean vocalisations and turtle flipper movement (Fig. 2.). Cetacean vocalisations, which were exclusively humpback whales (*Megaptera novaeangliae*), were detected in 455 acoustic datasets (median = 114 vocalisations per turtle, range: 54 – 173 vocalisations, n = 4; Fig. 3e). Cetacean vocalisations were sampled by all turtles across the study period (Fig. 6a); with peaks in positive detections occurring between dusk and dawn (Fig. 6b). Cetacean vocalisations were detected throughout the water column and time of detections coincided across individual turtles (Fig. 6c; identified by vertical clustering of coloured points).

DISCUSSION

Marine soundscapes are complex physical phenomena that vary over time and space and are uniquely experienced based upon receiver characteristics (Brumm & Slabbekoorn, 2005). Here we demonstrate the use of animal-borne sensors to undertake an investigation of the anthropogenic and biological sounds present within a leatherback turtle internesting environment; ultimately showcasing the characterisation of marine soundscapes by a mobile receiver.

The consistent presence of anthrophony within the study suggests it is a common component of coastal marine soundscapes that exist near sites of anthropogenic marine activity (Samuel *et al.*, 2005). The range of anthrophony intensities sampled reflects the heterogeneous nature of marine soundscapes and emphasise the findings that individuals experience unique soundscapes

based upon their horizontal and vertical location in addition to local water characteristics. The slight increasing of and variance of anthrophony with depth (Fig. 4a and b), despite the near-surface sampling bias (largely due to leatherback diving behaviour), suggests that spatially defining soundscapes may require the understanding of the interactions between marine sound propagation and mobile animal-borne sensors. Temporally (Fig. 4d), anthrophony varied significantly between sampling days; with median anthrophony intensities initially decreasing as turtles progressed through the internesting period, likely reflecting movement offshore. This decrease was mirrored by an increase in days prior to the subsequent nesting event, indicating a movement to shallower near-shore waters. Mapping median anthrophony levels on a 2D plane (Fig. 3c) revealed a complex and variable spatial pattern that likely reflects the mobile nature of the animal-borne hydrophone, the heterogeneity of sound in the water column and the variable sampling effort. This spatial pattern may highlight the need to use three dimensions to represent sound in space, a greater sampling duration and number of sensors, in addition to methods that incorporate sound perception from mobile animal-borne sensors. The mapping of shipping densities from Odwendo Port (Fig. 1b) and within the sampling area highlighted distinct shipping routes that pass through the turtle internesting region (Fig. 3b) and may be prime contributors to anthrophony levels recorded. When comparing shipping densities (Fig. 3b) to sampling effort (Fig. 3a), it is noticeable that turtles did not enter the area of highest shipping density at the opening of the estuary and sampling effort was most dense within the mid-shipping density zone found to the west of the nesting beach. Whether this is deliberate avoidance behaviour by the turtles (turtle 2 swam to the north, an area of low shipping density) or habitat displacement by anthropogenic activity cannot be determined with extant data. Loud noise events were detected within the mid-range (1.1 – 5 vessel trajectories per 1 km) shipping density area with a cluster to the west of the internesting area (Fig. 3d), which may suggest the loud noise events are a product of a particular vessel type. However, examining the temporal distribution of loud noise events (Fig. 5) shows no distinct grouping of loud noise events across sensors, indicating loud noise events were encountered from a range of vessels and that other factors (e.g. proximity to vessel, depth) may determine the occurrence of a loud noise event.

Low-intensity persistent anthrophony may be perceived as background noise by animals; a constant and normal character of the soundscape and one that does not induce abnormal behaviour. Alternatively, constant high-intensity anthrophony has shown to mask the vocalisations of marine animals (such as humpback whales) that communicate at similar low sound frequencies (Clark *et al.*, 2009; Dunlop *et al.*, 2010; Tennessen & Parks, 2016), increase stress in animals that inhabit the soundscape (Rolland *et al.*, 2012), and illicit avoidance behaviours in marine mammals (Bailey *et al.,* 2010; Koschoinkski *et al.*, 2003) and fish (Fewtrell & McCauley, 2012; Gerlotto *et al.*, 2004). However, in marine species of lesser acoustic reliance, such as turtles, the impacts of high-intensity anthrophony (constant or intermittent) have yet to be explored. As Samuel *et al.* (2005) suggests low-frequency anthrophony is a concern for all marine turtles as their hearing range of highest sensitivity (Piniak *et al.*, 2012a) is confined to the same low-frequencies. Acoustic communication has been detected in a few marine reptiles: female leatherbacks have been recorded sighing during nesting events (Mrosovsky, 1972), green turtle (*Chelonia mydas*) and leatherback turtle hatchlings have been recorded emitting sounds (Ferrara *et al.*, 2014a; Ferrara *et al.*, 2014b) perhaps to coordinate hatching events. Both adult and hatchling freshwater turtles (*Podeocnemis expansa*) vocalise to gather individuals for mass migration events (Ferrara *et al.*, 2013), and the non-vocal Galapagos marine iguanas (*Amblyrhynchus cristatus*) have shown recognition ability of heterospecific alarm calls and respond with appropriate predator-avoidance behaviour (Vitousek *et al.*, 2007); these studies may reflect the currently undocumented acoustic capabilities of adult marine turtles. Whether acoustic communication is vital to marine turtle ecology or not, the anthrophony intensities recorded in this study and, in particular, the loud noise events defined may represent behaviour-influencing noise levels. Probable affects to leatherback turtles from these loud noise events may include increased stress levels and avoidance behaviour that may impact reproductive output during the nesting season due to investment of energy into abnormal behaviours, physiological damage to the ear and temporary/permanent shifts in hearing thresholds (Kastak *et al.*, 1999; Lucke *et al.,* 2009) that may inhibit turtle behaviour to an unknown severity until the importance of acoustics for this species is more clearly defined. Further investigation is required to understand

the importance of acoustics in marine turtles and pair their behaviour with perceived sound.

Biophony within the study area revealed the presence of vocalising cetaceans; identified as male humpback whales. Humpbacks vocalise for a range of purposes (Parsons *et al.*, 2008), however at a known wintering ground (Rosenbaum & Collins, 2006) it could be seen as communicating with other individuals in the region to determine competition at foraging sites. Detection rates of vocalisations were greater at dawn and dusk throughout the study period (Fig. 6c), identifying vocalisation periods that should be considered if management of the marine soundscape or shipping routes were to incorporate environmental impact. Whilst information gleaned from biophony investigation provides useful insights into temporal distribution of cetacean vocalisation, we caution that detection may be influenced by the behaviour of the animals bearing the sensor and the spatial distribution determined from the sensor does not truly represent the location of the vocalising cetacean. Using multiple sensors may enable triangulation of sounds perceived at synchronised times, but would require additional information on marine sound propagation. Despite the spatial shortcomings, there is much use in determining the presence/absence of vocal marine species using acoustic monitoring methods.

With adjustments, animal-borne monitored marine soundscapes have research scope beyond characterisation of the acoustic environment. Combining continuous fine-scale movement datasets with continuous acoustic datasets would allow wild animal behavioural modelling in relation to sound events (Ellison *et al.*, 2016); an area that is being investigated in some marine species in regards to renewable energy (Madsen *et* al., 2006; Thompson *et al.*, 2013), but is still limited in marine turtles (Nelms *et al.*, 2016). Applying behavioural ecology to acoustic analysis would open up research pathways into behavioural adaptation in response to prolonged exposure to anthropogenic noise, spatial and temporal habitat selection and preference, and behavioural coping mechanisms for unfavourable noise conditions. Application of sensory ecology to acoustic datasets would enable greater examination of animal-perceived sound, shifting the focus from a human perception and creating scope for the generation of fine-scale, animal-centric soundscapes.

Mapping of acoustic environments requires interdisciplinary approaches to understand the complex relationships between marine sound propagation and ecological responses to such stimuli. We encourage the investigation of acoustic environments from an animal-borne sensor approach to aid in broad scale assessments of marine noise, biological monitoring of large marine areas and generation of marine soundscapes over time and space.

Here we provide novel marine soundscapes, which when combined with finer acoustic sensitivities of adult leatherback turtles may aid in understanding the impacts and management of marine anthrophony for this species. We add to the evidence that a vulnerable species is exposed to high intensity anthrophony during the reproductive season and encourage further investigation into quantifying the effects of this exposure.

CHAPTER 2

Fine-scale movements and effects of ambient acoustic environment on dynamic body acceleration of the leatherback turtle (*Dermochelys coriacea*) during an internesting interval

Jack A. Boyle[1], Pierre Didier Agamboue[2], Philip D. Doherty[1], Angela Formia[2], Brendan J. Godley[1], Lucy A. Hawkes[1], David A. Mann[3], Sara M. Maxwell[4], Richard J. Parnell[2,5], Guy-Phillipe Sounguet[2], Matthew J. Witt[1]

[1] University of Exeter, Penryn, Cornwall, UK

[2] Wildlife Conservation Society, Marine Program, Libreville, Gabon, Africa

[3] Loggerhead Instruments, Sarasota, Florida, USA

[4] Department of Biological Sciences, Old Dominion University, Norfolk, VA, USA

[5] For Agence Nationale des Parcs Nationaux, Libreville, Gabon, Africa

ABSTRACT

Concern of the potential impacts of marine noise is increasing; however the methodologies available to assess these impacts on lesser vocal marine species are under-developed. Combining tracking and acoustic monitoring technologies, we collected fine-scale data on the movement and acoustic environment of the leatherback turtle (*Dermochelys coriacea*), nesting in Gabon, Central Africa. A SPLASH10-AF satellite transmitter (Argos tracking), DSG-OpenTag (hydrophone and accelerometer tag) and VHF transmitter (for relocating individuals) were attached to four female turtles using direct carapacial attachment. Data were gathered throughout an entire internesting interval on behaviour (diving profiles), ambient acoustic environment (sampling rate: 20 seconds every 10 minutes, frequency: several Hz to 12.5 kHz; used to calculate sound energy across frequency bands) and tri-axial acceleration (used to calculate Vectoral Dynamic Body Acceleration; VeDBA). Using VeDBA as an energy proxy, we explored the fine-scale movement and modelled the effects of sound energy on individuals. Turtles spent an average of 21.3 ± 12.4 hours (mean ± 1SD, n = 4) at the surface, with an average diving depth of 13.7 ± 1.6

metres (mean ± 1SD, n = 4; max = 52 metres). VeDBA ranged from 0.005 – 0.171g and was significantly affected by depth and broadband sound energy (GLMM: $\chi^2_{1,6}$ = 8.62, p = <0.05). Individual turtle VeDBA was influenced by different sound frequencies within the turtle hearing range. We discuss the potential effects of marine acoustics on this species. Our findings provide a novel methodology for examining the effects of sound on wild marine fauna.

KEYWORDS

marine turtle; accelerometry; acoustics; dynamic body acceleration; diving behaviour

INTRODUCTION

Understanding the spatio-temporal distribution of movement has been pivotal to ecological studies for decades (Hebblewhite & Haydon, 2010). Animal movement studies have been conducted on fauna large and small, across the globe (Hussey *et* al., 2015; Kays *et al.*, 2015), giving insight into animal-environment usage, allowing researchers to identify sites for protection and inform conservation management strategies (Cooke, 2008; Wilson *et al.*, 2015).

Telemetry combines technology with biology to peer into the secret lives of fauna, with devices adapting over time with the development of satellites, microcomputers and computing (Kooyman, 2004). Due to associated environmental complexities (submergence, pressure, device retrieval) marine animal tracking may prove more difficult to implement than for terrestrial species, but has enabled researchers to detail trans-oceanic migrations (Block *et al.*, 2011; Doherty *et al.,* 2017a; Hays & Scott, 2013), define the boundaries, or lack of, marine animal ranges (Block *et al.*, 2005; Blumenthal *et al.*, 2006; Doherty *et al.*, 2017b), and pinpoint sites of conservation importance (Maxwell *et al.*, 2011; Simpfendorfer *et al.*, 2010). These discoveries are tied to the analysis of large-scale tracking data, however local conservation efforts require the knowledge of the fine-scale movements of individuals in a defined space (Christiansen *et al.*, 2017; Wilson *et al.*,2017; Wright *et al.*, 2017), which may

help to determine individual energetics and fitness costs (Bouyoucos *et al.*, 2017; Brownscombe *et al.*, 2017; Rosen *et al.*, 2017), whilst examining the impact of environmental factors on behaviour (Castellote *et al.*, 2012; Pine *et al.*, 2017; Southall *et al.*, 2016).

Biologging devices are capable of tracking fine scale movement of individuals and the surrounding environment they exist in; for example global positioning system (GPS) tags can be used to define individual locations (Hart & Hyrenbach, 2009), accelerometers are capable of tracking tri-axial acceleration (Lyons *et al.*, 2013; Brownscombe *et al.*, 2014; Nakamura *et al.*, 2015), on-board oceanographic sensors for salinity and dissolved oxygen provide insights into ocean structure (Boehlert *et al.*, 2001; Lydersen *et al.*, 2002; McMahon *et al.*, 2005), and hydrophones can be used to record ambient environmental noise (Lammers *et al.*, 2008; Sousa-Lima *et al.*, 2013). Combining data streams from multiple biologging devices enables researchers to delve further into the minutiae of animal movement; by combining location and tri-axial acceleration individual energy proxies may be examined (Gleiss *et al.,* 2011), whilst the addition of ambient acoustic data from hydrophones enables the creation of soundscapes (Coquereau *et al.*, 2017; Erbe *et al.,* 2015; Pine *et al.*, 2015) and provides a platform to investigate the effect of marine noise on wild animal behaviour (Bas *et al., 2017;* Magnhagen *et al.,* 2017).

Here we apply multichannel biologging technology to leatherback turtles (*Dermochelys coriacea)* nesting on the beaches of Gabon, to investigate the fine-scale movement of individuals during an internesting period and examine the affect of ambient marine noise on turtle behaviour. Marine turtles have a global distribution (Bowen & Karl, 2007) and gravid female turtles are large in body size, nesting terrestrially, depositing clutches multiple times per season with an in-water interval between each nesting attempt, termed the internesting period (Lutz *et al.*, 2002); making them an ideal species for device attachment, especially when gathered data are too large for repatriation to researchers by satellite. Documentation of trans-oceanic migrations is common with nesting females from this population migrating to equatorial Atlantic, South America, and southern Africa (Witt *et al.*, 2011), however the investigation of fine-scale movement at the nesting sites is sparse (Georges *et al.*, 2007; Witt *et al.*, 2008); despite such information having great potential in identifying the needs of and

risks to individuals during vulnerable parts of the life cycle (Lascelles *et al.,* 2014). Anthropogenic noise has been detected in a variety of marine ecosystems, and is shown to impact the behaviour (Nowacek *et al.*, 2007; Williams, *et al.,* 2015) induce trauma (André *et al.* 2011; De Soto *et al.,* 2013; Romano *et al.*, 2004), and possibly cause mortality in marine fauna across the globe. The effects of marine noise on turtles is largely unknown (Nelms *et al.*, 2016) perhaps due to the unknown role of acoustics in marine turtle ecology, despite the species existing in areas of marine noise pollution (Samuel *et al.*, 2005), such as Gabon port (Fig. 1b). This Gabon leatherback turtle nesting population provides an opportunity to combine fine-scale behavioural and acoustic data in attempt to understand diving behaviour during the nesting season and explore novel sampling and analysis of acoustic and movement datasets.

We present new data on the fine-scale diving behaviour and movement of nesting leatherback turtles during a nesting season and propose a novel methodology for investigating the effects of marine noise on wild marine animals. Generating information that may inform local management strategies for the nesting population and a methodology that could be adapted and applied to a wide range of acoustic-sensitive animals, capable of supporting biologging technology.

METHODS

Study site and turtle monitoring

Female leatherback turtles were encountered during the early nesting season (October) at Pongara National Park, Gabon, Central Africa (Fig. 1a and 1b; 0.1289° N, 9.6119° E). The Kingere zone within the National Park was surveyed by foot and quad bike to locate nesting leatherback turtles for instrumentation. Bathymetry surrounding the Kingere zone represents a shallow inshore shelf (Fig. 1b), reaching depths of 50 metres twenty-five kilometres from the nesting beach.

Tag specification and attachment procedure

Three devices were attached to the medial ridge of each of six turtles (Fig. 1c; curved carapace length, mean ± 1SD = 152. ± 10.4 cm; estimated mass (Georges & Fossette, 2006), mean ± 1SD = 321 ± 54.3 kg). Fitted devices were a Fastloc-GPS enabled Argos-linked satellite tag (SPLASH10-AF; Wildlife Computers, Redmond, Washington, USA), a sound and movement tag (DSG-OpenTag; Loggerhead Instruments, Sarasota, Florida, USA) and a VHF tag (Sirtrack, NZ) (Fig. 1d). The area of tag attachment was cleansed with sterile water and Hibiscrub (Regent Medical Oversea Ltd; Manchester, UK), before narrow channels were made laterally into the medial ridge using individual-use, sterile, veterinary, anti-skid drill bits. Tags were secured to the carapace with nylon coated braided stainless wire loops, closed with slow degrading ferrule to ensure release later of tags should the instrumented turtles not be re-encountered for physical device retrieval. A pad of hypoallergenic dental putty (Equinox 35; Smooth-On Inc.; Pennsylvania, US) was inserted between each device and the carapace surface to prevent device movement, reduce friction and improve hydrodynamic flow around each device. Turtles selected for instrumentation were in good physical condition, had no visible external injuries and exhibited no atypical nesting behaviour. Scientific procedures were subject to ethical review by the University of Exeter (UK) and by Agence National des Parcs Nationaux (Gabon).

Data sampling

Satellite tags collected GPS location (longitude, latitude; coordinate system World Geodetic System 84). Satellite tags were programmed to gather one valid GPS quality location every hour from up to four attempts. Satellite tags transmitted these data to overpassing satellites (Argos System; www.argos-system.org) when tags were at the sea surface.

Fine-scale movements were sampled via the accelerometer contained within the sound and movement tag. Tri-axial acceleration (surge, pitch and roll) of instrumented turtles, also pressure (depth) and temperature data were sampled at 10-millisecond frequency and archived to a SD card for later download.

An in-built hydrophone in the sound and motion tag sampled the ambient acoustic environments for 20 seconds periods at 10 minute intervals at a rate of 50 kHz with a decimation factor of 4; providing an effective frequency range of several Hz to 12.5 kHz. This frequency range encompasses the acoustic range of marine turtles; determined to be 50 – 1200 Hz (with a sensitivity range of 100 to 400 Hz) based on auditory evoked potentials in leatherback turtles hatchlings (Piniak *et al.*, 2012), and so for adult leatherback turtles this range is likely smaller and potentially lower due to aging and physiological changes, while remaining within these bounds.

Data collection periods for all tags encompassed one internesting period (approximately 10 days). Instrumented turtles were actively relocated during subsequent night patrols. An Argos System hand-held receiver (TSUR-400; Teleonics) detected transmissions made by satellite tags as turtles neared the nesting beach. A VHF receiver and antenna (Ultra; Sirtrack, NZ) were used to detect signals from the VHF tag as turtles emerged onto the beach for nesting. Once instrumented turtles were located, the sound and movement and VHF tags were removed and data downloaded. Depth and temperature data were also downloaded *in-situ* from satellite tags; these tags remained attached for the remainder of the breeding season and into post-nesting migrations.

Data processing

Data from the multiple devices were aligned for onward analysis using time-based matching and concatenated to the lowest common sampling rate (hydrophone at 20 second sampling periods at 10 minute intervals) to prepare them for analysis.

Fastloc-GPS location data underwent interpolation (Tremblay *et al.*, 2006) to provide tracks across the internesting period and location data at 10 minute intervals, aligning with acoustic data sampling time periods.

Accelerometer-sampled pressure data were used to determine depth and generate dive profiles for individual turtles. Diving behaviour (time at surface, average and maximum diving depths) were subsequently calculated for each turtle during the internesting period.

Tri-axial acceleration data were used to calculate Vectoral Dynamic Body Acceleration (VeDBA), a quantitative measure of fine-scale body movement that may be used as an energy proxy (Gleiss *et al.*, 2011); using the calculations provided in Qasem *et al.* (2012). Subsequently, a VeDBA sum and mean average per acoustic sampling period were generated for further analysis.

Only sub-surface acoustic files were used in analysis (verified by audible inspection and confirmed by assigned depth values; depth ≥ 0.5 m) and were processed using PAMGuide (Merchant *et al.*, 2015). PAMGuide enables data calibration to instrument specifications, quantification of sound energy within defined acoustic frequency ranges, and visualisation of audio data. Sound energy, per third-octave bands (TOBs; a frequency band whose upper band-edge frequency is the lower band frequency times the cube root of two) across the broadband range were calculated for each acoustic sampling period.

Diving behaviour and VeDBA were examined across time and individuals. A generalised linear mixed model (GLMM) with an inverse Gaussian error structure was used to investigate the interactions between depth and broadband sound energy on mean average VeDBA per acoustic sampling period, with individuals fitted as a random factor. To determine if particular energy within particular sound frequencies significantly impacted individual VeDBA, general linear models (GLM) with an inverse Gaussian error and log link function were fitted for each turtle; using sound energy within third-octave bands that encompassed the leatherback turtle acoustic range as defined by Piniak (2012). Models were simplified to contain only significant variables.

Data manipulation, analysis and mapping were conducted in MATLAB (The MathWorks, R2014b) and R v3.0.1 (R Core Team 2013).

RESULTS

The modal internesting duration was 10 days (range: 9 – 10 days; n = 4), with turtles moving a mean (±1SD) minimum straight line distance of 321.2 ± 16.9 km. Turtles 1, 3 and 4 had internesting ranges no further than 25 km (radial distance) from the tagging site. Turtle 2 undertook a short foray north of the

nesting beach across the Gabon estuary, moving 50 km from the tagging site prior to returning 10 days later for a subsequent nesting attempt.

Turtles spent an average of 21.3 ± 12.4 hours (Fig. 7; mean ± 1SD, n = 4) at the surface, 0.09 ± 0.05 % (mean ± 1SD, n = 4) of the internesting period (modal duration = 10 days, n = 4). Average diving depth was 13.7 ± 1.6 metres (mean ± 1SD, n = 4) with max diving depth reaching 52 metres (range: 47 – 52 metres, n = 4). Internesting diving profiles (Fig. 7) indicate no turtle maintained a horizontal depth for a prolonged period, undertaking continuous vertical ascents and descents.

Mean VeDBA was 0.17 ± 0.01 g (mean ± 1SD, n = 4; range: 0.005 – 0.171 g) and varied significantly amongst individual turtles (Kruskal-Wallis rank sum test: χ^2_3 = 70.39, P = <0.01). VeDBA was significantly influenced by depth (Fig. 8), broadband sound energy (Fig. 9) and the interaction between both predictors (GLMM: $\chi^2_{1,6}$ = 8.62, p = <0.05; Table 1), with depth having a significantly larger negative relationship with VeDBA in comparison to the positive effect of broadband sound energy; the interaction between both predictors had a minor positive effect on VeDBA. VeDBA in all individuals was significantly affected by multiple TOBs (range = 3 to 6 significant TOBs, n = 4), with each individual being affected by different TOBs within the leatherback turtle acoustic range (Table 2). Turtle 1 VeDBA was affected by sound energy in the smallest range of TOBs (GLM: $\chi^2_{1,677}$ = 42.3, P = 0.17) within the acoustic sensitive range (100 – 500 Hz). Turtle 2 VeDBA was affected by sound energy across the whole acoustic range ($\chi^2_{1,748}$ = 37.1, P = 0.18). Turtle 3 VeDBA was affected by sound energy of TOBs within the middle to upper sound frequencies ($\chi^2_{1,748}$ = 37.1, P = 0.18), encompassing the acoustic sensitive rang. Turtle 4 VeDBA was affected by the greatest range of TOBs from the lower and upper frequencies (3 significant TOBs; $\chi^2_{1,469}$ = 41.0, P = 0.12), none of which lied in the acoustic sensitive range.

DISCUSSION

Here we have explored the internesting behaviour, energy proxies and acoustic sensitivities of three leatherback turtles; exploring the behaviour of an

endangered species at a reproductive site using novel biologging devices and data sampling methods.

Three of four turtles undertook similar internesting movements, swimming only to the west of the nesting beach; turtle 2 undertook a foray to the north of the nesting beach, across the Gabon estuary, resulting in a greater distance travelled than the other three turtles. Whilst the reasons for difference in internesting range cannot be inferred, the large distance travelled by turtle 2 may have led the individual to experience a greater range of underwater acoustic environments as it transited through the shipping channel from Gabon port.

Diving profiles (Fig. 7) revealed an active internesting period for all individuals, with constant vertical movement throughout the sampling period. Depths reported reflect local bathymetry (Fig. 1b); potentially indicating individuals were diving close to the sea floor and back to the surface repeatedly. With little time spent at the surface and dive profiles showing no prolonged periods spent at one horizontal depth (i.e. remaining stationary), it would seem turtles do not rest during internesting periods. As capital breeders (Lutz *et al.,* 2002), it is assumed turtles do not feed at nesting beaches and may aim to reduce diving to invest more energy into reproductive events. Whilst collected data does not allow the inference of feeding events, data may suggest internesting diving behaviour is a considered reproductive energy cost by individuals, or that diving is not a costly behaviour for turtles due to physiology, and therefore has no significant impact on reproductive output.

The VeDBA range reported support the active, or at least non-stationary, internesting interval portrayed by the diving profiles (Fossette *et al.*, 2012). The density of low VeDBA values sampled (Fig. 8) may also reflect the low-energy nature of diving for turtles, conserving energy to invest directly into terrestrial reproductive events. Whilst no other studies have reported VeDBA for leatherback turtles, the values reported here reflect similar values and variance as the Overall Dynamic Body Acceleration (ODBA) found in other marine turtle species (Enstipp *et al.*, 2011; Halsey *et al.*, 2011; Shepard *et al.*, 2008).

The results of the GLMM to investigate the influence of depth and broadband sound energy on turtle VeDBA, highlighted a significant effect of both fixed

effects and the interaction between them (Table 1). This may suggest position in the water column and ambient acoustic environment may lead to a change in dynamic body acceleration and infer diving ascent/descent; perhaps representing reactions to sound events (Small *et al.*, 2017), such as avoidance behaviour, or disorientation behaviour (Holles *et al.*, 2013). By modelling the effect of third-octave bands on VeDBA, we determine which frequencies within the turtle acoustic range had the greatest impact. Results from VeDBA-sound models should be taken with consideration due to the non-significance of individual turtle models. Individual VeDBA was affected by different TOBs frequencies within the known turtle acoustic range (Table 2). This may highlight individual difference in hearing due to aging and health, but does not necessarily indicate an increased sensitivity to particular TOBs. Significant TOBs may have been those that the individual perceived greatest sound energy from, which in turn may be influenced further by depth and proximity to the sound source. Piniak *et al.* (2012) identified an acoustic sensitive range in leatherback turtle hatchlings at 100 – 400 Hz, however results from the models show VeDBA was influenced by TOB frequencies that ranged above, below and throughout this acoustic sensitive range. Regardless of which TOB frequencies most affect turtle VeDBA, we provide evidence of sound-influenced movement that may suggest turtles react to the ambient acoustic environment and would reinforce the concern of marine noise pollution from shipping and the hydrocarbon industry on marine organisms (Simmonds *et al.*, 2014).

This study presented a novel methodology for investigating marine animal movement and the effects of marine noise on individuals. The fine-scale nature of such variables requires high-resolution tracking to identify the minute variations in both sound and body movement. Whilst technological capabilities may limit sampling techniques, this study would greatly benefit from a greater number of individuals sampled and repeats of internesting sampling periods both within and across nesting seasons; helping to refine models and better understand the interactions between body movement and sound energy. Using this methodology in an area of known marine pollution, and anthropogenic activity (i.e. seismic surveying, pile driving) may provide further evidence of responses to impulsive sound sources with a quantifiable source. Currently, our

study provides potential avenues for further investigation into the field of sound-induced marine animal movement.

GENERAL DISCUSSION

The use of multiple biologging devices has allowed us to examine the spatiotemporal patterns of a marine acoustic environment; deconstructing it to visualise and interrogate sound components and generate a marine soundscape, which enabled us, in tandem with fine-scale movement data, to examine the effect of marine sound on a free-ranging marine species. The studies utilised novel methodologies that combined technology and ecological knowledge to investigate the internesting activities and acoustic environment of leatherback turtles, and whilst results should be considered carefully, the research presented here provides a foundation for investigating the effects of marine sound and noise pollution across the globe.

THIS RESEARCH

Conceptually, the marine soundscapes presented in chapter 1 make the marine acoustic environment accessible, both visually and analytical. The deconstruction of components enables researchers to select the most relevant data for hypothesis and aid in identifying the interactions between sound and organisms that perceive it. The novelty in this style of acoustic monitoring comes from the animal-borne sensors, which record the sound at the level of the individual, applying animal context to a human-centric of acoustic environments (Francis & Barber, 2013). The duration of this study does not allow ambient acoustic phenomena with oscillation larger than 10 days to be resolved; scaling up data collection periods may elucidate temporal patterns in the soundscape, which would aid in management of anthrophony (Van Parijs *et al.*, 2009) and the logistics of studies aimed at specific acoustic events (loud noises, anthrophony sources).

The perhaps serendipitous biophony data inspired the idea of animals as acoustic biodiversity monitors. Observation of fauna within the marine realm is often difficult, so monitoring bioacoustics may be a viable method of surveying an area for acoustic emitting species. Whilst this may exclude species that do not emit sounds, it would be ideal for small marine habitats such as coral reefs,

where biophony is abundant (Parsons *et al.*, 2016; Radford *et al.*, 2014). An extension of biophony analysis is the characterisation of sound signatures and assignation of them to extant species; an acoustic library of marine animal noises. Biophony sound signatures could be characterised in terms of sound frequencies, sound intensities and durations they occur; potentially using machine learning techniques (Kotsiantis *et al.*, 2007; Schindelin *et al.*, 2012) to analyse spectrograms and help to mass analyse acoustic datasets.

Application of this methodology to specific anthrophony events (i.e. those we perceive as damaging to the environment) would be of interest. Whilst logistically it may prove difficult (syncing of device deployment on individuals with the anthrophony) the information obtained from such research would be of much use in generating quantitative data on sound intensities perceived by individuals within populations. For example, animal-borne acoustic monitoring of seismic surveys would enable the assessment of sound, and the potential impact, in the context of an individual, which in turn can be coupled with movement data to see if the individual responds (akin to our study in chapter 2).

The use of VeDBA as an energy proxy enables empirical investigation of environmental impacts on individuals, opening up evolutionary and physiological explanations for marine fauna behaviour. The knowledge to be obtained from marine VeDBA studies is vast, but requires expertise in data handling of time-series and novel experimental designs to couple the movement data with other variables. Whilst the results presented in chapter 2 should be considered with care, they represent methods and analysis that could be utilised in understanding the increasing concerns of marine noise on marine fauna (Nelms *et al.*, 2016; Simmonds *et al.*, 2014). Improved experimental design or data sampling frequencies may provide results of greater reliability, as the fine-scale changes in both dynamic body acceleration and acoustic environment may benefit from a continuous sampling period rather than discrete snapshots. A study centred around specific high intensity anthrophony events, as previously mentioned, would be ideal in design; enabling dosage experimental designs (before, during, after sound event) and analysis to be applied to the animal movement.

THE FUTURE OF MARINE BIOLOGGING

Biologging devices provide a wealth of data, and information if the appropriate scientific planning and procedures are supplied. Whilst there may be a desire to amass datasets, we stress the need to consider hypotheses and experimental design before deploying devices as data rich may not equal information rich (Hebblewhite & Haydon, 2010). We envision animal monitors contributing to global oceanography datasets (Moustahfid *et al.*, 2011; O'Dor & Stokesbury, 2009), devices capable of accompanying animals to extreme depths, devices small enough to equip to vertebrates, and a shift in analysis from 2D to 3D to better represent the complexity of the marine environment and the movement of fauna who reside there. Marine biologging is a world of innovation and adaptation, tying the brilliance of technology with ecology in an effort to reveal the secrets of the marine realm.

CONCLUSION

Here we have presented high-resolution and archival tracking of leatherback sea turtles to investigate the marine acoustic environment and its effect on leatherback turtle behaviour. Our studies showcased novel methodologies and analysis of fine-scale datasets, elucidating the complexity of acoustic environments and the potential impacts it may have on individuals during a nesting season. The marine acoustic environment requires greater research attention and the effects of marine noise should be incorporated into local management strategies for species within the area.
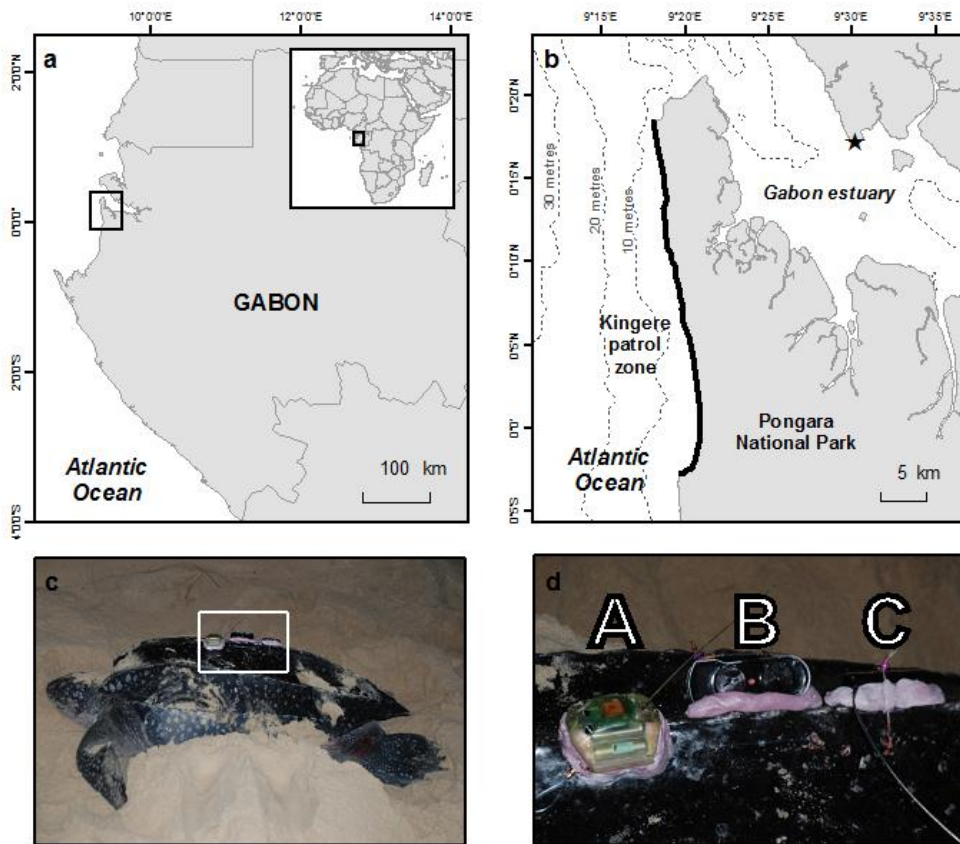
Figure 1. Geographic context and electronic data tags. (a) Gabon, Atlantic coast of Central Africa and African continent (inset). Extent of part b (bold black polygon). (b) Pongara National Park and the Kingere zone (solid black line). Black star denotes location of Owendo Port, Libreville. (c) Lateral profile of instrumented female leatherback turtle; total mass of instrument packages 650g. Extent of part b (white polygon). (d) Fastloc-GPS Argos-linked satellite tag (A); sound and motion tag (B) and VHF tag (C).
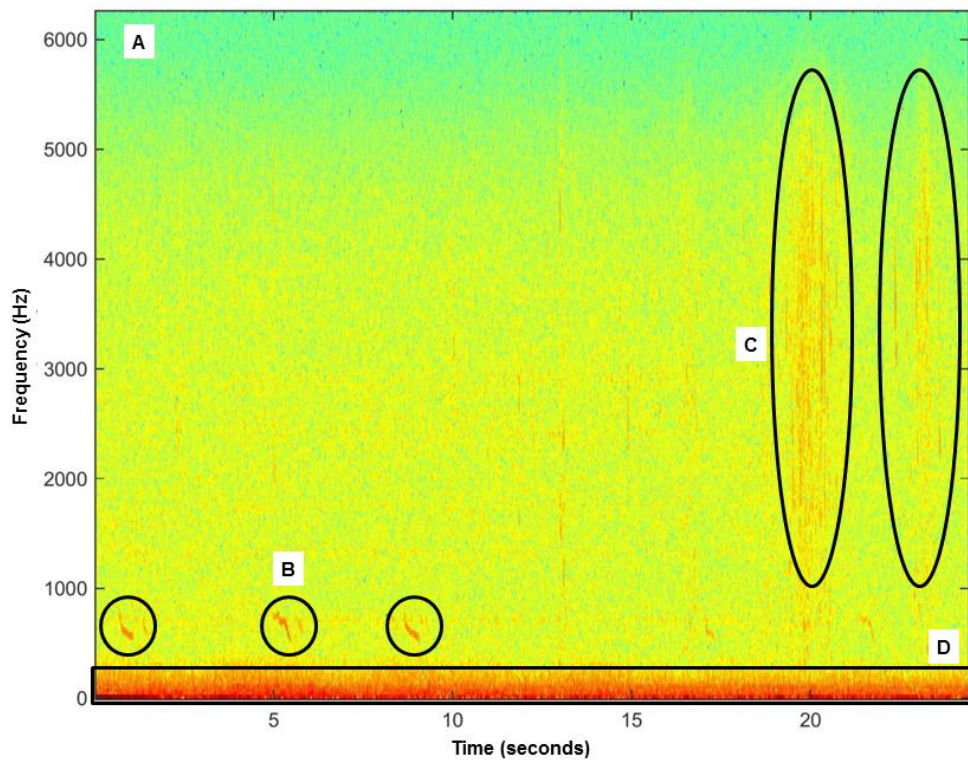
Figure 2. Example spectrogram. Visual representation of an acoustic file produced as an output option from PAMGuide (Merchant *et al.*, 2015). Colours represent sound intensity (i.e. decibels, dB); with blue representing low intensity sound and red high intensity sound. This particular spectrogram contains multiple soundscape components and sound signatures (A-D). Geophony (A): broad frequency spectrum, low intensity sound. Biophony (B): cetacean vocalisations, distinct sound signatures of high sound intensity. Biophony (C): turtle flipper movements, distinct broad frequency sound signature. Anthrophony (D): shipping activity, typically low frequency and high intensity sounds of longer durations.
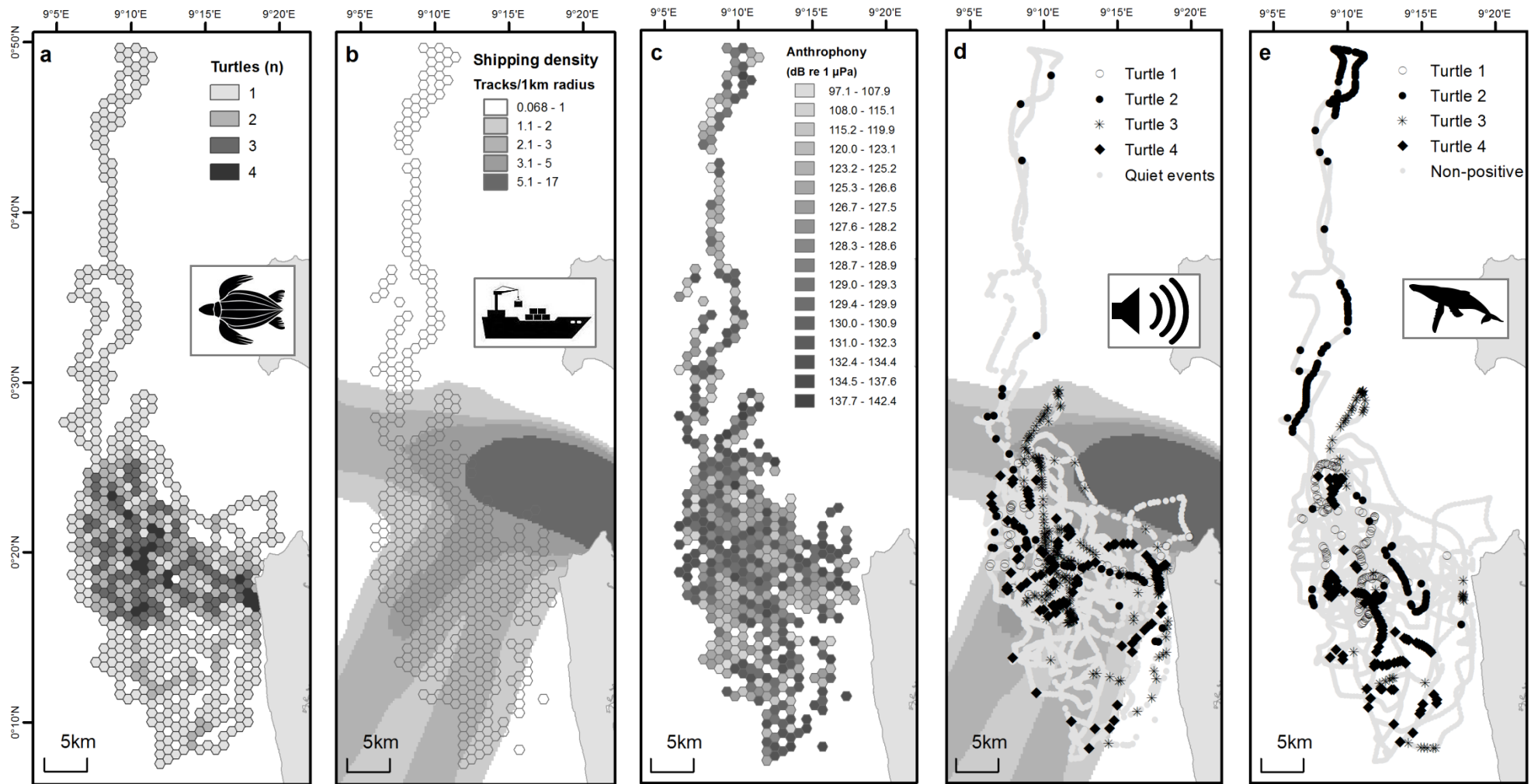
Figure 3. Marine soundscape components. (a) Interpolated turtle survey effort; density of turtle tracks per 1 km^2 hexagon. (b) Shipping density; shipping density (vessel trajectories per 1km radius) for the duration of the acoustic sampling period and a hexagrid to show study survey area. (c) Anthrophony; median anthrophony per 1km² hexagon, for all individuals across the whole sampling period. (d) Loud noise events with shipping density underlay. (e) Detections of whale vocalisations.
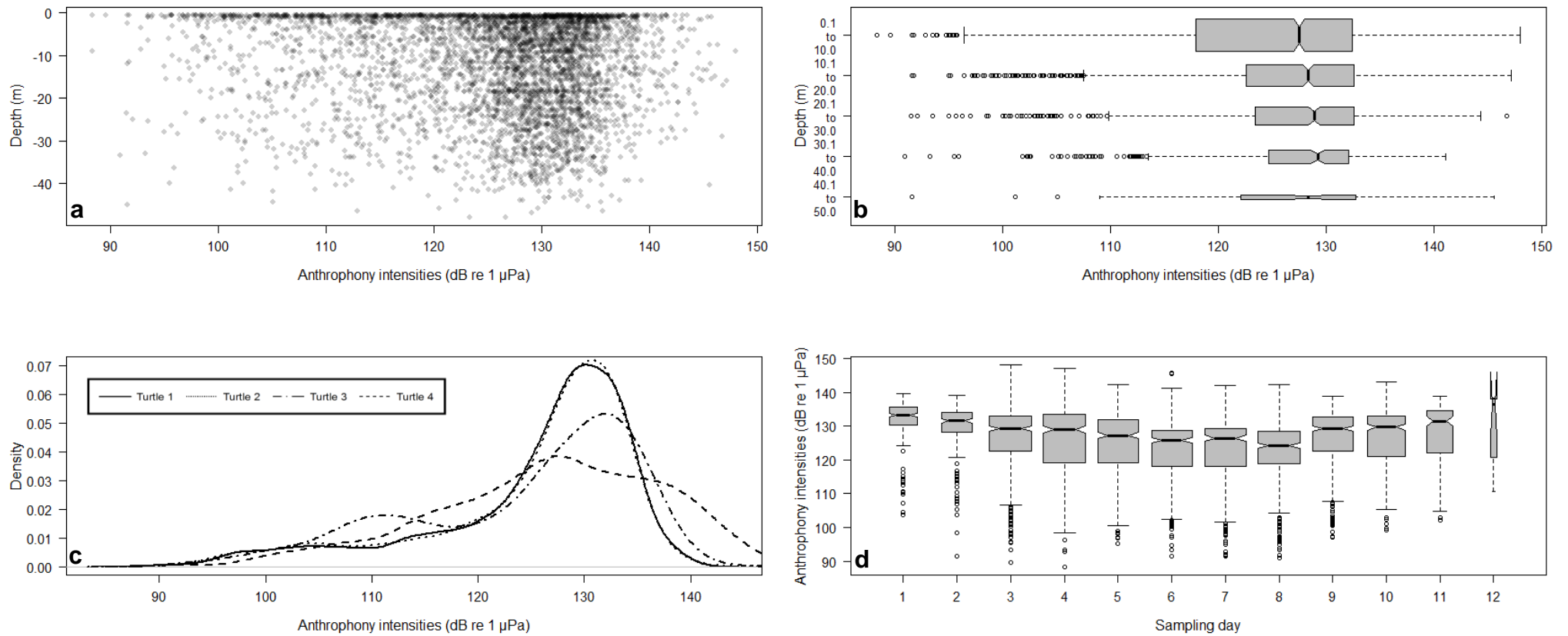
Figure 4. Anthrophony. (a) Anthrophony sampling across the water column; each point represents one interpolated location for acoustic data sampling sites. (b) Comparison of anthrophony intensities when grouped into depth ranges; boxplot width has been scaled to number of samples per depth bin. (c) Density plots of anthrophony intensities per acoustic monitor. (d) Anthrophony intensities per day of sampling; box plots width scaled to number of samples per hour.

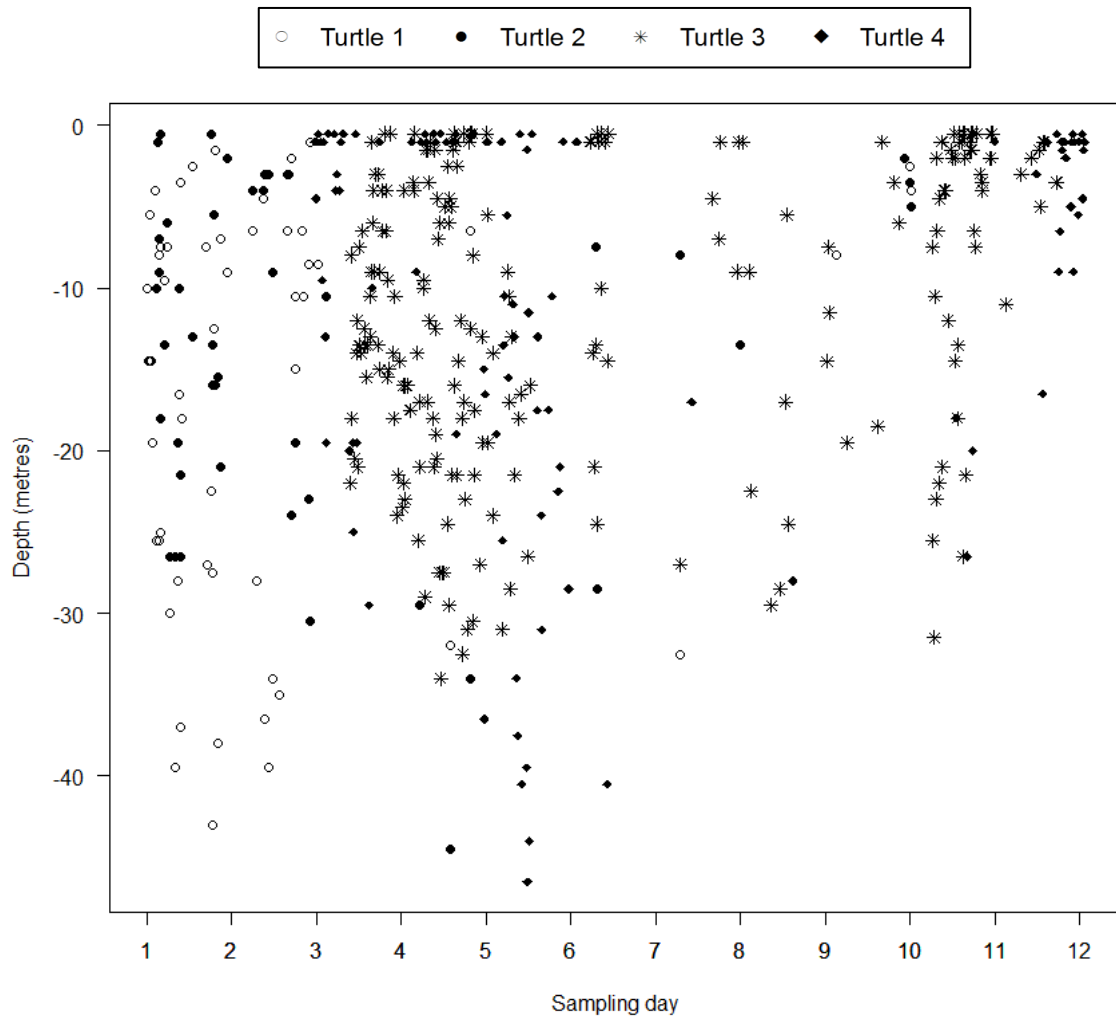Figure 5. Loud noise events. Distribution of loud noise event across sampling period (October 26th – November 6th) and depth of water column.
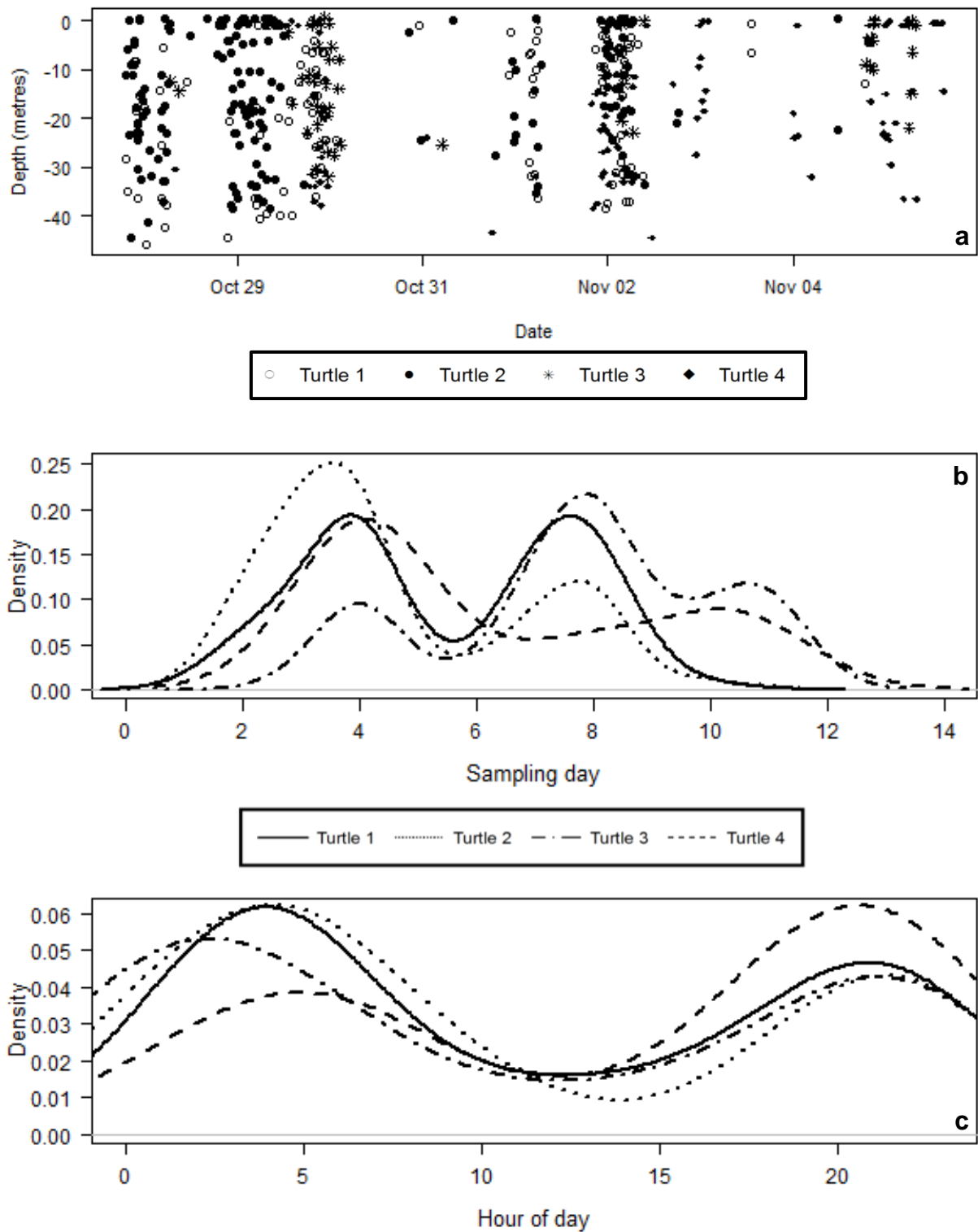
Figure 6. Biophony: cetacean vocalisations. (a) Temporal and depth distributions of positive detections of whale vocalisations. (b) Density of positive detections of cetacean vocalisations over the whole sampling period. (c) Density of positive detections of cetacean vocalisations per hour of the day; line styles represent individual turtles.
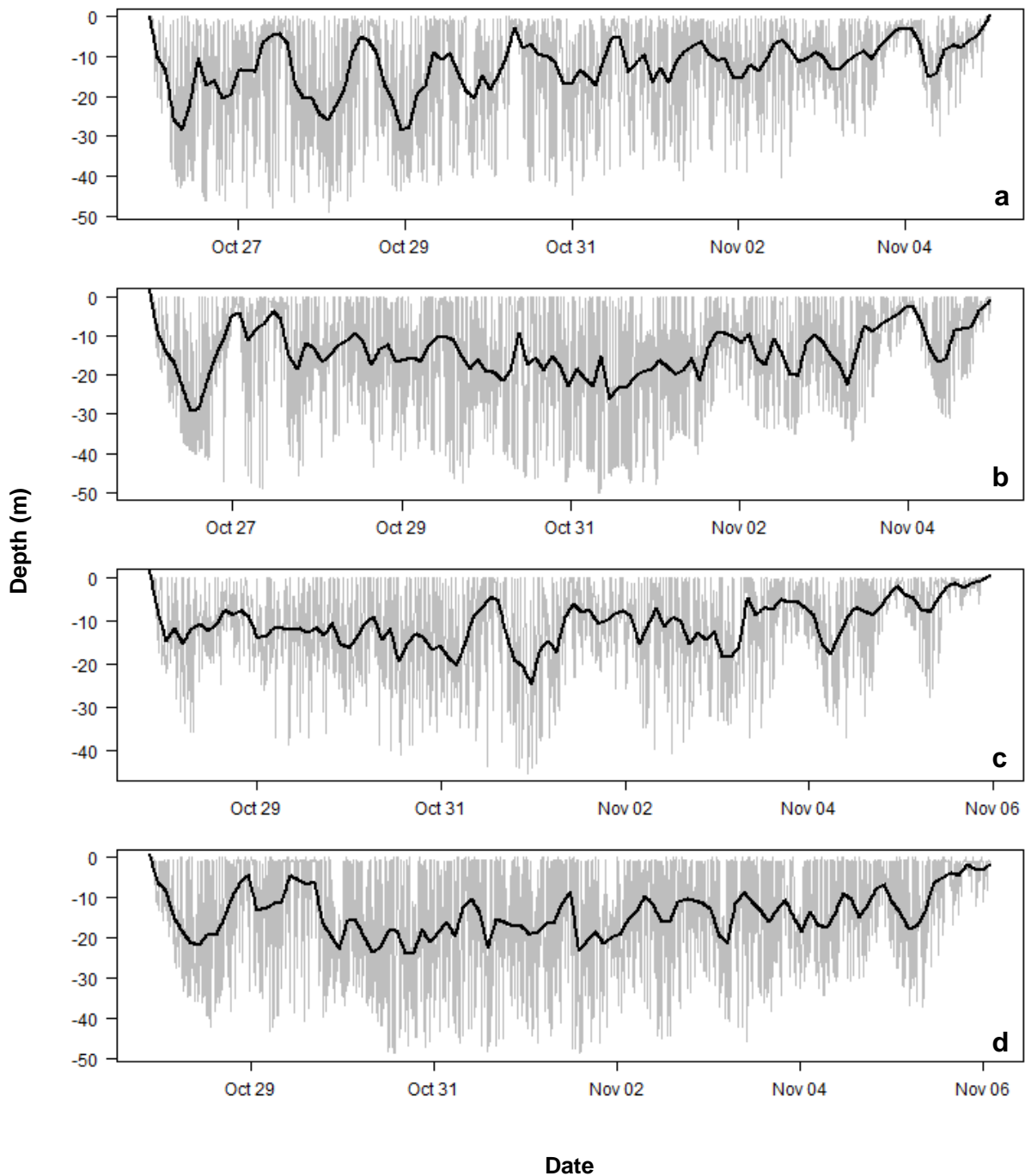
45

Figure 7. Dive profiles. (a-d) Individual turtle dive profiles, turtles 1 – 4 respectively, for the sampling period. Grey line represents raw data downloaded from satellite tags; black line represents a smoothing of the raw data at a 0.02 frequency.
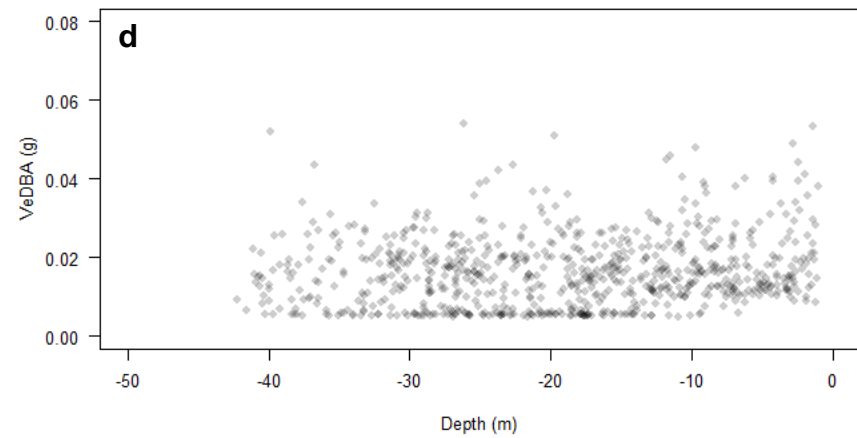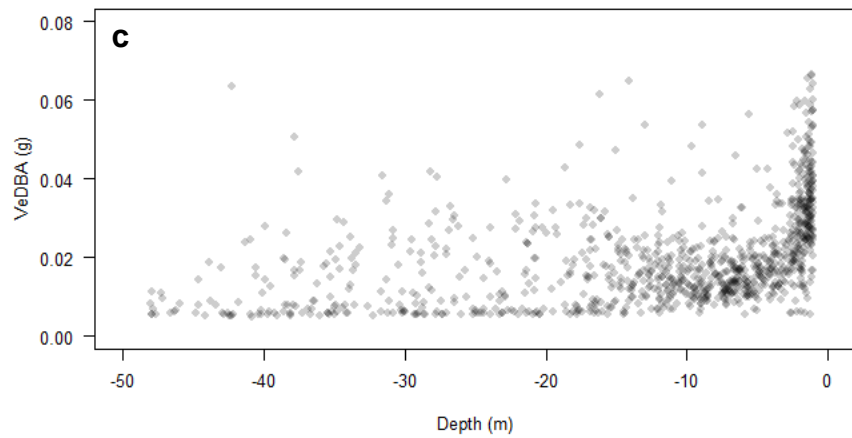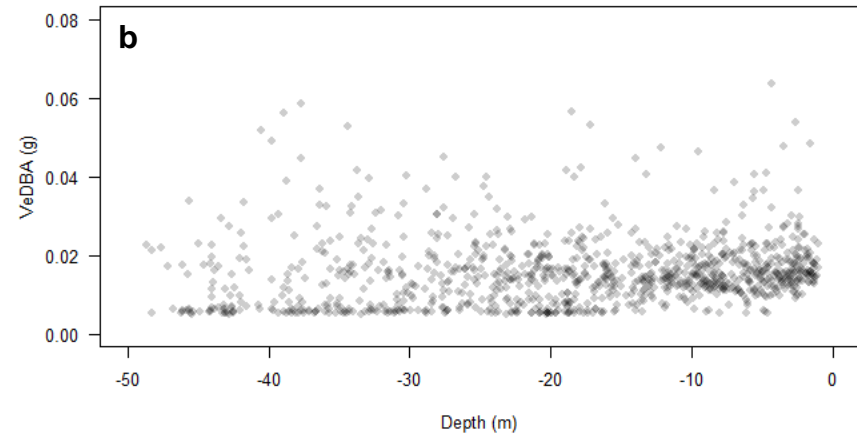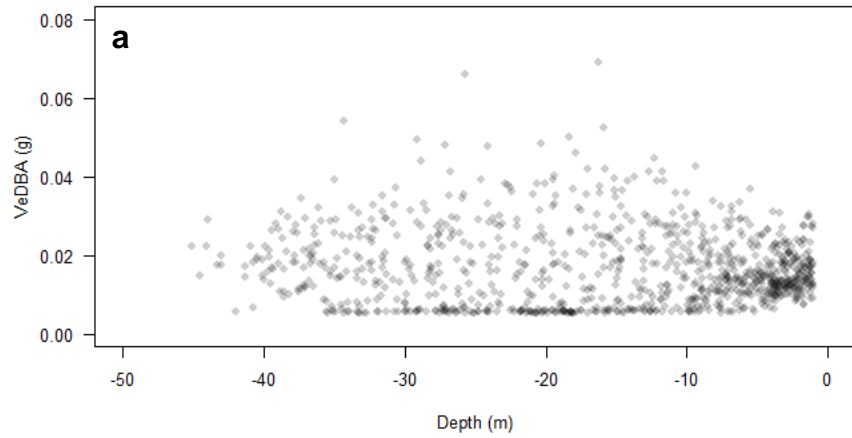
Figure 8. VeDBA at depth. (a-d) Individual VeDBA against depth plots, turtles 1 – 4 respectively, for the sampling period. Points are transparent, with darker areas representing a high density of data points. Axis limits have been optimised for display, some points lay outside of plot extent.
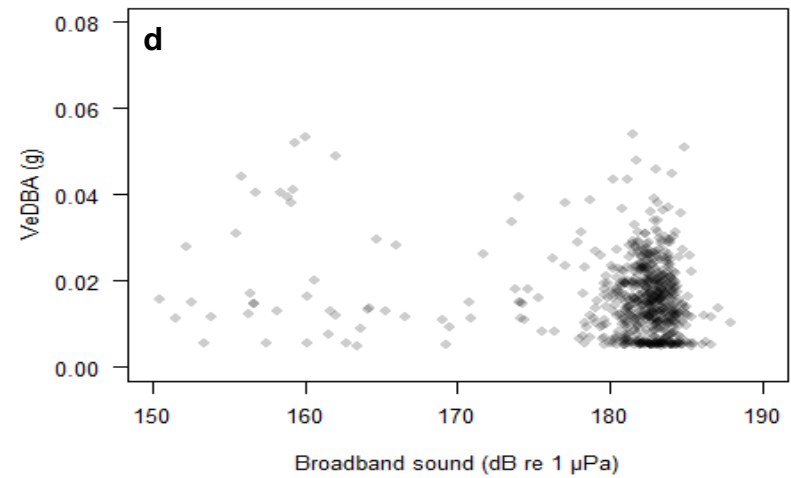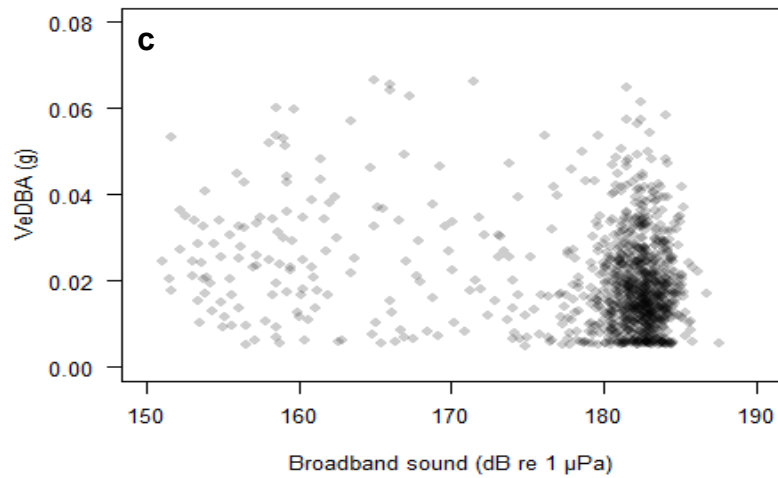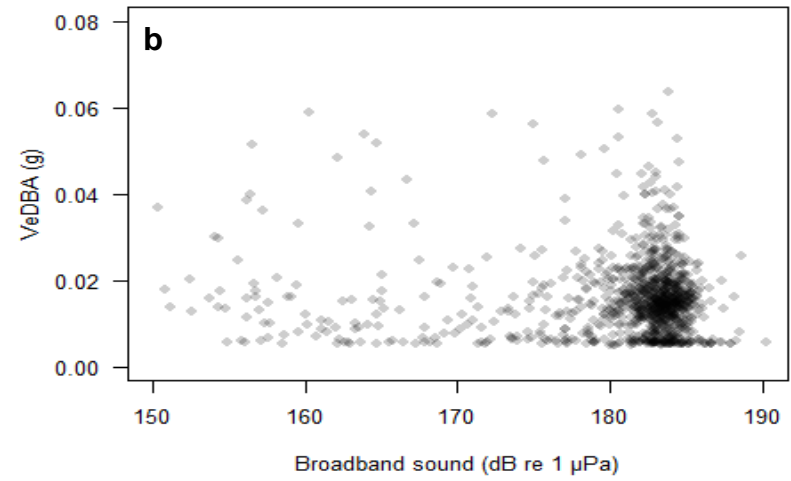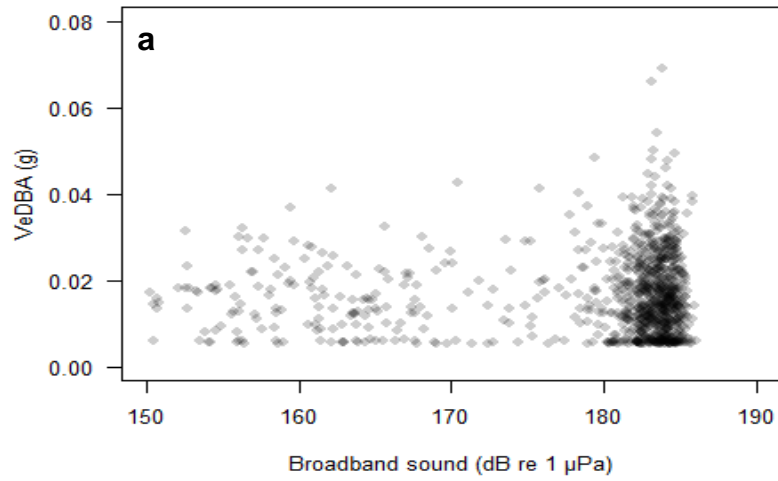
Figure 9. VeDBA in relation to broadband sound energy. (a-d) Individual plots for turtles 1 – 4 respectively. Points are transparent, with darker areas representing a high density of data points. Axis limits have been optimised for display, some points lay outside of plot extent.

Table 1. VeDBA GLMM output. Results of GLMM analysis to determine the effect of depth, broadband sound energy and the interaction between them on turtle VeDBA. All fixed effects were significant.

Fixed term	Estimated effect ± SE	Df	F-statistic	P
Constant	-6243.0 ± 33.1			
Broadband sound energy	47.0 ± 0.6	1	56.9	<0.05
Depth	-564.17 ± 26.8	1	101.8	<0.05
Interaction	2.72 ± 17.9	1	7.6	<0.05

Table 2. Individual turtle VeDBA model outputs. All third-octave bands (TOBs) used in GLMs included in table, significant frequencies shown by '***' for each turtle.

TOB centre frequency (Hz)	Turtle			
	1	2	3	4
50				
63		***		***
79		***		
100				
125				***
158	***	***	***	
199			***	
251	***	***	***	
316			***	
398	***			
501	***			
630			***	
794			***	
1000		***		
1258				***
Significant TOBS	4	5	6	3

REFERENCES

Alfaro-Shigueto, J., Dutton, P.H., Van Bressem, M-F. & Mangel, J. (2007). Interactions Between Leatherback Turtles and Peruvian Artisanal Fisheries. *Chelonian Conservation and Biology*, 6, 129-134.

André, M., Solé, M., Lenoir, M., Durfort, M., Quero, C., Mas, A., Lombarte, A, van der Schaar, M., López-Bejar, M., Morell, M., Zaugg, S. & Houégnigan, L. (2011). Low-frequency sounds induce acoustic trauma in cephalopods. *Frontiers in Ecology and the Environment*, 9, 489-493.

Au, W.W.L. & Banks, K. (1998). The acoustics of the snapping shrimip *Synalpheus parneomeris* in Kaneohe Bay. *The Journal of the Acoustical Society of America*, 103, 41-47.

Bailey, H., Senior, B., Simmons, D., Rusin, J., Picken, G. & Thompson, P.M. (2010). Assessing underwater noise levels during pile-driving at an offshore windfarm and its potential effects on marine mammals. *Marine Pollution Bulletin*, 60, 888-897.

Barbour, A.B. & Adams, A.J. (2012). Biologging to examine multiple life stages of an estuarine-dependent fish. *Marine Ecology Progress Series*, 457, 241-250.

Bartol, S.M., Musick, J.A. & Lenhardt, M.L. (1999). Auditory Evoked Potentials of the Loggerhead Sea Turtle (*Caretta caretta*). *Copeia*, 3, 836-840.

Bas, A.A., Christianen, F., Öztürk, A.A., Öztürk, B. & McIntosh, C. (2017). The effects of marine traffic on the behaviour of Black Sea harbour porpoises (*Phocoena phocoena relicta*) within the Istanbul Strait, Turkey. *PLoS ONE*, 12, e0172970.

Bidder, O.R., Qasem, L.A. & Wilson, R.P. (2012). On Higher Ground: How well Can Dynamic Body Acceleration Determine Speed in Variable Terrain? *PLoS One,* 7, 1-7.

Block, B.A., Teo, S.L.H., Walli, A., Boustany, A., Stokesbury, M.J.W., Farwell, C.J., Weng, K.C., Dewar, H. & Williams, T.D. (2005). Electronic tagging and population structure of Atlantic Bluefin tuna. *Nature*, 434, 1121-1126.

Block, B.A., Jonsen, I.D., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.-L., Ganong, J.E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W. & Costa, D.P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, 0, 1-5.

Blumenthal, J.M., Solomon, J.L., Bell, C.D., Austin, T.J., Ebanks-Petrie, G., Coyne, M.S., Broderick, A.C. & Godley, B.J. (2006). Satellite tracking highlights the need for international cooperation in marine turtle management. *Endangered Species Research*, 2, 51-61.

Boehlert, G.W., Costa, D.P., Crocker, D.E., Green, P., O'Briend, T., Levitus, S. & Le Boeuf, J. (2001). Autonomous Pinniped Environmental Samplers: Using Instrumented Animals as Oceanographic Data Collectors. *Journal of Atmospheric and Oceanic Technology*, 18, 1882-1893.

Bouyoucos, I.A., Montgomer, D.W., Brownscombe, J.W., Cooke, S.J., Suski, C.D., Mandelman, J.W. & Brooks, E.J. (2017). Swimming speeds and metabolic rates of semi-captive juvenile lemon sharks (*Negaprion brevirostris,* Poey) estimated with acceleration biologging devices. *Journal of Experimental Marine Biology and Ecology*, 486, 245-254.

Bowen, B.W. & Karl, S.A. (2007). Population genetics and phylogeography of sea turtles. *Molecular Ecology*, 16, 4886-4907.

Brownscombe, J.W., Gutowsky, L.F.G., Danylchuk, A.J. & Cooke, S.J. (2014). Foraging behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologging devices. *Marine Ecology Progress Series*, 505, 241-251.

Brownscombe, J.W., Cooke, S.J. & Danylcuk, A.J. (2017). Spatiotemporal drivers of energy expenditure in a coastal marine fish. *Behavioral Ecology*, 183, 689-699.

Brumm, H. & Slabbekoorn, H. (2005). Acoustic Communication in Noise. *Advances in the Study of Behaviour*, 35, 151-209.

Castellote, M., Clark, C.W. & Lammers, M.O. (2012). Acoustic and behavioural changes by fin whales (*Balaenoptera physalus)* in response to shipping and airgun noise. *Biological Conservation*, 147, 115-122.

Chambault, P., Pinaud, D., Vantrepotte, V., Kelle, L., Entraygues, M., Guinet, C., Berzins, R., Bilo, K., Gaspar, P., de Thoisy, Benoît, Maho, Y.L. & Chevallier, D. (2015). Dispersal and Diving Adjustments of the Green Turtle *Chelonia mydas* in Response to Dynamic Environmental Conditions during Post-Nesting Migration. *PLOS One*, 10, 1-19.

Charrassin, J-B., Park, Y-H., Le Maho, Y. & Bost, C-A. (2002). Penguins as oceanographers unravel hidden mechanisms of marine productivity. *Ecology Letters*, 5, 317-319.

Christiansen, F., Esteban, N., Mortimer, J.A., Dujon, A.M. & Hays, G.C. (2017). Diel and seasonal patterns in activity and home range size of green turtles on their foraging grounds revealed by extended Fastloc-GPS tracking. *Marine Biology*, 164, 1-11.

Clark, C.W., Ellison, W.T., Southall, B.L. Hatch, L., Van Parijs, S.M., Frankel, A. & Ponirakis, D. (2009). Acoustic masking in marine ecosystems: intuitions, analysis, and implication. *Marine Ecology Progress Series,* 395, 201-222.

Cooke, S.J. (2008). Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. *Endangered Species Research*, 4, 165-185.

Coquereau, L., Lossent, J., Grall, J. & Chauvaud, L. (2017). Marine soundscape shaped by fishing activity. *Royal Society open science*, 4, 160606.

Costa, D.P., Breed, G.A. & Robinson, P.W. (2012). New Insights into Pelagic Migrations: Implications for Ecology and Conservation. *Annual Review of Ecology, Evolution, and Systematics*, 43, 73-96.

Cowen, R.K. & Sponaugle, S. (2009). Larval Dispersal and Marine Population Connectivity. *Annual Review of Marine Science*, 1, 443-466.

Crossin, G.T., Cooke, S.J., Goldbogen, J.A. & Phillips, R.A. (2014). Tracking fitness in marine vertebrates: current knowledge and opportunities for future research. *Marine Ecology Progress Series*, 496, 1-17.

Dahlheim, M. & Castellote, M. (2016). Changes in the acoustic behaviour of gray whales *Eschrichtius robustus* in response to noise. *Endangered Species Research*, 31, 227-242.

De Soto, N.A., Delorme, N., Atkins, J., Howard, S., Williams, J. & Johson, M. (2013). Anthropogenic noise causes body malformations and delays development in marine larvae. *Scientific reports*, 3, 2831.

Doherty, P.D., Baxter, J.M., Gell, F.R., Godley, B.J., Graham, R.T., Hall, G., Hall, J., Hawkes, L.A., Henderson, S.M., Johnson, L., Speedie, C. & Witt, M.J. (2017). Long-term satellite tracking reveals variable seasonal migration strategies of basking sharks in the north-east Atlantic. (2017a). *Scientific Reports*, 7, 1-10.

Doherty, P.D., Baxter, J.M., Godley, B.J., Graham, R.T., Hall, G., Hall, J., Hawkes, L.A., Henderson, S.M., Johnson, L., Speedie, C. & Witt, M.J. (2017b). Testing the boundaries: Seasonal residency and inter-annual site fidelity of basking sharks in a proposed Marine Protected Area. *Biological Conservation*, 209, 68-75.

Dunlop, R.A., Cato, D.H. & Noad, M.J. (2010). Your attention please: increasing ambient noise levels elicits a change in communication behaviour in humpback whales (*Megaptera novaeangliae). Proceedings of the Royal Society B*, 277, 2521-2529.

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 Sand Point, St. Croix, U.S. Virgin Islands. *Herpetologica*, 42, 381-388.

Ellison, W.T., Racca, R., Clark, C.W., Streever, B., Frankel, A.S., Fleishman, E., Angliss, R., Berger, J., Ketten, D., Guerra, M., Leu, M., McKenna, M., Sformo, T., Southall, B., Suydam, R. & Thomas, L. (2016). Modeling the aggregated exposure and responses of bowhead whales *Balena mysticetus* to multiple

sources of anthropogenic underwater sound. *Endangered Species Research*, 30, 95-108.

Enstipp, M.R., Ciccione, S., Gineste, B., Milbergue, M., Ballorain, K., Ropert-Coudert, Y., Kato, A., Plot, V. & Georges, J-Y. (2011). Energy expenditure of freely swimming adult green turtle (*Chelonia mydas*) and its link with body acceleration. *The Journal of Experimental Biology*, 214, 4010-4020.

Erbe, C. (2013). Underwater passive acoustic monitoring & noise impacts on marine fauna – a workshop report. *Acoustics Australia: Technical Note*, 41, 211-217.

Erbe, C., Verma, A., McCauley, R., Gavrilov, A. & Parnum, I. (2015). The marine soundscape of the Perth Canyon. *Progress in Oceanography*, 17, 38-51.

Erbe, C., McCauley, R. & Gavrilov, A. (2016). Characterizing Marine Soundscapes. *Effects of Noise on Aquatic Life II*, 875, 265-271.

ESRI. (2013). ArcGIS Desktop: Release 10.1. *Environmental Systems Research Institute*, Redlands, CA.

Estabrook, B.J., Ponirakis, D.W., Clark, C.W. & Rice, A.N. (2016). Widespread spatial and temporal extent of anthropogenic noise across the northeastern Gulf of Mexico shelf ecosystem. *Endangered Species Research*, 30, 267-282.

Esteban, N., van Dam, R.P., Harrison, E., Herrera, A. & Berkel, J. (2015). Green and hawksbill turtles in the Lesser Antilles demonstrate behavioural plasticity in inter-nesting behaviour and post-nesting migration. *Marine Biology*, 162, 1153-1163.

Fedak, M., Lovell, P., McConnell, B. & Hunter, C. (2002). Overcoming the Constraints of Long Range Radio Telemetry from Animals: Getting More Useful Data from Smaller Packages. *Integrative and Computational Biology,* 42, 3-10.

Fedak, M. (2004). Marine animals as platforms for oceanographic sampling: a "win/win" situation for biology and operational oceanography. *Memoirs of National Institute of Polar Research Special Issue*, 58, 133-147.

Ferrara, C.R., Vogt, R.C. & Sousa-Lima, R.S. (2013). Turtle vocalizations as the first evidence of posthatching parental care in Chelonians. *Journal of Comparative Psychology*, 127, 24-32.

Ferrara, C.R., Mortimer, J.A. & Vogt, R.C. (2014a). First evidence that hatchlings of *Chelonia mydas* emit sounds. *Copeia*, 2, 245-247.

Ferrara, C.R., Vogt, R.C., Harfush, M.R., Sousa-Lima, R.S., Albavera, E. & Tavera, A. First evidence of leatherback turtle (*Dermochelys coriacea*) embryos and hatchlings emitting sounds. (2014b). *Chelonian Conservation and Biology*, 13, 110-114.

Fewtrell, J.L. & McCauley, R.D. (2012). Impact of air gun noise on the behaviour of marine fish and squid. *Marine Pollution Bulletin*, 64, 984-993.

Fischer, D.T., White, J.W., Botsford, L.W., Largier, J. & Kaplan, D.M. (2011). A GIS-Based Tool for Representing Larval Dispersal for Marine Reserve Selection. *The Professional Geographer*, 63, 489-513.

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. *The Journal of Experimental Biology*, 213, 4074-4083.

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. *Functional Ecology*, 26, 324-333.

Francis, C.D. & Barber, J.R. (2013). A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Frontiers in Ecology and the Environment,* 11, 305-313.

Frankel, A.S. Ellison, W.T., Vigness-Raposa, K.J., Giard, J.L. & Southall, B.L. (2016). Stochastic Modeling of Behavioral Response to Anthropogenic Sounds. *Effects of Noise on Aquatic Life II,* 875, 321-329.

Garrett, J.K., Blondel, Ph. Godley, B.J., Pikesley, S.K., Witt, M.J. & Johanning, L. (2016). Long-term underwater sound measurements in the shipping noise

indicator bands 63 Hz and 125 Hz from the port of Falmouth Bay UK. *Marine Pollution Bulletin*, 110, 438-448.

Gedamke, J., Costa, D.P. & Dunstan, A. (2001). Localization and visual verification of a complex minke whale vocalization. *The Journal of the Acoustical Society of America*, 109, 3038-3047.

Georges, J-Y. & Fossette, S. (2006). Estimating body mass in leatherback turtles *Dermochelys coriacea*. *Marine Ecology Progress Series*, 318, 255-262.

Georges, J-Y., Fossette, S., Billes, A., Ferraroli, S., Fretey, J., Grémillet, Le Maho, Y., Myers, A.E., Tanaka, H. & Hays, G.C. (2007). Meta-analysis of movements in Atlantic leatherback turtles during the nesting season: conservation implications. *Marine Ecology Progress Series*, 338, 225-232.

Gerlotto, F., Castillo, J., Saaverdra, A., Barbieri, M.A., Espejo, M. & Cotel, P. (2004). Three-dimensional structure and avoidance behaviour of anchovy and common sardine schools in central southern Chile. *ICES Journal of Marine Science*, 61, 1120-1126.

Gleiss, A.C., Wilson R.P. & Shepard, L.C. (2011). Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution*, 2, 23-33.

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. *Journal of Experimental Marine Biology and Ecology*, 287, 119-134.

Godley, B.J., Barbosa, C., Bruford, M., Broderick, A.C., Catry, P., Coyne, M.S., Formia, A., Hays, G.C. & Witt, M.J. (2010). Unravelling migratory connectivity in marine turtles using multiple methods. *Journal of Applied Ecology*, 47, 769-778.

Goldbogen, J. & Meir, J. (2014). The device that revoluntionized marine organismal biology. *The Journal of Experimental* Biology, 217, 167-8.

Graf, P.M., Wilson, R.P., Qasem, L., Hackländer, K. & Rosell, F. (2015). The Use of Acceleration to Code for Animal Behaviours: A Case Study in Free-Ranging Eurasian Beavers *Castor fiber*. *PLoS One,* 10, 1-17.

Graham, R.T., Witt, M.J., Castellanos, D.W., Remolina, F., Maxwell, S., Godley, B.J. & Hawkes, L.A. (2012). Satellite Tracking of Manta Rays Highlights Challenges to Their Conservation. *PLoS ONE*, 7, e36834.

Griffin, D.B., Murphy, S.R., Frick, M.G., Broderick, A.C., Coker, J.W., Coyne, M.S., Dodd, M.G. Godfrey, M.H., Godley, B.J., Hawkes, L.A., Murphy, T.M., Williams, K.L. & Witt, M.J. (2013). Foraging habitats and migration corridors utilized by a recovering subpopulation of adult female loggerhead sea turtles: implications for conservation. *Marine Biology*, 160, 3071-3086.

Halsey, L.G., Jones, T.T., Jones, D.R., Liebsch, N. & Booth, D.T. (2011). Measuring Energy Expenditure in Sub-Adult and Hatchling Sea Turtles via Accelerometry. *PLoS ONE,* 6, 1-9.

Hamann, M., Godfrey, M.H., Seminoff, J.A., Arthur, K, Barata, P.C.R., Bjorndal, 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., 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., Tomás, 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. *Endangered Species Research,* 11, 245-269.

Hart, K.M. & Hyrenbach, K.D. (2009). Satellite telemetry of marine megavertebrates: the coming of an experimental science. *Endangered Species Research*, 10, 9-20.

Hart, K.M., Lamont, M.M., Fujisaki, I., Tucker, A.D. & Carthy, R.R. (2012). Common coastal foraging areas for loggerheads in the Gulf of Mexico: Opportunities for marine conservation. *Biological Conservation*, 145, 185-194.

Hatch, L.T., Wahle, C.M., Gedamke, J., Harrison, J., Laws, B., Moore, S.E., Stadler, J.H.& Van Parijs, S.M. (2016). Can you hear me here? Managing acoustic habitat in US waters. *Endangered Species Research*, 30, 171-186.

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 turtle. *Diversity and Distributions*, 13, 447-457.

Hawkes, L.A., Tomás, J., Revuelta, O., León, Y.M., Blumenthal, J.M., Broderick, A.C., Fish, M., Raga, J.A., Witt, M.J. & Godley, B.J. (2012). Migratory patterns in hawksbill turtles described by satellite tracking. *Marine Ecology Progress Series*, 461, 223-232.

Hays, G.C., Houghton, J.D.R. & Myers, A.E. (2004). Pan-Atlantic leatherback turtle movements. *Nature*, 429, 522.

Hays, G.C. (2008). Sea turtles: A review of some key recent discoveries and remaining questions. *Journal of Experimental Marine Biology and Ecology*, 356, 1-7.

Hays, G.C. & Scott, R. (2013). Global patterns for upper ceilings on migration distance in sea turtles and comparison with fish, birds and mammals. *Functional Ecology*, 27, 748-756.

Hazen, E.L., Maxwell, S.M., Bailey, H., Bograd, S.J., Hamann, M., Gaspar, P., Godley, B.J. & Shillinger, G.L. (2012).Ontogeny in marine tagging and tracking science: technologies and data gaps. *Marine Ecology Progress Series,* 457, 221-240.

Hebblewhite, M. & Haydon, D.T. (2010). Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B*, 365, 2303-2313.

Holles, S., Simpson, S.D., Radford, A.N., Berten, L. & Lecchini, D. (2013). Boat noise disrupts orientation behaviour in a coral reef fish. *Marine Ecology Progress Series*, 485, 295-300.

Hooker, S.K. & Boyd, I.L. (2003). Salinity sensors on seals: use of marine predators to carry CTD data loggers. *Deep-Sea Research I*, 50, 927-939.

Houghton, J.D.R., Doyle. T.K., Davenport, J., Wilson, R.P. & Hays, G.C. (2008). The role of infrequent and extraordinary deep dives in leatherback turtles (*Dermochelys coriacea*). *The Journal of Experimental Biology*, 21, 2566-2575.

Hovem, J.M. & Korakas, A. (2014). Modeling Low-Frequency Anthropogenic Noise in the Oceans: A Comparison of Propagation Models. *Marine Technology Society Journal*, 48, 72-80.

Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Koelk, J.F., Flemming, J.E.M. & Whoriskey, F.G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Ecology*, 348, 1221-1231.

Iorio, L.D., Gervaise, C., Jaud, V., Robson, A.A. & Chauvaud, L. (2012). Hydrophone detects cracking sounds: Non-intrusive monitoring of bivalve movement. *Journal of Experimental Marine Biology and Ecology*, 432, 9-16.

Kastak, D., Schusterman, R.J., Southall, B.L. & Reichmuth, C.J. (1999). Underwater temporary threshold shift induced by octave-band noise in three species of pinniped. *Journal of the Acoustical Society of America*, 106, 1142-1148.

Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, 348, 1222-1231.

Kight, C.R. & Swaddle, J.P. (2011). How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecology Letters*, 14, 1052-1061.

Kooyman, G.L. (1966). Maximum Diving Capacities of the Weddell Seal, Leptonychotes weddelli. *Science*, 151, 1553-1554.

Kooyman, G.L., Drabek, C.M., Elsner, R. & Campbell, W.B. (1971). Diving Behaviour of the Emperor Penguin, *Aptenodytes forsteri. The Auk*, 88, 775-795.

Kooyman, G.L. (1976). Northern Fur Seal Diving Behaviour: A New Approach to Its Study. *Science*, 193, 411-412.

Kooyman, G.L. (2004). Genesis and evolution of bio-logging devices: 1963 – 2002. *Memoirs National Polar Research* Institute, 58, 15-22.

Koschinski, S., Culik, B.M., Henriksen, O.D., Tregenza, N., Ellis, G., Jansen, C. & Kathe, G. (2003). Behavioural reactions of free-ranging porpoise and seals to the noise of simulated 2 MW windpower generator. *Marine Ecology Progress Series*, 265, 263-273.

Kotsiantis, S.B., Zaharakis, I. & Pintelas, P. (2007). Supervised machine learning: A review of classification techniques. 3-24.

Kuehne, L.M., Padgham, B.L. & Olden, J.D. (2013). The Soundscapes of Lakes across an Urbanization Gradient. *PLoS ONE*, 8, 4-10.

Laidre, K.L., Heide-Jørgensen, Logsdon, M.L., Delwiche, L. & Nielsen, T.G. (2010). A whale of an opportunity: Examining the vertical structure of chlorophyll-*a* in high Arctic waters using instrumented marine predators. *Marine Biology Research*, 6, 519-529.

Lammers, M.O., Brainard, R.E., Au, W.W.L, Mooney, A. & Wong, K.B. (2008). An ecological acoustic recorder (EAR) for long-term monitoring of biological and anthropogenic sounds on coral reefs and other marine habitats. *The Journal of the Acoustical Society of America*, 123, 1720-1728.

Lascelles, B., Di Sciara, G.N., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., Hoyt, E., Llewellyn, F., Louzao, M., Ridoux, V. & Tetley, M.J. (2014). Migratory marine species: their status, threats and conservation management needs. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 24, 111-127.

Lavender, A.L., Bartol, S.M. & Bartol, I.K. (2014). Ontogenetic investigation of underwater hearing capabilities in loggerhead sea turtles (*Caretta caretta*) using a dual testing approach. *The Journal of Experimental Biology*, 217, 2580-2589.

Le Boeuf, B.J., Costa, D.P. & Huntley, A.C. (1986). Pattern and depth of dives in Northern elephant seals, *Mirounga angustirostris*. *Journal of Zoology*, 208, 1-7.

Lucke, K., Siebert, U., Lepper, P.A. & Blanchet, M-A. (2009). Temporary shift in masked hearing thresholds in a harbour porpoise (*Phocoena phocoena*) after exposure to seismic airgun stimuli. *Journal of the Acoustical Society of America*, 125, 4060-4070.

Lutz, P.L., Musick, J.A. & Wyneken, J. eds. (2002). Reproduction in Sea Turtles. *The Biology of Sea Turtles*, 2, 56. CRC press.

Lydersen, C., Nøst, O.A., Lovell, P., McConnell, B.J., Gammelsrød, T., Hunter C., Fedak, M.A. & Kovacs, K.M. (2002). Salinity and temperature structure of a

freezing Arctic fjord – monitored by white whales (*Delphinapterus leucas*). *Geophysical Research Letters*, 29, 34-38.

Lyons, G.N., Pope, E.C., Kostka, B., Wilson, R.P., Dobrajc, Z., & Houghton, J.D.R. (2013). Tri-axial accelerometers tease apart discrete behaviours in the common cuttlefish *Sepia officinalis. Journal of the Marine Biological Assocation of the United Kingdom*, 93, 1389-1392.

MacDonald, B.D., Madrak, S.V., Lewison, R.L., Seminoff, J.A. & Eguchi, T. (2013). Fine scale diel movement of the east Pacific green turtle, *Chelonia mydas,* in a highly urbanized foraging environment. *Journal of Experimental Marine Biology and Ecology*, 443, 56-64.

Madsen, P.T., Wahlberg, M., Tougaard, J., Lucke, K. & Tyack, P. (2006). Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs. *Marine Ecology Progress Series*, 309, 279-295.

Magnhagen, C., Johansson, K. & Sigray, P. (2017). Effects of motorboat noise on foraging behaviour in Eurasian perch and roach: a field experiment. *Marine Ecology Progress Series,* 564, 115-125.

Martin, K.J., Alessi, S.C., Gaspard, J.C., Tucker, A.D., Bauer, G.B. & Mann, D.A. (2012). Underwater hearing in the loggerhead turtle (*Caretta caretta*): a comparison of behavioural and auditory evoked potential audiograms. *The Journal of Experimental Biology*, 215, 3001-3009.

Martin, S.B. & Cott, P.A. (2015). The under-ice soundscape in Great Slave Lake near the city of Yellowknife, Northwest Territories, Canada. *Journal of Great Lakes Research*, 42, 248-255.

MATLAB and Statistics Toolbox. (2014b). *The MathWorks*, Inc., Natick, Massachusetts, United States.

Maxwell, S.M., Breed, G.A., Nickel, B.A., Makanga-Bahouna, J., Pemo-Makaya, E., Parnell, R.J., Formia, A., Ngouessono, S., Godley, B.J., Costa, D.P., Witt, M.J. & Coyne, M.S. (2011). Using Satellite Tracking to Optimize Protection of Long-Lived Marine Species: Olive Ridley Sea Turtle Conservation in Central Africa. *PLoS ONE*, 6, 1-10.

McIntyre, T. (2014). Trends in tagging of marine mammals: a review of marine mammal biologging studies. *African Journal of Marine Science*, 36, 409-422.

McMahon, C.R., Autret, E., Houghton, J.D.R., Lovell, P., Myers, A.E. & Hays, G.C. (2005). Animal-borne sensors successfully capture the real-time thermal properties of ocean basins. *Limnology an Oceanography: Methods*, 3, 392-398.

McWilliam, J.N. & Hawkins, A.D. (2013). A comparison of inshore marine soundscapes. *Journal of Experimental Marine Biology and Ecology,* 446, 166-176.

Merchant, N.D., Pirotta, E., Barton, T.R. & Thompson, P.M. (2014). Monitoring ship noise to assess the impact of coastal developments on marine mammals. *Marine Pollution Bulletin*, 78, 85-95.

Merchant, N.D., Fristrup, K.M., Johnson, M.P., Tyack, P.L., Witt, M.J., Blondel, P. & Parks, S.E. (2015). Measuring acoustic habitats. *Methods in Ecology and Evolution,* 6, 257-65.

Merchant, N.D., Brookes, K.L., Faulkner, R.C., Bicknell, A.WJ., Godley, B.J. & Witt, M.J. (2016). Underwater noise levels in waters. *Scientific Reports*, 6, 1-10.

Miksis-Olds, J.L. (2016). Global Trends in Ocean Noise. *Effects of Noise on Aquatic Life II*, 875, 713-718.

Morreale, S.J., Standora, E.A., Spotila, J.R. & Paladino, F.V. (1996). Migration corridor for sea turtles. *Nature,* 384, 319-320.

Moustahfid, H., Grimes, C., Kocik, J., Block, B., Hollad, K., Payne, J., Fox, D., Seitz, A. & Alexander, C. (2011). Toward a National Animal Telemetry Observing Network (ATN) for Our Oceans, Coasts, and Great Lakes: Workshop Synthesis Report. *US Department of Commerce, NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFSC-482*.

Mrosovsky, N. (1972). Spectrographs of the sound of leatherback turtles. *Herpetologica*, 28, 256-258.

Naito, Y., Sakamoto, W., Uchida, I., Kureha, K. & Ebisawaw, T. (1989). Estimation of migration route of the loggerhead turtle *Caretta caretta* around the

nesting ground. *Bulletin of the Japanese Society for the Science of Fish*, 56, 255-262.

Nakamura, I., Goto, Y. & Sato. K. (2015). Ocean sunfish rewarm at the surface after deep excursions to forage for siphonophores. *Journal of Animal Ecology*, 84, 590-603.

Nedelec, S.L., Campbell, J., Radford, A.N., Simpson, S.D. & Merchant, N.D. (2016). Particle motion: the missing link in underwater acoustic ecology. *Methods in Ecology and Evolution*, 7, 1-7.

Nelms, S.E., Piniak, W.E.D., Weir, C.R. & Godley, B.J. (2016). Seismic surveys and marine turtle: An underestimated global threat? *Biological Conservation*, 193, 49-65.

Noda, T., Okuyama, J., Koizumi, T., Arai, N. & Kobayashi, M. (2012). Monitoring attitude and dynamic acceleration of free-moving aquatic animals using a gyroscope. *Aquatic Biology*, 16, 265-176.

Nowacek, D.P., Thorne, L.H., Johnston, D.W. & Tyack, P.L. (2007). Responses of cetaceans to anthropogenic noise. *Mammal Review*, 37, 81-115.

O'Dor, R.K. & Stokesbury, M.J. (2009). The Ocean Tracking Network – Adding Marine Animal Movements to the Global Ocean Observing System. *Tagging and tracking of marine animals with electronic devices*, 91-100. Springer Netherlands.

Padman, L., Costa, D.P., Bolmer, T., Goebel, M.E., Huckstadt, L.A., Jenkins, A., McDonald, B.I. & Shoosmith, D.R. (2010). Seals map bathymetry of the Antarctic continental shelf. *Geophysical Research Letters,* 37, 1-5.

Parks, S.E., Johnson, M., Nowacek, D. & Tyack, P.L. (2011). Individual right whales call louder in increased environmental noise. *Biology* Letters, 7, 33-35.

Parks, S.E., Miksis-Olds, J.L. & Denes, S.L. (2014). Assessing marine ecosystem acoustic diversity across ocean basins. *Ecological Informatics*, 21, 81-88.

Parsons, E.C.M., Wright, A.J. & Gore, M.A. (2008). The nature of humpback whale (*Megaptera novaeangliae*) song. *Journal of Marine Animals and Their Ecology*, 1, 22-31.

Parsons, M.J.G., Salgado Kent, C.P., Recalde-Salas, A. & McCauley, R.D. (2016). Fish choruses off Port Hedland, Western Australia. *Bioacoustics*, 1-18.

Pichegru, L., Grémille, Crawford, R.J.M. & Ryan, P.G. (2010). Marine no-take zone rapidly benefits endangered penguin. *Biology Letters,* 6, 498-501.

Pijanowski, B.C., Farina, A., Gage, S.H., Dumyahn, S.L. & Krause, B.L. (2011). What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology*, 26, 1213-1232.

Pijanowski, B.C. (2016). Terrestrial Soundscapes: Status of Ecological Research in Natural and Human-Dominated Landscapes. *Effects of Noise on Aquatic Life II*, 875, 838-846.

Piniak, W.E.D., Eckert, S.A., Harms, C.A. & Stringer, E.M. (2012a). Underwater hearing sensitivity of the leatherback sea turtle (*Dermochelys coriacea*): Assessing the potential effect of anthropogenic noise. *Bureau of Ocean Energy Management*, 01156, 1-25.

Piniak, W.E.D., Mann, D.A., Eckert, S.A. & Harms, C.A. (2012b). Amphibious hearing in sea turtles. *Advances in Experimental Medicine and Biology*, 730, 83-87.

Pine, M.K., Radford, C.A. & Jeffs, A.G. (2015). Eavesdropping on the Kaipara Harbour: characterising underwater soundscapes within a seagrass bed and a subtidal mudflat. *New Zealand Journal of Marine and Freshwater Research*, 49, 247-258.

Pine, M.K., Wang, K. & Wang, D. (2017). Fine-scale habitat use in Indo-Pacific humpback dolphins, *Sousa chinensis*, may be more influenced by fish rather than vessels in the Pearl River Estuary, China. *Marine Mammal Science*, 33, 291-312.

Priede, I.G. & French, J. (1991). Tracking of marine animals by satellite. *International Journal of Remote Sensing*, 12, 667-680.

Plötz, J., Bornemann, H. & Knust, R. (2002). Foraging behaviour of Weddell seals, and its ecological implications. *Polar Biology*, 24, 901-909.

Poonian, C.N.S., Hauzer, M.D., Allaoui, A.B., Cox, T.M., Moore, J.E., Read, A.J., Lewison, R.L. & Crowder, L.B. (2008). Rapid Assessment of Sea Turtle and Marine Mammal Bycatch in the Union of the Comoros. *Western Indian Ocean Journal of Marine Science,* 7, 207-216.

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L.G., Shepard, E.L.C., Gleiss, A.C. & Wilson, R. (2012). Tri-Axial Dynamic Acceleration as a Proxy for Animal Energy Expenditure; Should We Be Summing Values or Calculating the Vector? *PLoS One*, 7, 1-8.

Radford, C.A., Stanley, J.A. & Jeffs, A.G. (2014). Adjacent coral reef habitats produce different underwater sound signatures. *Marine Ecology Progress Series*, 505, 19-28.

Rako, N., Vilibić, I. & Mihanović. (2013). Mapping underater sound noise and assessing its sources by using a self-organizing maps method. *The Journal of the Acoustical Society of America,* 133, 1368-76.

R Core Team. (2013). R: A Language and Environment for Statistical Computing, *R Foundation for Statistical Computing*, Vienna, Austria, https://www.R-project.org.

Rees, A.F., Al-Kiyumi, A., Broderick, A.C., Papathanasopoulou, N. & Godley, B.J. (2012). Conservation related insights into the behaviour of the olive ridley sea turtle *Lepidochelys olivacea* nesting in Oman. *Marine Ecology Progress Series*, 420, 195-205.

Reina, R.D., Abernathy, K.J., Marshall, G.J. & Spotila, J.R. (2005). Respiratory frequency, diver behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. *Journal of Experimental Marine Biology and Ecology*, 316, 1-16.

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. *Marine Biology*, 6, 1415-1426.

Rodriguez, A., Gasc, A., Pavoine, S., Grandcolas, P., Gaucher, P. & Sueur, J. (2014). Temporal and spatial variability of animal sound within a neotropical forest. *Ecological Informatics*, 21, 133-143.

Rolland, R.M., Parks, S.E., Hunt, K.E., Castellote, M., Corkeron, P.J., Nowacek, D.P., Wasser, S.K. & Kraus, S.D. (2012). Evidence that ship noise increases stress in right whales. *Proceedings of the Royal Society B*, 279, 2363-2368.

Romano, T.A., Keogh, M.J., Kelly, C., Feng, P., Berk, L., Schlundt, C.E., Carder, D.A. & Finneran, J.J. (2004). Anthropogenic sound and marine mammal health: measures of the nervous and immune systems before and after intense sound exposure. *Canadian Journal of Fisheries and Aquatic Sciences*, 61, 1124-1134.

Ropert-Coudert, Y., Beaulieu, M., Hanuise, N. & Kato, A. (2009). Diving into the world of biologging. *Endangered Species Research,* 1, 21-27.

Rosen, D.A.S., Hindle, A.G., Gerlinsky, C.D., Goundie, E., Hastie, G.D., Volpov, G.D. & Trites, A.W. (2017). Physiological constraints and energetic costs of diving behaviour in marine mammals: a review of studies using trained Steller sea lions diving in the open ocean. *Journal of Comparative Physiology B*, 187, 29-50.

Rosenbaum, H. & Collins, T. (2006). The ecology, population characteristics and conservation efforts for humpback whales (*Megaptera novaeangliae*) on their wintering grounds in the coastal waters of Gabon. *Bulletin of the Biological Society of Washington*, 12, 425-436.

Rutz, C. & Hays, G.C. (2009). New frontiers in biologging science. *Biology Letters*, 5, 289-292.

Rutz, C. & Troscianko, J. (2013). Programmable, miniature video-loggers for deployment on wild birds and other wildlife. *Methods in Ecology and Evolution*, 4, 114-122.

Samuel, Y., Morreale, S.J., Clark, C.W., Greene, C.H. & Richmond, M.E. (2005). Underwater, low-frequency noise in a coastal sea turtle habitat. *Journal of the Acoustical Society of America*, 117, 1465-1772.

Schindelin, J. Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B. & Tinevez, J.Y. (2012). Fiji: an open-source platform for biological-image analysis. *Nature methods*, 9, 676-682.

Scott, R., Biastoch, A., Roder, C., Stiebens, V.A. & Eizaguiree, C. (2014). Nano-tags for neonates and ocean-mediated swimming behaviours linked to rapid dispersal of hatchling sea turtles. *Proceedings of the Royal Society B*, 281, 1-9.

Scott, R., Biastoch, A., Agamboue, P.D., Bayer, T., Boussamba, F.L., Formia, A., Godley, B.J., Mabert, B.D., Manfoumbi, J.C., Schwarzkopf, F.U., Sounguet, G-P., Wagner, P. & Witt, M.J. (2017). Spatio-temporal variation in ocean current-driven hatchling dispersion: Implications for the world's largest leatherback sea turtle nesting region. *Diversity and Distributions*, 1-11.

Scholander, P.F. (1940). Experimental investigations on the respiratory function in diving mammals and birds. *Hvalrådets Skrifter*, 22, 1-131.

Shaver, D.J., Hart, K.M., Fujisaki, I., Rubio, C., Sartain, A.R., Peña, J., Burchfield, P.M., Gamez, D.G. & Ortiz, J. (2013). Foraging area fidelity for Kemp's ridleys in the Gulf of Mexico. *Ecology and Evolution*, 3, 2002-2012.

Shepard, E.L.C., Wilson, R.P., Halsey, L.G., Quintana, F., Laich, A.G., Gleiss, A.C., Liebsch, N., Myers, A.E. & Norman, B. (2008). Derivation of body motion via appropriate smoothing of acceleration data. *Aquatic Biology*, 4, 235-241.

Shepard, E.L.C., Wilson, R.P., Ress, W.G., Grundy, E., Lambertucci, S.A. & Vosper, S.B.. (2013). Energy Landscapes Shape Animal Movement Ecology. *The American Naturalist*, 182, 298-312.

Shillinger, G.L., Swithenbank, A.M., Bailey, H., Bograd, S.J., Cstelton, 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. *Marine Ecology Progress Series*, 422, 275-289.

Shillinger, G.L., Bailey, H., Bograd, S.J., Hazen, E.L., Hamann, M., Gaspar, P., Godley, B.J., Wilson, R.P. & Spotila, J.R. (2012). Tagging through the stages: technical and ecological challenges in observing life histories through biologging. *Marine Ecology Progress Series*, 457, 165-170.

Simmonds, M.P., Dolman, S.J., Jasny, M., Parsons, E.C.M., Weilgart, L. Wright, A.J & Leaper, R. (2014). Marine noise pollution – Increasing recognition but need for more practical action. *Journal of Ocean Technology,* 9, 71-90.

Simpfendorger, C.A., Wiley, T.R. & Yeiser, B.G. (2010). Improving conservation planning for an endangered sawfish using data from acoustic telemetry. *Biological Conservation*, 143, 1460-1469.

Slabbekoorn, H., Bourton, N., van Opzeeland, I., Coers, A., ten Cate, C. & Popper, A.N. (2010). A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends in Ecology and Evolution*, 7, 419-427.

Small, R.J., Brost, B., Hooten, M., Castellote, M. & Mondragon, J. (2017). Potential for spatial displacement of Cook Inlet beluga whales by anthropogenic noise in critical habitat. *Endangered Species Research*, 32, 43-57.

Sousa-Lima, R.S., Norris, T.F., Oswald, J.N. & Fernandes, D.P. (2013). A Review and Inventory of Fixed Autonomous Records for Passive Acoustic Monitoring of Marine Mammals. *Aquatic Mammals*, 39, 23-51.

Southall, B.L., Nowacek, D.P., Miller, P.J.O. & Tyack, P.L. (2016). Experimental field studies to measure behavioral responses of cetaceans to sonar. *Endangered Species Research,* 31, 293-315.

Staaterman, E.R., Clark, C.W., Gallagher, A.J., Claverie, T. & Patek, S.N. (2011). Rumbling in the benthos: acoustic ecology of the California mantis shrimp *Hemisquilla californiensis*. *Aquatic Biology*, 13, 97-105.

Stokes, K.L., Broderick, A.C., Canbolat, A.F., Candan, O., Fuller, W.J., Glen, F., Levy, Y., Rees, A.F., Rilov, G., Snape, R.T., Stott, I., Tchernov. D. & Godley, B.J. (2015). Migratory corridors and foraging hotspots: critical habitats identified for Mediterranean green turtles. *Diversity and Distributions*, 1-10.

Tennessen, J.B. & Parks, S.E. (2016). Acoustic propagation modelling indicates vocal compensation in noise improves communication range for North Atlantic right whales. *Endangered Species Research,* 30, 225-237.

Teo, S.L.H, Kudela, R.M., Rais, A., Perle, C., Costa, D.P. & Block, B.A. (2009). Estimating chlorophyll profiles from electronic tags deployed on pelagic animals. *Aquatic Biology*, 5, 195-207.

Thompson, P.M., Hastie, G.D., Nedwell, J., Barham, R., Brookes, K.L., Cordes, L.S., Bailey, H. & McLean, N. (2013). Framework for assessing impacts of pile-driving noise from offshore wind farm construction on a harbour seal population. *Environmental Impact Assessment Review*, 43, 73-85.

Towsey, M., Wimmer, J., Williamson, I. & Roe, P. (2013). The use of acoustic indices to determine avian species richness in audio-recordings of the environment. *Ecological Informatics*, 21, 110-119.

Tremblay, Y., Shaffer, S.A., Fowler, S.L., Kuhn, C.E., McDonald, B.I., Weise, M.J., Bost, C-A., Weimerskirch, H., Crocker, D.E., Goebel, M.E. & Costa, D.P. (2006). Interpolation of animal tracking data in a fluid environment*. The Journal of Experimental Biology*, 209, 128-140.

Truax, B. & Barrett, G.W. (2011). Soundscape in a context of acoustic and landscape ecology. *Landscape Ecology*, 26, 1201-1207.

Tomkiewicz, S.M, Fuller, M.R., Kie, J.G. & Bates, K.K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transaction of the Royal Society B,* 365, 2163-2176.

Tuomainen, U. & Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biological Reviews,* 86, 640-657.

Tyack, P.L. (2008). Implications for marine mammals of large-scale change in the marine acoustic environment. *Journal of Mammalogy*, 89, 549-558.

Van Dam, R.P., Ponganis, P.J., Ponganis, K.V., Levenson, D.H. & Marshall, G. (2002). Stroke frequencies of emperor penguins diving under sea ice. *The Journal of Experimental Biology*, 205, 3769-3774.

Van Parijs, S.M., Clark, C.W., Sousa-Lima, R.S., Parks, S.E., Rankin, S., Risch, D. & Van Opzeeland, I.C. (2009). Management and research application of real-

time and archival passive acoustic sensors over varying temporal and spatial scales. *Marine Ecology Progress Series*, 395, 21-36.

Vitousek, M.N., Adelman, J.S., Gregory, N.C. & St Clair, J.J.H. (2007). Heterospecific alarm call recognition in a non-vocal reptile. *Biology Letters*, 3, 632-634.

Votier, S.C., Bicknell, A.B., Cox, S.L., Scales, K.L. & Patrick, S.C. (2013). A Bird's Eye View of Discard Reforms: Bird-Borne Cameras Reveal Seabird/Fishery Interactions. *PLOS One*, 8, 1-6.

Wallace, B.P., Lewison, R.L., McDonald, S.L., McDonald, R.K., Kot, C.Y., Kelez, S., Bjorkland, R.K., Finkbeiner, E.M., Helmbrecht, S. & Crowder, L.B. (2010). Global patterns of marine turtle bycatch. *Conservation Letters*, 3, 131-142.

Wallace, B.P., Zolkewitz, M. & James, M.C. (2015). Fine-scale foraging ecology of leatherback turtles. *Frontiers in Ecology and Evolution*, 3.

Weilgart, L.S. (2007). The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Canadian Journal of Zoology*, 85, 1091-1116.

Whiteaker, T. (2013). Create Hexagon Tesellation. *ArcGIS Geoprocessing Package*, available at: https://goo.gl/HG5AoK.

Whittock, P.A., Pendoley, K.L. & Hamann, M. (2014). Inter-nesting distribution of flatback turtles *Natator depressus* and industrial development in Western Australia. *Endangered Species Research*, 26, 25-38.

Williams, R., Wright, A.J., Ashe, E., Blight, L.K., Bruintjes, R., Canessa, R., Clark, C.W., Cullis-Suzuki, S., Dakin, D.T., Erbe, C., Hammond, P.S., Merchant, N.D., O'Hara, P.D. & Purser, J. (2015). Impacts of anthropogenic noise on marine life: Publication patterns, new discoveries, and future directions in research and management. *Ocean & Coastal Management*, 115, 17-24.

Wilmers, C.C, Nickel, B., Bryce, C.M., Smith, J.A., Wheat, R.E. & Yovovich, V. (2015). The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology*, 96, 1741-1753.

Wilson, R.P. & Bain, A.R. (1984). An Inexpensive Depth Gauge for Penguins. *The Journal of Wildlife Management*, 48, 1077-1084.

Wilson, R.P. & Wilson, M.P. (1988). Dead reckoning – a new technique for determining penguin movements at sea. *Meeresforsching – Reports on Marine Research*, 32, 155-158.

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. *Endangered Species Research*, 4, 123-137.

Wilson, R.P., Quintana, F. & Hobson, V.J. (2012). Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proceedings of the Royal Society B*, 279, 975-980.

Wilson, A.D.M, Wikelski, M., Wilson, R.P & Cooke, S.J. (2015). Utility of biological sensor tags in animal conservation. *Conservation Biology*, 29, 1065-1075.

Wilson, K., Littnan, C., Halpin, P. & Read, A. (2017). Integrating multiple technologies to understand the foraging behaviour of Hawaiian monk seals. *Royal Society open science*, 4, 1-14.

Witt, M.J., Broderick, A.C., Coyne, M.S., Formia, A., Ngouessono, S., Parnell, R.J., Sounguet, G-P & Godley, B.J. (2008). Satellite tracking highlights difficulties in the design of effective protected area for Critically Endangered leather turtles *Dermochelys coriacea* during the inter-nesting period. *Oryx*, 42, 296-300.

Witt, M.J., Baert, B., Broderick, A.C., Formia, A., Fretey, J., Gibudi, A., Mounguengui, G.A.M., Moussanda, C., Ngouessono, S., Parnell, R.J., Roumet, D., Sounguet, G-Y., Verhage, B., Zogo, A. & Godley, B.J. (2009). Aerial surveying of the world's largest leatherback turtle rookery: A more effective methodology for large-scale monitoring. *Biological Conservation,* 142, 1719-1727.

Witt, M.J., Bonguno, E.A., Broderick, A.C., Coyne, M.S., Formia, A., Gibudi, A., Mounguengui, G.A.M., Moussounda, C., Nsafou, M., Nougessono, S., Parnell, R.J., Sounguet, G-P., Verhage, S. & Godley, B.J. (2011). Tracking leatherback

turtles from the world's largest rookery: assessing threats across the South Atlantic. *Proceedings of the Royal Society B*, 278, 2338-2347.

Woakes, A.J., Butler, P.J. & Bevan, R.M. (1995). Implantable data logging system for heart rate and body temperature: its application to the estimation of field metabolic rates in Antarctic predators. *Medical & Biological Engineering & Computing*, 145-151.

Work, P.A., Sapp, A.L., Scott, D.W. & Dodd, M.G. (2010). Influence of small vessel operation and propulsion system on loggerhead sea turtle injuries. *Journal of Experimental Marine Biology and Ecology*, 393, 18-175.

Wright, B.M., Ford, J.K.B., Ellis, G.M., Deecke, V.B., Shaprio, A.D., Battaile, B.C. & Trites, A.W. (2017). Fine-scale foraging movements by fish-eating killer whales (*Orcinus orca*) relate to vertical distributions and escape responses of salmonid prey (Oncorhynchus spp.). *Movement Ecology*, 5, 1-18.

Yasuda, T. & Arai, N. (2005). Fine-scale Tracking of Marine Turtles Using GPS-Argos PTTs. *Zoological Science*, 22, 547-553.