The role of Accelerometry in the Conservation of two Coastal Marine Vertebrates

Submitted by Jessica Louise Rudd to the University of Exeter as a thesis for the degree of Masters of Science by Research in Biosciences in January 2021

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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.

Signature: JRudd

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Abstract

This thesis advances the understanding of the spatial and behavioural ecology of two endangered species, basking sharks (*Cetorhinus maximus*) and green turtles (*Chelonia mydas*) at their coastal foraging sites while highlighting the pragmatic application of biologging technology in informing conservation. **Chapter 1** of this thesis is a general introduction to tracking technologies, covering how the advancements of biologging have revolutionised the field of ecology, with an emphasis on how accelerometers can be used in conservation. **Chapters 2** explores the use of accelerometers on three basking sharks in the western Scottish Isles to understand their fine-scale behaviour. I present early evidence of potential behavioural lateralisation, and the first direct records of 67 breaches over 41 days, with sharks breaching on average twice a day, both during night and day and increasing energy expenditure by at least 30 times to breach. While the function of breaching remains unclear, owing to its energetic cost, breaching is likely to have an important fitness function. In **Chapter 3**, accelerometers were deployed on 16 juvenile green turtles in The Bahamas to investigate the behavioural and energetic costs of translocation. Turtles rehomed in as little as 15 hours following translocation of 4 km and allocated twice as much time to energetically demanding behaviours compared to resident turtles at their foraging grounds, highlighting that translocation is not a suitable conservation practice for sea turtles. **Chapter 4** summarises both data chapters and discusses how their findings provide further evidence of how tracking technologies can be ideal tools for conservation practitioners by monitoring animal movement, behaviour and health as well as assisting with the designation of protected areas by identifying important life history events. Chapter 4 concludes on the challenges and limitations of the thesis as well as the future directions in the use of tracking technologies in conservation ecology.

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Abbreviations

DD: Daily Diary tags
DEE: Daily Energy Expenditure
DSF: Dominant Stroke Frequency (Hz)
FBA: Flipper Beat Amplitude (Hz)
GPS: Global Positioning System
RM: Routine Metabolism (MJ.day^{-1})
TBA: Tail Beat Amplitude (Hz)
VeDBA: Vectorial Dynamic Body Acceleration (g)

Author’s Declaration

Field work for Chapter 2 carried out by Drs Matthew Witt and Lucy Hawkes and Dr Suzanne Henderson. I carried out tag calibrations, data analysis, thesis writing and formatting.

The data collected in Chapter 3 was carried out at the Cape Eleuthera Institute, The Bahamas. Experimental design for the turtle tracking study was designed by Annabelle Brooks, Dr Lucy Hawkes and myself. Fieldwork was supervised by Annabelle Brooks and Meagan Gary who supported me in the tag design and preparation, subject collection, tag deployment, search and recovery. Habitat mapping and environmental data collection was based upon previous methodology designed by Meagan Gary, and coordinated, supervised and conducted by myself and Isobel Lake. I also co-lead and coordinated an Island School Research Class, during which students assisted with the data collection for Chapter 3 as well as Eartwatch Institute volunteers. Following the data collection, I carried out tag calibration, data analyses, thesis writing and formatting.
Guidance and comments from Dr Matthew Witt and Dr Lucy Hawkes throughout the project, as well as Annabelle Brooks for Chapter 3.

All materials that are not my original work have been referenced in this thesis, including imagery for which links have been provided for access.

Chapter 1: Introduction

The emergence of ‘biologging’, the use of animal-borne tags for logging and/or relaying data on an animal’s movement, behaviour, physiology or environment (Rutz & Hays 2009), has revolutionised the field of ecology over the past 50 years (Hussey et al. 2015, (Kays et al. 2015, Wilmers et al. 2015). This has been made possible through advances in tag technology, including device miniaturisation, reduction of cost per unit, increase in battery life and memory capacity, providing unprecedented insight into animals’ internal and/or external environments from a sub-second scale to distances of several thousands of kilometres (den Ujil et al. 2017 Alerstam et al. 2019). Biologging tags comprise technologies ranging from radio-transmitted telemetry (LeMunyan et al. 1959, Millspaugh & Marzluff 2001) to archival multi-sensor Daily Dairy tags recording temperature, depth, speed, light levels, wet-dry sensor, tri-axial accelerometry and magnetometry (Wilson et al. 2008). These tools have provided novel understanding into previously unknown distribution and home range (Alonso et al. 2018), physiology (Gallagher et al. 2014 Sherub et al 2017), ecology (Williams et al. 2017, Nourani et al. 2019), behaviour (Whitney et al. 2010, Rattenborg et al. 2016), response to climate change (Abrahms et al. 2018, Chmura et al. 2018), predator-prey and social interactions of species (Jacoby et al. 2016, Cusack et al. 2020) by tracking free-ranging animals in their natural environment. Tags record unbiased, continuous high-resolution data, which would otherwise likely be missed by visual survey alone (Cooke 2008, Hebblewhite & Haydon 2010).

The use of biologging tags has been useful for animals that were previously challenging to observe, and for which basic biology was largely lacking until recently such as for cryptic and/or aquatic species, and younger age classes (Mansfield et al. 2012, Wilmers et al. 2015, Edwards et al. 2019), as well as used to assess threats to population and their conservation status (i.e. IUCN Red List) (Cooke 2008). The use of telemetry in combination with sensors, video footage or remote sensing has helped to provide social (Sutton et al. 2015, Barkley et al.

2020), behavioural (Williams et al. 2014, Tackaberry et al. 2020), physiological (Williams et al. 2016, Græsli et al. 2020) and environmental (Benoit et al. 2020, Jewell et al. 2020) context to movement patterns. Changes in chlorophyll-*a* concentrations has be found to drive some species distribution, including the timing of migration in basking sharks (Sims et al. 2003a), fin whales (*Balaenoptera physalus*) (Littaye et al. 2004), and leatherback turtles (*Dermochelys coriacea*) (Sherril-Mix et al. 2008). Furthermore, biologging has enabled an integrative approach to understanding species responses to anthropogenic environmental change (Cherry et al. 2016, Chmura et al. 2018). Tracked animals have also played an integral part in monitoring the ocean by becoming observation platforms, collecting oceanographic parameters such as temperature, salinity, chlorophyll and conductivity at a fine temporal and spatial scale, which satellite imagery or hydrographic buoys may fail to capture (Harcourt et al. 2019). This has resulted in approximately 70% of all oceanographic profiles south of 60˚ S to being recorded by sensors on animals (Wilmers et al. 2015), playing an instrumental role in detecting change in remote locations (Treasure et al. 2017, Miloslavich et al. 2018, Harcourt et al. 2019). More recently, biologging tags have been deployed as novel surveillance of fishing vessels onboard seabirds, enabling effective and cost-efficient targeted monitoring of illegal fishing activity, particularly in the high seas where surveillance is challenging for political and logistical reasons (Weimerskirch et al. 2020).

A disconnect remains between the volume of existing tracking data and their use in conservation and management actions (Nguyen et al. 2018, Hays et al. 2019, Sequeira et al. 2019). Hays et al. (2016) highlighted key questions and priority research for marine megafauna movement ecology and the need to increase engagement with policy makers to help translate tracking data into real-world conservation benefits and effective resource management (Lennox et al. 2017). Tracking data can therefore contribute towards policy change, and has informed evidence-based conservation management strategies on local (Lea et al 2016) and regional scales (Trathan et al. 2014, Hays et al. 2019), such as the recommendation of new (Doherty et al. 2017a) and success of existing marine protected areas (MPA) (Farmer & Ault 2011), or the need to amend current protected area boundaries (Graham et al. 2016, Reynold et al. 2017). Biologging can be crucial for identifying animal fluxes, and consequently to predict the spread of nuisance species or disease (Daversa et al. 2018), provide near real-time mitigation against human activity at sea such as vessel strikes (Sequeira et al. 2019), as well as inform decisions regarding fisheries openings and quotas (Hobday et al. 2010, Young et al. 2013). Accelerometry data in particular can directly influence conservation action by identifying stress responses to human activity (Chivers et al. 2016, Barnett et al. 2016, Huveneers et al. 2018) and inform best practice in animal tagging and handling protocols, which can be put into practice immediately by scientists, commercial and recreational fisheries alike (Donaldson et al. 2013, Brownscombe et al. 2013, Bouyoucos et al. 2017).

Tri-axial accelerometers are one of the most simple and powerful biologging sensors that record data revealing two acceleration components of moving animals (i) static acceleration relating to posture and (ii) dynamic acceleration relating to the changes in velocity linked to patterns of the animal’s movement (Shepard et al. 2008). Owing to the unique wave signatures of stereotyped movements, accelerometers can identify locomotion (Sherub et al. 2017, Corbeau et al. 2020), reproduction (Whitney et al. 2010) and foraging activities (Okuyama et al. 2009, Wang et al. 2015, Yoshino et al. 2020). More subtle micro-movements can also be detected, informing on internal state including animals’ response to disease (Wilson et al. 2014). Dynamic Body Acceleration (DBA) derived from accelerometry data (Wilson et al. 2006, Gleiss et al. 2011) has been validated as a proxy for energy expenditure (Grémillet et al. 2017, Wilson et al. 2020a), allowing for insights into field metabolic rates of free-ranging animals in their natural environment (Udyawer et al. 2017, Lear et al. 2020). For example, DBA has revealed the energetic costs of prey capture dives in orcas (*Orcinus orca*) (Tennessen et al. 2019), and hunting in pumas (*Puma concolor*) (Williams et al. 2014). Behaviours can then be quantified temporarily into time-activity budgets (Okuyama et al. 2013, Bouyoucos et al. 2018a), and spatially into energetic landscapes (Scharf et al. 2016). Accelerometry is therefore particularly powerful when combined with other sensors (Williams et al. 2017), and an important tool for conservation physiology (Sherub et al. 2017), understanding environmental change (Williams et al. 2016), and effect of human activity (Benoit et al. 2020).

This thesis sets out to apply biologging, particularly accelerometry, to the conservation of two highly mobile marine vertebrate species, the basking shark (*Cetorhinus maximus*) and the green turtle (*Chelonia mydas*). Both species are listed as endangered following centuries of overexploitation (Compagno 2001, Jackson et al. 2001, McClenachan et al. 2006), bycatch (Wallace et al. 2010, Sims 2008) and habitat degradation (Whittock et al. 2017), and display periods of coastal foraging (Sims et al. 2000, Senko et al. 2010, Francke et al. 2013, Morais et al. 2014, Shimada et al. 2016, Di Beneditto et al. 2017, Doherty et al. 2017a, Doherty et al. 2017b, Dolton et al. 2020). Basking sharks form summer feeding aggregations off the coast of the UK (Witt et al. 2012), while green turtles, which generally live in tropical to sub-tropical waters, undergo an ontogenetic shift in habitat to neritic developmental grounds (Arthur et al. 2008). In the last few decades, biologging has provided insight on the movement (Braun et al. 2018), habitat preference (Makowski et al. 2006, Austin et al. 2019) and site fidelity (Fukuoka et al. 2015, Doherty et al. 2017b) of both species, with the first ever satellite tag to be used in the marine environment deployed on a basking shark in 1984 (Priede 1984). Biologging has also shed light on both species diving patterns (Hazel et al. 2009, Queiroz et al. 2017), diel behaviour (Shepard et al. 2006, Christiansen et al. 2017) and energetics (Okuyama et al. 2014, Johnston et al. 2018). However, much of green turtles' and basking sharks' basic biology remains unclear (navigational abilities or timing and location of reproduction for basking sharks), as well as fine scale behavioural or physiological responses to human activities.

The second chapter of this thesis will investigate how multi-sensor tags (incorporating temperature, depth, and tri-axial accelerometry) can be used to study breaching in basking sharks. Breaching, the act of leaping partially or completely out of the water is a behaviour displayed by a number of marine species (Halsey & Iosilevskii 2020). Owing to its extreme energetic cost, breaching is likely to have a fitness benefit, although its function in elasmobranchs when not linked to feeding remains unclear. (Kotiaho et al. 2001, Halsey & Iosilevskii 2020). This work is the first to gain long-term insight into the fine-scale movements of basking sharks, and highlights how biologging tags can be used not only to shed light on the fine-scale sub-surface behaviour and daily energy expenditure of basking sharks at their summer aggregation sites, but also infer important habitat supporting this behaviour by identifying the unique accelerometry signature of breaching events. This knowledge can be integrated into the design of MPAs and policy extending to wildlife watching guidelines and management of fisheries within and outside of designated areas.

Translocation, involving the intentional human-mediated movement of a living organism from one area to release at another (IUCN 2013) has been increasingly used as conservation method to mitigate against a range of anthropogenic and environmental threats (Barham et al. 2006, Hayward et al. 2007, Johnson et al. 2010, Devan-Song et al. 2016) but has shown varying levels of success (Batson et al. 2015, Wolfe et al. 2018). By combining GPS telemetry data with accelerometer-derived metrics (Wilson et al. 2006, Grémillet et al. 2018), the third chapter of this thesis aims to test whether translocation away from threats can be an effective conservation strategy for juvenile green turtles, by estimating the behavioural differences and energetic costs of homing behaviour following translocation. This study highlights how biologging can be used as an essential tool by wildlife managers to identify the outcomes of translocation by not only determining site fidelity to or dispersion from the release location, but also provide continuous monitoring to assess the immediate, short-term and possibly long-term effects on animal movements, behaviour, energetics and physiology. This is particularly pertinent for aquatic species where biologging can shed light into cryptic animals, save time and resources in long-term monitoring, as well as provide valuable insight to practitioners on best protocols to minimise handling stress prior to release.

Chapter 2: Fantastic breaches and where to find them: first insights into basking shark breaching behaviour

Abstract

Basking sharks (*Cetorhinus maximus*), the world's second largest fish, are endangered in the northeast Atlantic following two centuries of large-scale exploitation for their oily livers. They seasonally gather in key sites, including the western Scottish Isles, where they feed on plankton. Using high-resolution three-axis accelerometry and dive logging, this study investigated the energetics ans spatio-temporal variation of breaching behaviour, the act of leaping partially or completely out of the water. I present the first direct records of 67 breaches by basking sharks over 41 days at a feeding aggregation site in the Inner Hebrides. Basking sharks were found to breach both during the night and day, twice a day on average. Breaching events were highly repeatable both between and among sharks following similar ascent rate and angles, starting and finishing at 20 metres depth. Basking sharks can breach up to four times in surprisingly short succession (47 seconds), and likely increase energy expenditure by at least 30 times to breach, requiring 10 to 11.5 kJ of mechanical energy. The chapter also present early evidence of potential lateralisation in basking sharks. While the function of breaching remains unclear, given its energetic cost, breaching is likely to have a significant fitness function, highlighting the importance of the Sea of Hebrides for this species.

Introduction

Basking sharks (*Cetorhinus maximus*) are the world's second largest fish, reaching up to 12 metres in length and 4 tonnes in weight (Sims 2008). They have a circumglobal distribution (Braun et al 2018, Dewar et al. 2018), grow slowly and have low fecundity and long gestation periods (Matthews 1950, Pauly et al. 1997). Following two centuries of large-scale exploitation for their oily livers (Compagno 2001, Sims 2008) they are now listed as Vulnerable under the IUCN Red List on a global scale (Fowler 2009), are considered endangered regionally in the Northeast Atlantic and North Pacific (Fowler 2009). The species has been listed under Appendix II of the Convention on International Trade of Endangered Species since 2003 (CITES 2017), Appendices I and II of the Convention on Migratory Species since 2005 (CMS 2016) and in waters of the European Union under the Common Fisheries Policy since 2007 (Council Regulation (EU) No. 2018/120). They are also susceptible to modern fisheries bycatch (Speedie et al. 2009).

The emergence of animal tracking technologies (Hussey et al. 2015, Kays et al. 2015) over the past 50 years has provided invaluable insight into movements (Hussey et al 2015), physiology (Enstipp et al. 2016, Bouyoucos et al. 2018b), ecology (William et al. 2017), lateralisation (Payne et al. 2016), behaviour (Gleiss et al. 2017a, Gleiss et al. 2017b), energetics (Cooke et al. 2016, Bouyoucos et al. 2017), and social interactions (Jacoby et al. 2016) of a wide variety of species. Biologging tags allow for the continuous recording of high-resolution data that would otherwise likely be missed by visual survey alone (Cooke 2008). Due to their wide-range of applications, animal-borne tags have been used as a tool to assess threats to populations as well as their conservation status (i.e. IUCN Red List) (Cooke 2008, Jeffers & Godley 2016) by identifying overlaps with anthropogenic activities (Ellenberg et al. 2013, Maxwell et al. 2013) that have contributed to species decline worldwide (Hays et al. 2003, Queiroz et al. 2016, Harrison et al. 2018).

Biologging has been used on basking sharks to identify their long distance (Braun et al. 2018, Skomal et al. 2009) and seasonal migration patterns (Sims et al. 2003a, Doherty et al. 2017a) in relation to environmental conditions (Siders et al. 2013), and has been used to describe their habitat preferences (Curtis et al. 2014, Miller et al. 2015, Austin et al. 2019), foraging and diving patterns (Gore et al. 2008, Queiroz et al. 2017), and diel behaviour (Shepard et al. 2006). Basking sharks are obligate ram filter-feeders and feed at ocean fronts where abundance of primary (phytoplankton) and secondary (zooplankton) productivity is high (Skomal et al. 2004, Southall et al. 2005). Their diving behaviour, which varies between habitat types (Sims et al. 2003b, Sims et al. 2005), is thought to be tightly linked to the diel vertical movement of their prey through the water column, as well as tidal patterns (Shepard et al. 2006). The UK appears to host three conspicuous seasonal foraging aggregations, forming in late spring and summer: (i) Western Ireland, (ii) the Isle of Man, and (iii) the west coast of Scotland in the Sea of Hebrides (Witt et al. 2012). This last site has been subject to scientific study to improve the evidence base for discussions concerning a proposed Marine Protected Area and to investigate long-range movements of sharks present there (Speedie et al. 2009, Doherty et al. 2017a, Doherty et al. 2017b). While sharks likely visit there to feed (Crowe et al. 2018, Gore et al. 2019), these aggregations may also provide opportunity for social interactions and courtship (Southall et al. 2006, Jacoby et al. 2012, Miller et al. 2015, Gore et al. 2019).

Despite the advances in knowledge of basking sharks' spatial ecology, comparatively little is known about their below surface fine-scale behaviour during summer aggregations. Using GPS data, it has been possible to show the movements of basking sharks around the Sea of the Hebrides and further afield with a spatial resolution of approximately 100 metres (Doherty et al. 2017a). However, such data does not reveal aspects of movement and behaviour at sub-second scales. In addition, basking sharks are known to breach, leaping partially or completely out of the water (Hayes et al. 2018, Gore et al. 2019, Johnston et al. 2018). This behaviour has also been observed in white sharks (Sperone et al. 2012), reef mantas (Marshall & Bennett 2010), spinner sharks, dolphins (De Carli et al. 2018) and humpback whales (Maricato et al. 2017). The function of these leaping events in different marine species has been associated with parasite dislodgment (Félix et al. 2006), communication (Pyle et al. 1996, Kavanagh et al. 2017), signalling (Pearson 2017), response to human activity (Amrein et al. 2020), predation (Martin et al. 2005, Papastamatiou et al. 2018a, Semmens et al. 2019), mate finding (Marshall & Bennett 2010, Lusseau 2006, Félix & Botero-Acosta 2012, Stevens et al. 2018), mate guarding (Willis & Dill 2007), and even fun (Kuczaj & Eskelinen 2014). For non-air-breathing vertebrates the role of breaching, if it is not directly associated with feeding (Martin et al. 2005, Semmens et al. 2019), remains unclear. Basking sharks have recently been found to breach at greater vertical speeds than predatory ambushes performed by great white sharks (Johnston et al. 2018), requiring as much as 5-6% of its daily standard metabolic rate for a single breaching event. Because breaching has been estimated to be relatively energetically demanding (Halsey & Iosilevskii 2020, Segre et al. 2020), it is likely to have a fitness benefit (Kotiaho et al. 2001).

While basking shark surface behaviour has been studied at their feeding aggregations (Gore et al. 2016, Gore et al. 2019), these have been limited to coarse resolution (Doherty et al. 2017b) or visual observation made at the surface, which are restricted both by daylight hours and environmental conditions (Hayes et al. 2018) providing only “snapshots” into their behaviour. High resolution animal-borne multi-channel tags offer exceptionally fine scale (i.e. sub-second) recordings of environmental and biological parameters such as temperature, depth and speed, as well as used to derive the energetic requirement of behaviours (Wilson et al. 2008, Walker et al. 2015). Dynamic Body Acceleration, which is derived from measurements of raw acceleration, can be used to estimate energetic expenditure and to discriminate different types of activities (Halsey et al. 2011, Metcalfe et al. 2015). Should breaching have an important fitness function, it is then valuable to elucidate the timing, location and frequency of breaching events to highlight the importance of the Sea of Hebrides for basking sharks, and heighten management to aid species recovery.

The present study used accelerometry combined with temperature depth measurements and satellite telemetry to show, the depths, swimming speed and forces required for basking sharks to breach. I also describe the fine-scale behaviour of breaching events and the diel behaviours of basking sharks at coastal aggregation sites in Scotland.

Methods

Study area and tagging

All work was carried out in accordance with the UK HM Government Home Office under the Animals (Scientific Procedures) Act 1986 (Project Licence P23C6EFD) and under the Wildlife & Countryside Act 1981 (as amended) (Licence: 124812), and were reviewed and approved by the University of Exeter's animal welfare and ethics review board (AWERB). Three basking sharks (2 females, one unidentified sex) were tagged in the waters of Coll and Tiree, Inner Hebrides, Scotland (N 56˚33', W 6˚41') with Daily Diary tags ("DD tags", TDR10-DD-278A, Wildlife Computers, WA, USA, 7.4 x 5.7 x 3.6 cm, 117 g in air https://wildlifecomputers.com) between 2nd August and 4th September 2017. Sharks were tagged by approaching them from behind using a 10 m vessel, until close enough to apply the tags, with tagging attempts limited to three to reduce disturbance. DD tags recorded accelerometry and magnetometry at 8 Hz on three orthogonal planes corresponding to the dorso-ventral, anterior-posterior and lateral axes of the animal. DD tags also recorded swim speed ($m.s^{-1}$), depth (m) and temperature (C˚) at 1 Hz and whether the tag was wet or dry using a salt water switch sensor recording at 4 Hz. Tags were attached using a custom-made darting system to the body at the base of the dorsal fin that held the tags flush to the body (Fig. 2.1). A programmable timed-release mechanism (Wildlife Computers, WA, USA) released the tag from the shark 30 days following attachment. Each tag was deployed with a hydrodynamic syntactic bead floatation system (AZ-FLOAT-006, Wildlife Computers, Redmond, WA, USA, 16.9 x 4.1 x 10.5 cm, 80 g in air) and a SPOT6 satellite tracking tag to aid relocation of DDs once tags had detached from the study animals. Each tag system also comprised of a second satellite tag, a SPOT5 towed tag, which tracked the sharks' movements during the DD-tag deployment, and remained on the sharks after the DD tag detached. Following detachment, DD tags were retrieved and data downloaded.

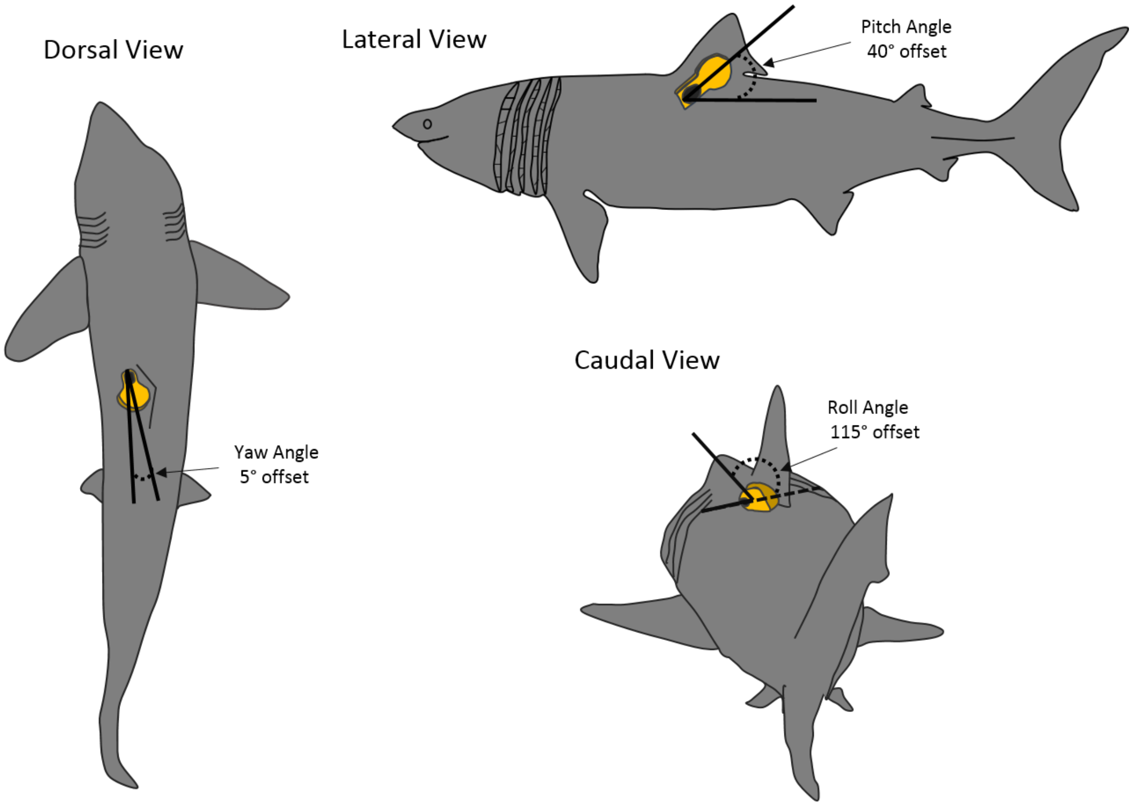


Figure 2.1: Schematic of a Daily Diary tag deployed on a basking shark viewed from the lateral, caudal and dorsal side of the shark. The pitch, roll and yaw angle of the tag attachment is highlighted in each view. The offset angles of each tag were corrected during the calibration process.

Accelerometry and behavioural analysis

There were small differences in the angles at which tags were deployed on sharks, so to correct the orientation of the tags to the sharks' body axes, accelerometry data were calibrated (following rotation of known angles) using the 'tagtools' package (https://github.com/stacyderuiter/TagTools). Accelerometry data were calibrated to one unit of gravity (9.8 m.s^{-1}) by rotating the DD through known angles in all three spatial planes. The sharks' body pitch and roll were extracted from the raw accelerometry data using additional 'tagtools' functions, with positive and negative angles indicative of an upward and downward pointing direction, respectively. Temperature and depth data were linearly interpolated to match the accelerometry and magnetometry 8 Hz sampling frequency. Swimming speeds for shark 3 were omitted due to likely entrapment of material preventing rotation of the speed wheel, making the data quality poor. Magnetometry data were omitted due to the metal base-plate on which the DD-tags were attached that caused false readings by the magnetometer.

Accelerometry data comprises two components, (i) low-frequency static acceleration and (ii) high-frequency dynamic acceleration. The static component relates to the inclination of the tag with respect to the earth's gravitational field (which is analogous to the shark's body posture) and was obtained by individually smoothing each of the three acceleration channels with a running mean of three seconds (Wilson et al. 2006, Shepard et al. 2008). These smoothed values were then subtracted from the raw data for the corresponding axis, leaving three-dimensional dynamic acceleration, relating to the changes in velocity owing to the patterns of the animal's movement (Gleiss et al. 2011). The three-dimensional dynamic acceleration was then used to make a summary metric describing effort, VeDBA (Vectorial Body Dynamic Acceleration) calculated as follows:

$$VeDBA = \sqrt{(A_x^2 + A_y^2 + A_z^2)}$$

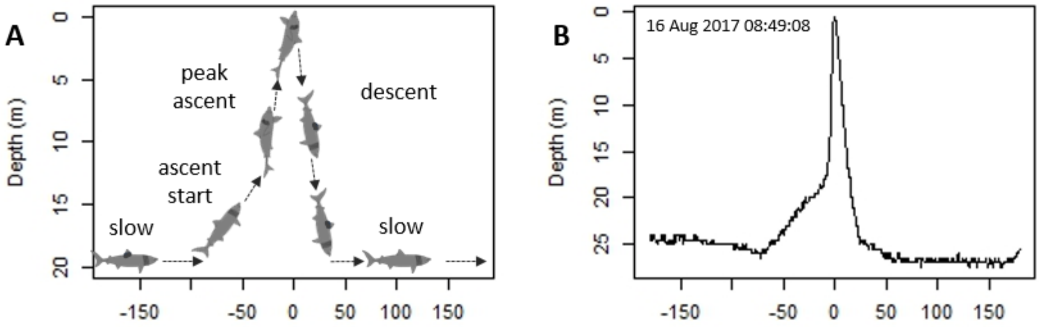
VeDBA is considered a proxy for the rate of energy expenditure, when tag orientation varies over time (Qasem et al. 2012, Wright et al. 2014).

Sharks' mean swimming speed, VeDBA, depth and tail beat amplitude (TBA – see below, hereafter referred to as 'swimming metrics') were compared for diel differences between sunrise and sunset times for the study site (https://www.tidetimes.org.uk/gott-bay-tide-times). A spectrogram of the dorso-ventral acceleration (z-axis) was generated in Ethographer ver. 2.04 (Sakamoto et al. 2009) in Igor Pro (Igor Pro 8, WaveMetrics Inc., Lake Oswego, USA), calculated by continuous wavelet transformation using the Marlet wavelet function with a minimum cycle of 0.125 seconds and maximum cycle of 1 second (Sakamoto et al. 2009). TBA was calculated for each 1 second interval using the Peak Tracer function. The resulting values were linearly interpolated to match the

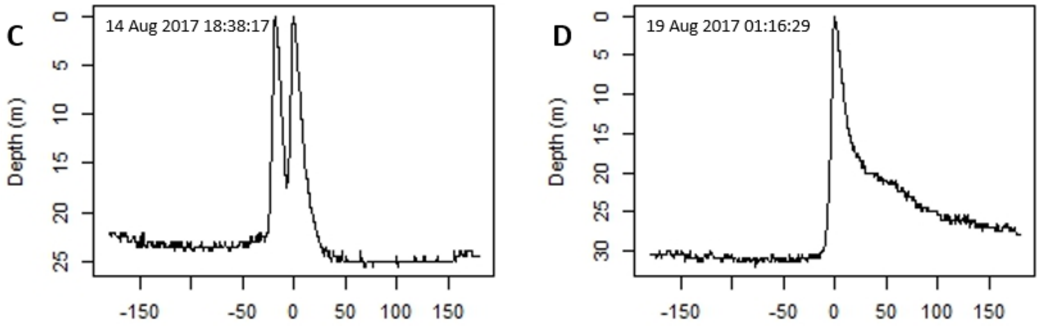
8 Hz sampling frequency of the Daily Diary, as above.

Breaching behaviour analysis

Breaching events were identified by the wet/dry sensor (recording at 4 Hz) as events where the tag broke the surface of the water. As the DD tags were attached flush to the shark's body, the tag should only break the surface when the shark breached or swam with the entire dorsal fin exposed above the surface. Data were individually inspected, looking for rapid depth changes coinciding with peaks in dynamic acceleration to identify breaching events. For each breach, the ascent and descent phase of breaching events were described by changes in depth, VeDBA, speed and TBA, including the maximum and absolute mean pitch and roll angles, the ascent and descent depths and duration. The ascent phase began when the sharks made a directed, sustained swim to the surface and usually terminated in a shorter, peak ascent phase, where the period of burst speed exceeded ≥ 1.5 $m.s^{-1}$ before breaching. The descent phase was the period between the end of the breach until the sharks' depth levelled (Fig. 2.2A).

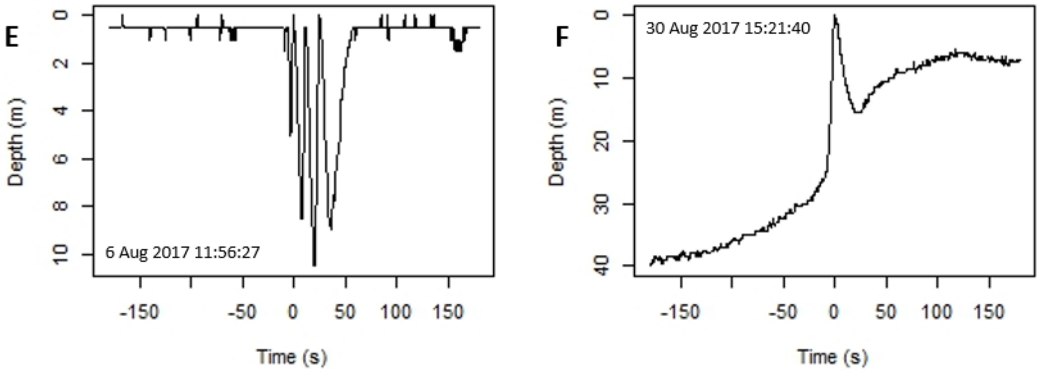


(i) Breach with gradual ascent



(ii) Spike breach

(iii) Breach with gradual descent



(iv) Surface breach

(v) Other breach types

Figure 2.2: **Basking shark breaching profile types.**

(**A**) A schematic diagram showing a stylised breach by a basking shark over time, starting and finishing at 20 metres depth. Breaches by basking sharks could be generalised into five different types as follows (examples show real data from sharks, as stated on each plot): (**B**) sharks switched from swimming along the sea floor to a short slow ascent before starting the peak ascent phase, breaching, and returning to similar depth (8% of the breaches recorded, n=4 breaches); (**C**) sharks made rapid ascents to the surface and descended to similar depths, here shown for a double breach, (45%, n=21); (**D**) sharks made a rapid ascent to the surface but returned gradually to shallower depth (27%, n=13); (**E**) sharks started near the surface, dived to reach depths from which to breach, and returned to the surface afterwards (4, n=2); and (**F**) breaches that do not fit in the other four categories (15%, n=7).

Energetic analysis

The morphometric measurements of shark appendages, fork length and mass were calculated as described in Johnston et al. (2018). Shark 1 was estimated to weigh 678 kg and measure 5 m, while sharks 2 and 3 were both estimated to weight, 1171 kg and measure 6 m. To derive the mechanical power of each breach (E_m), expressed in kJ, as:

1) $E_m = \frac{k_E}{\eta_k} . \frac{mv^2}{2}$

where k_E is a parameter likely ranging between 1.3 and 1.5 reflecting the acceleration profile of the shark during a breach, the hydrodynamic propulsion efficiency η_k is estimated at 0.7, the mass of the shark *m* in kg, and the speed of shark *v* in $m.s^{-1}$ (see Johnston et al. 2018 for calculations). Since the speed *v* was derived from the speed wheel, the mechanical power of breaches could only be calculated for sharks 1 and 2.

Sharks' daily energy expenditure was estimated using mean daily summed VeDBA, and compared to an estimate of daily routine metabolism (in $kJ.day^{-1}$) using a generalised relationship between mass and routine metabolism standardised at 15˚ C for 17 species of fish, including five shark species, given in Parsons (1990) defined as:

2) $y = 13.0(\log(x))^{0.602}$

Where x is the weight in grams and y is the routine metabolism in $kcal.kg.day^{-1}$, subsequently converted into $kJ.day^{-1}$. Since temperature is widely recognised as the most important factor driving metabolic rate in ectotherms (Clarke & Johnston 1999, Gillooly et al. 2001, Kingslover 2009), the routine metabolic rate was corrected for the mean water temperature experienced by each shark (14.3˚C for sharks 1 and 3, and 14.6˚C for shark 2) based on the equation:

3) $R_2 = R_1 . {Q_{10}}^{(\frac{T_2 - T_1}{10})}$

Where R_1 is routine metabolic rate (in kJ.day^{-1}) derived from the equation 2 estimated at T_1 of 15˚C and R_2 is the temperature corrected routine metabolism at temperature T_2. Q_{10} is the interspecific temperature coefficient of 2.23 (Ste-Marie et al. 2020) which fits within the assume Q_{10} range for elasmobranchs (Brett & Groves 1979). Routine metabolism was also calculated at the temperature ranges experienced by all three sharks (14˚C to 15˚C for shark 1, 10.7˚C to 15.4˚C for shark 2, and 13.8˚C to 15˚C for shark 3). The wet mass of copepods required to meet the sharks' daily energetic expenditure was calculated from the calorific value of copepods of 5.04 kJ.g^{-1} (Båmstedt 1986). Since zooplankton densities were not measured *in situ* for the present study, a prey concentration range was used to estimate the amount of time necessary for the sharks to filter-feed the amount of prey needed to meet energetic demand, where the minimum density was the average theoretical threshold (0.62 g.m^3) for prey concentration estimated in Sims (1999), while the maximum density was 2.41 g.m^3 as reported in the same paper. In the present study, as foraging events could not be identified from accelerometry data, the filtration rates for both the 5 m and 6 m sharks were derived from Sims (1999) estimates and adjusted to the average swimming speed recorded by the DD tags (0.4 m.s^{-1} and 0.2 m.s^{-1} respectively). While the gape area of a 5 m shark was reported at 0.2 m^2 in Sims (1999), it was estimated at 0.3 m^2 for a 6 m shark based on the 1:10 gape length – total body length ratio (Sims 1999), with resulting filtration rates of 207 m^3.h^{-1} and 123 m^3.h^{-1} respectively (Fig. S2.1).

Tracking data

Argos location data from SPOT 5 tags were filtered for quality, retaining location classes 1, 2, 3, A and B (Witt et al. 2010). Location data collected during deployment of the DD tags were only received for Shark 2, as no SPOT 5 tag was deployed on shark 3, and no location data were transmitted for shark 1. The locations of breaching events for shark 2 were recorded as the closest Argos position received within 30 min of each breach.

Time-activity budget analysis

To determine the time-activity budget of basking sharks, accelerometry data were separated into three categories: (i) slow swimming, (ii) strong swimming, (iii) and breaching through visual inspection of the raw lateral acceleration (z-axis) and using tail beat amplitude (TBA). Slow swimming was defined as a TBA < 0.2 Hz, stronger swimming characterised by a TBA of 0.21 to 1.69 Hz, and breaching identified by a TBA > 1.7 Hz**.** The proportion of time allocated to each behaviour was measured for each shark throughout the entire tracking period as well as the overlapping 4-day deployment period when all three tags were contemporaneously attached.

Postural data analysis

To describe changes in the sharks posture during particular behaviours, the static acceleration of all three acceleration axes were plotted in a three dimensional scatter plot (hereafter termed a ‘g-sphere’) (Walker et al. 2015). The shark’s body orientation is represented by the position on the sphere, with the “north pole” (top of the sphere) denoting a horizontal swimming posture. All deviations from the north pole represent different orientations of the shark relative to its horizontal position. The ‘Dubai plot’ function generates a three-dimensional histogram of the frequency of postural data in each facet of the sphere, with the height of each bar equivalent to the proportion of time spent by the shark in a given posture. The posture of the shark during breaching was then quantified visually as breaching forward, backwards, to the left or right side. The last three breaches made by shark 2 (5%) were disregarded in the analysis due to potential shifts in the position of the DD tag and providing likely misleading postural data.

Statistical analysis

For each shark, diel differences in mean swimming metrics were compared between daytime and night time using Mann-Whitney U-test, or Welch t-test following a square root transformation if the data were not normal. To visualise these diel differences, the hourly means of swimming depth, VeDBA, speed and TBA were plotted using the 'radial.plot' function in the R package plotrix (https://www.rdocumentation.org/packages/plotrix/versions/3.7-2/topics/polar.plot). To test whether sharks displayed similar patterns of diel differences to one another, a Kruskal-Wallis test was used. To identify whether breaching occurred at particular times of the day, the frequency distribution of breaches throughout the 24-hour cycle was tested using Rayleigh test of uniformity with the R package 'CircStats' (https://cran.r-project.org/web/packages/CircStats/CircStats.pdf). Statistical differences between variables describing the ascent and descent phases of breaching events (depth, VeDBA, TBA, speed, pitch and roll angles) were tested with paired t-tests or Wilcoxon signed-rank test depending on normality. Additionally, the relationship between each swimming metric during the ascent phase of breaches was measured using linear least square regressions. Breaching may be expected to be energetically expensive, and multiple breaches to be progressively more demanding. Thus, to test whether breaching multiple times was different to breaching just once, swimming metrics (changes in depth, VeDBA, Speed and TBA, maximum and absolute mean pitch and roll angles, the starting ascent and finishing descent depths, and dive duration) were compared using paired t-tests or Wilcoxon signed-rank test depending on whether they met assumptions of normality. Due to the energetic demands of breaching, sharks may require a recovery period following breaching events. Mean VeDBA, depth, speed and TBA were therefore calculated for a 15 min window following the last (or only) breach, and one hour later, and compared using paired t-tests or Wilcoxon signed-rank test depending on normality for single and multi-breaching events. Lateralisation, the preference for one side (left or right) that is consistent across events (Canning et al. 2011), was investigated by comparing the roll and pitch direction during breaching. Due to limited sample size of breaching events for sharks 1 and 3 (n=2 and n=5 respectively) only sideways breaches made by shark 2 were included in the lateralisation analysis. Chi-squared test with Yates continuity correction were used to test for the association between direction of the roll and diel period.

Results

Diel behaviour

All three Daily Diary tags were recovered from the sharks providing access to a cumulative 41 days of data, with tags from shark 1 and shark 3 releasing prematurely (after 4 days 19 hours, and 5 days 11 hours respectively) and shark 2 recording for 31 days 19 hours. All sharks spent more time at the surface (0 to 3 m depth) during daylight hours than during the night (shark 1's mean time at the surface during day time 0.8 % ± 1.7 s.d. vs night time 0.2 % ± 0.4 s.d. Wilcoxon rank sum test: W=90.5 p=0.23; shark 2 day 59.6 % ± 23.9 vs night 7.9 % ± 16.1, W=135.5, p<0.001; shark 3: day 9.2 % ± 9.2 vs night 0.4 % ± 0.8, W=132, p<0.001; Fig. 2.3). Shark 3 swam significantly deeper overall than the other two sharks (Kruskal-Wallis rank sum test: χ^2=49.76, df=2, p<0.001, mean 23.7 m ± 6), but did not show any overall diel differences in depth use (day 22.4 m ± 5.5 vs night 25.8 ± 6.3, Wilcoxon rank sum test: W=49, p=0.24; Fig. 2.4).

Sharks 1 and 2 displayed reverse diel vertical migration, swimming significantly deeper at night than during the day (shark 1 day 16.3 m ± 1.6 vs night 18.8 m ± 2.3, Wilcoxon signed rank test V=20, p<0.01; shark 2 day 5.6 m ± 3.4 vs night 13.8 m ± 2.3 V=8, p<0.001) and spending significantly more time at depth greater than 20 m at night than during the day (shark 1 day 24.2 % ± 9.5 vs night 43.5 % ± 15.6, W=23, p=0.05; and shark 2 day 4.2 ± 6.1 vs night 13.5 % ± 13.7, W=137, p<0.001; Fig. 2.4, Fig. 2.5). Only shark 2 exhibited clear diel differences in VeDBA, speed and tail beat amplitude (TBA), being significantly more active during daylight hours (mean VeDBA: day 0.5 g ± 0.2 vs night 0.3 ± 0.1, Welch two-sample t-test: t=0.09, df=22, p<0.001; mean speed: day 0.3 $m.s^{-1}$ ± 0.1 vs night 0.2 $m.s^{-1}$ ± 0.04, Welch two-sample t-test with log transformation t=6.99, df=22, p<0.001 ; mean TBA: day 0.1 Hz ± 0.01 vs night 0.07 Hz ± 0.02, Wilcoxon rank sum test: W=137.5, p<0.001; Fig. 2.5).

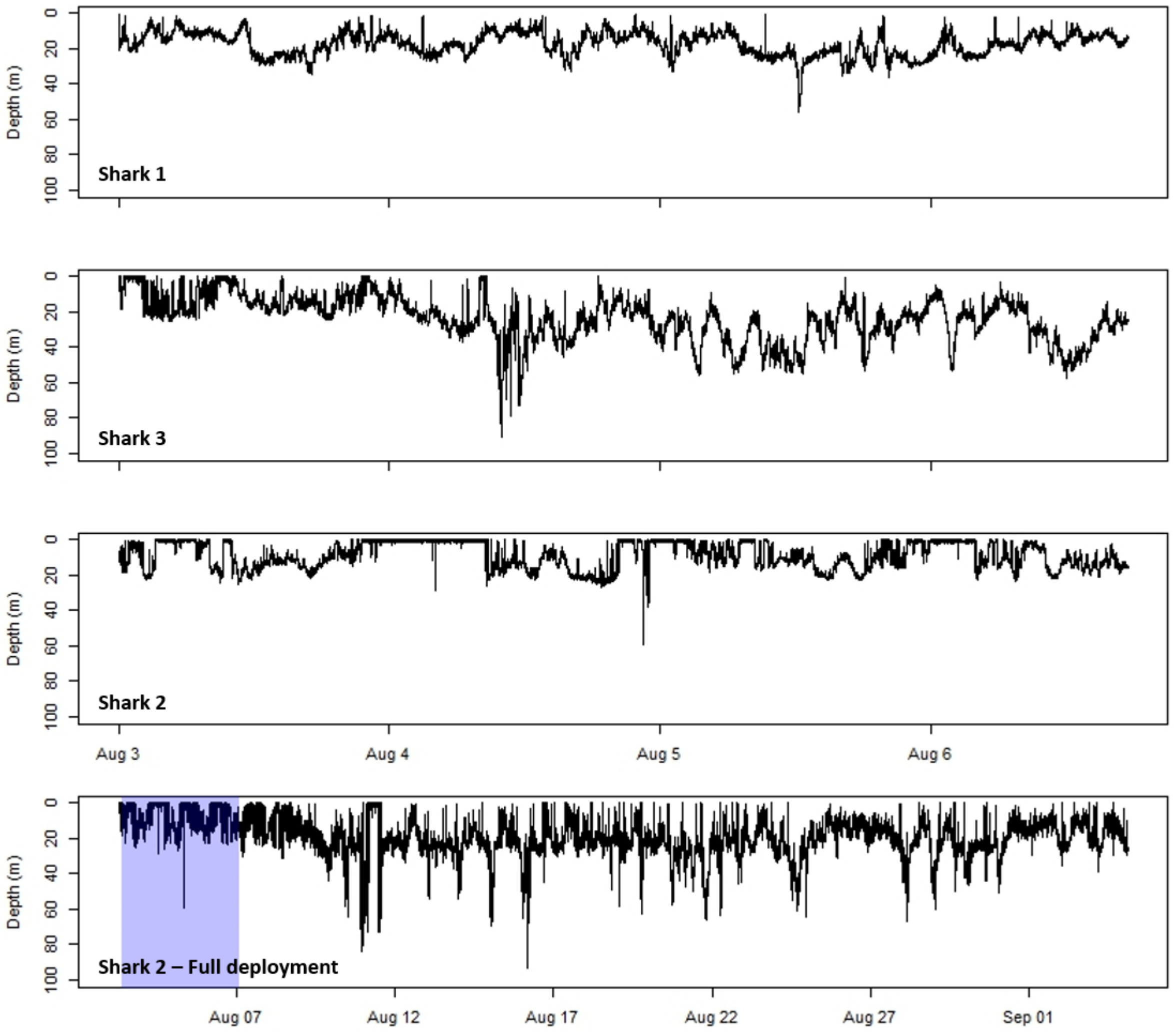


Figure 2.3: Depth profile for shark 1, 2 and 3 showing different fine scale vertical movement during the contemporaneous tag deployment period (09:31:00 2 Aug 2017 – 03:00:00 7 Aug). The last panel depicts the total 32 day deployment of shark 2’s tag, with the shaded extent representing the range of the contemporaneous period.

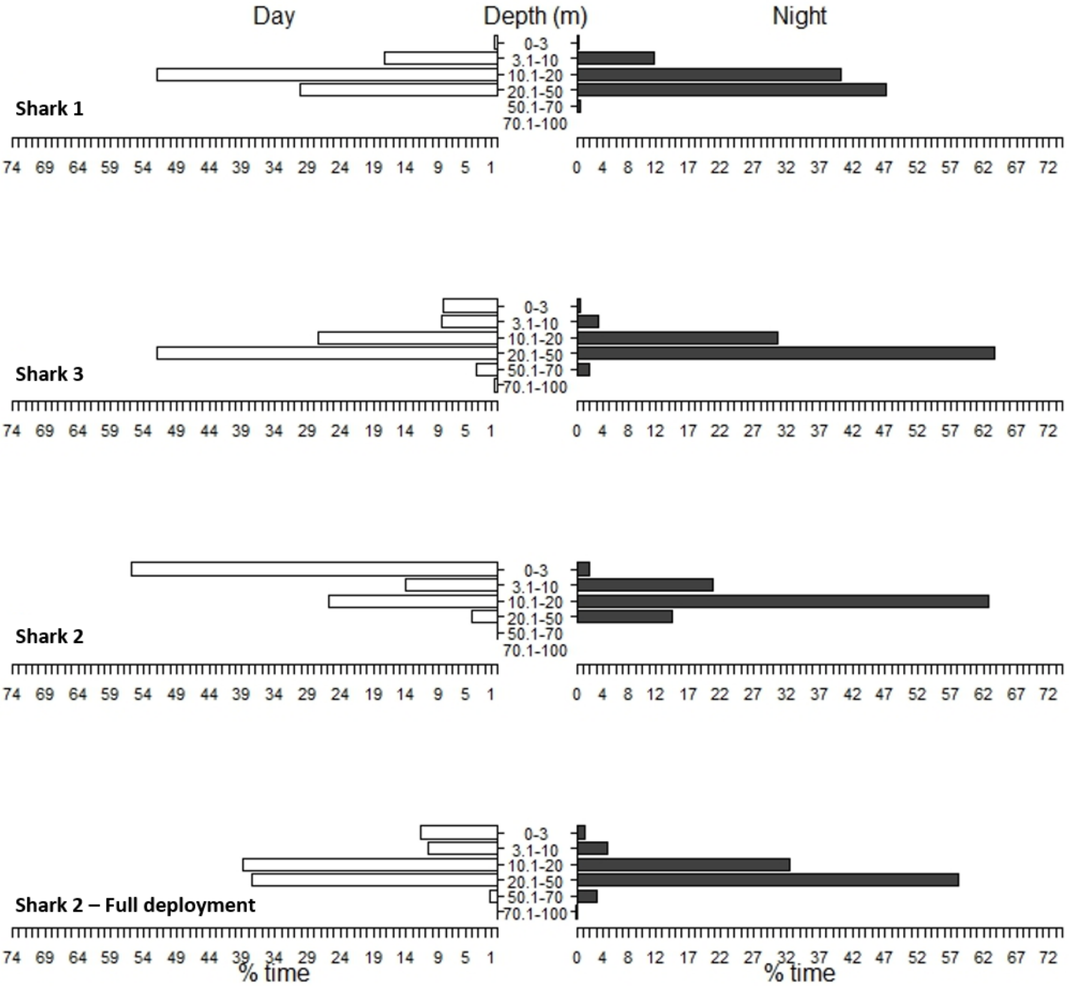


Figure 2.4: Histogram of the proportion of time sharks spent within six depth ranges during daylight hours (white), and at night (black) for sharks 1, 2 and 3 during the contemporaneous tracking period (09:31:00 2 Aug 2017 – 03:00:00 7 Aug), and for the full 32-day deployment of shark 2's tag in the last panel.

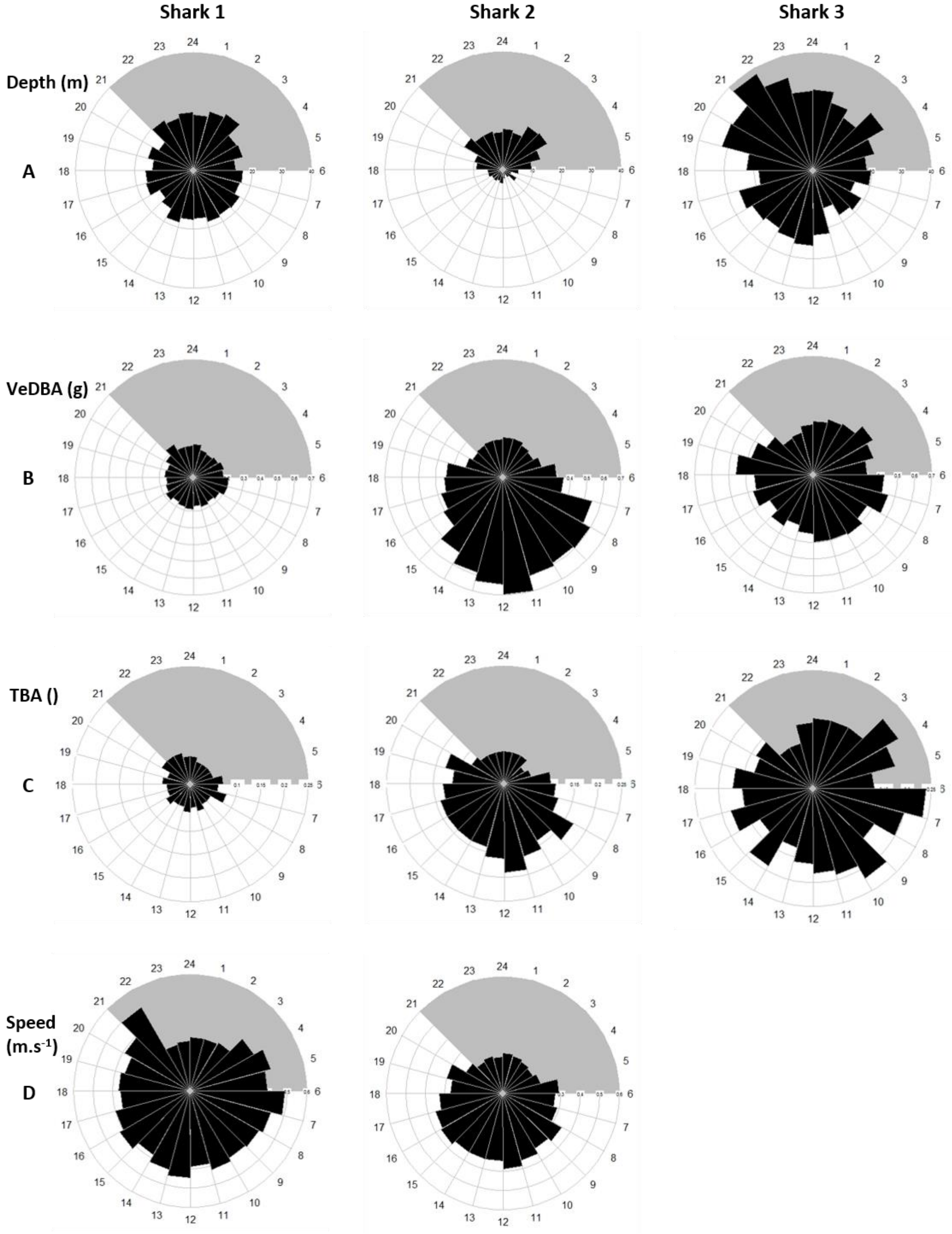


Figure 2.5: Radial plots highlighting the diel differences in depth, VeDBA, tail beat amplitude and speed for three tagged sharks. White and shaded portions of the background show the daylight and nocturnal periods respectively. The length of each black segment represents the mean hourly value of the corresponding metric, highlighting temporal differences in activity between sharks. Shark 2 displayed the greatest diel differences in behaviour, with lowest VeDBA, TBA and speed represented by shorter segments during the night time compared to longer segments during the daylight hours. No speed data were recorded for shark 3.

Fine scale breaching characteristics

Sixty-seven breaches were recorded (Fig. 2.6A), of which 28 were single breaches, 13 were double breaches, 3 were triple breaches and one shark breached four times in 47 seconds (Fig. 2.6E). Shark 1 carried out one double breach during the tracking period, shark 2 carried out 60 breaches, and shark 3 breached five times. Breaching occurred in 54% (n=22) of the 41 tracking days, and sharks breached on average two times per day (max six times in 24 hours). The time interval between breaching events varied between sharks, ranging from 6.7 ± 9 hours for shark 3 to 12.6 ± 22.3 hours for shark 2. Shark 1 carried out just one double breach, 32 seconds apart. The time interval between consecutive breaches within multi-breaching events was 18.2 s ± 5.7 (range 12 to 47 s) for sharks to dive to sufficient depth to gain momentum to propel themselves back out of the water. Breaching occurred throughout the diel cycle (Fig. 2.6B). Both sharks 1 and 3 appeared to predominantly breach at night (shark 1: 100 % n=2, shark 3: 80 % n=4). In contrast, shark 2 did not show any temporal pattern in the timing of breaching events, which were uniformly distributed throughout the diel period (Rayleigh test of uniformity: $\vec{R}$ = 0.12, p=0.39, Fig 2.4 B). The peak number of breaches recorded for all sharks occurred before dawn, between 4 and 5 AM.

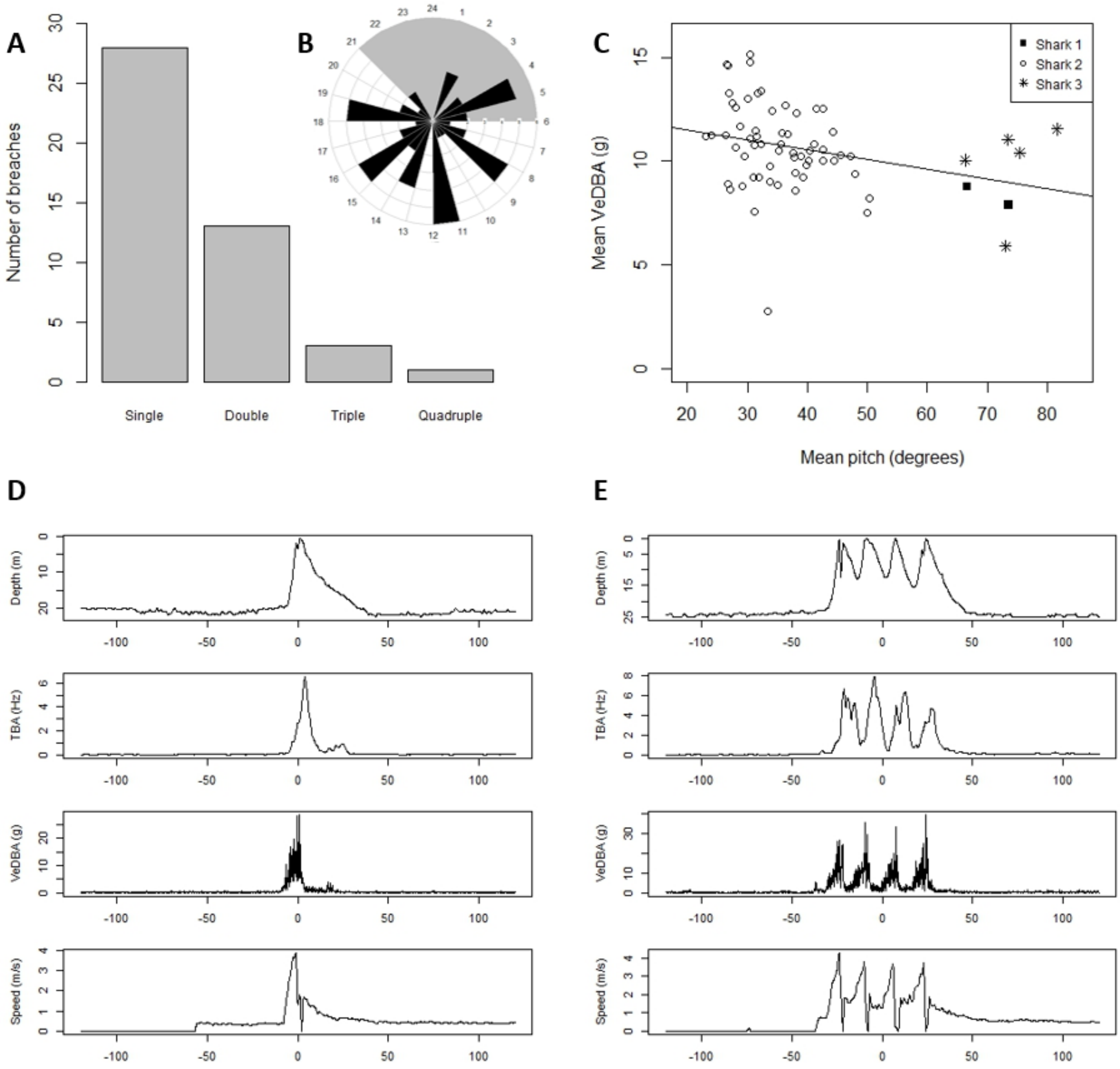


Figure 2.6: Breaching dynamics of basking sharks. (**A**) Histogram of the number of single and multi-breaches recorded for all three basking sharks (single= 28, double= 13, triple= 3 and quadruple=1). (**B**) Radial plot showing the number of breaches by the time of day performed by shark 2. Each segment represents the hour at which the shark breached, with the respective length indicating the total number of breaches recorded during that given hour. (**C**) Relationship between the mean VeDBA during the ascent phase of first breaches and the mean pitch angle at which the sharks swam to the surface. Values for shark 1 are represented by black squares, shark 2 by clear circles, and shark 3 by stars. Breaching profiles of a single (**D**) and a quadruple breaching event performed in 47 seconds (**E**), highlighting changes and consistencies in depth, TBA, VeDBA and speed differences over a 4 min window.

Breaches could be classified into five categories based on their depth and speed profiles: (i) breach with gradual ascent (n=4), (ii) spiked breach (n=21), (iii) breach with gradual descent (n=13), (iv) surface breach (n=2), and (v) breaches that fit neither of the other four categories (n=7) (Fig. 2.2). Sharks switched from slow swimming at an average speed of 0.3 $m.s^{-1}$ to ascending to the surface almost 25 times faster at 2 $m.s^{-1}$ ± 1.10 (range 0.1 to 3.8 $m.s^{-1}$), reaching the surface in 41.8 s ± 80.7 (range 2 s to 6.4 min) from 18.5 m ± 9.05 deep (range 5 to 57 m). Breaching was an estimated thirty-fold (32 times) more energetically demanding than routine swimming (VeDBA: 7.7 g ± 4.5, range 0.4 to 14.7 g), with a tail beat amplitude of 1.5 Hz ± 1.1 (range 0.1 to 5.1 Hz). A peak ascent phase of the breaches was observed when the rate of ascent and swimming speed suddenly increased to more than 1.5 $m.s^{-1}$. Breaching metrics were calculated separately for this phase, with sharks ascending to the surface considerably faster in 6 s ± 2.1 (range 2 to 17 s) from 14.8 m ± 5 deep (range 4.6 to 28 m) at 2.7 $m.s^{-1}$ ± 0.5 (range 1.2 to 3.8 $m.s^{-1}$), almost ten-fold faster than the sharks' average swimming speed. Sharks swam to the surface at mean angle of 36.1° ± 13.4 (range 23.1 to 81.6°) before exiting the water almost vertically at 76° ± 9 (range 43.3 to 87.9°) at a maximum speed of 3.9 $m.s^{-1}$ ± 0.59 (range 2.2 to 5.6 $m.s^{-1}$), 13 times faster and 45 times more energetically demanding than during slow swimming (mean VeDBA 10.6 g ± 2.18, range 1.1 to 15.1; Fig. 2.6). There was a negative relationship between mean pitch of ascent and VeDBA (Linear least squares regression: R^2=0.06, f=4.16, t=8.11, df=64, p=0.045, VeDBA =14.44-0.05*pitch), as well as TBA (R^2=0.06, f=4.02, t=4.02, df=64, p=0.049, TBA=3.68-0.02*pitch; Fig. 2.6C).

There were 14 breaches for which an Argos location was received within 30 minutes of the breach. Comparing the shark's depth profile to the bathymetry around Coll & Tiree, sharks likely started ascending to the surface from the sea floor, before propelling themselves at speed out of the water at a near vertical angle (76°). All recorded breaches with associate geographical locations were within the proposed boundaries of the Sea of Inner Hebrides MPA, and were predominantly within Gunna Sound (71%, n=10), with the remaining occurring south west of Tiree in deeper waters (Fig. 2.7). Breaching events were highly repeatable, both between and among sharks (Fig. S2.2). While the starting depth varied between sharks and breaches, each shark followed a similar pattern in ascent-rate, swimming speed and VeDBA (Table S2.1). Sharks did not display any significant differences in starting depth, VeDBA, speed, TBA, duration, mean and maximum pitch or roll during between the ascents of single breaches or the first ascent of multi-breaching events for either the total or peak ascent phase (Table S2.1). Perhaps surprisingly, during multiple breaching events, the ascent rate, swimming speed and VeDBA were similar for every subsequent breach when comparing the peak ascent phase phases of the first and second breaches of multi breaching events (n=17) (Table S2.2). Sharks displayed similar patterns between consecutive breaches despite starting at significantly greater depths (Wilcoxon signed-rank test, V=122.5, p=0.03, first breach 16.7 m ± 5.8, second breach 13.8 m ± 2.6) and stronger tail beats (V=33, p=0.04, first breach 1.6 Hz ±2.1, second breach 2.1 Hz ± 0.9).

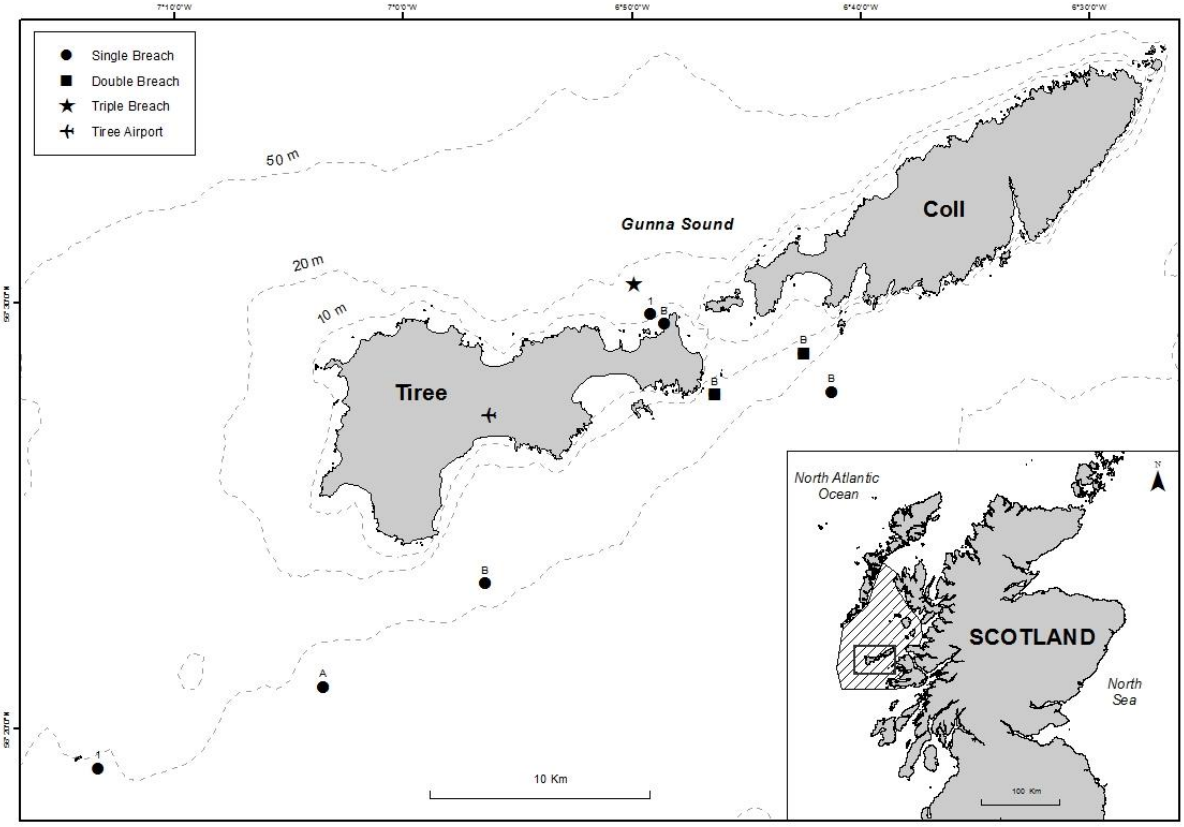


Figure 2.7: Map showing 14 locations closest to where a breach occurred. Single (n=5), double (n=3) and triple (n=1) breaches are represented by circles, square

and stars respectively. The Argos location class is labelled for each breach, denoting location accuracy of the possible location of the breach based on the closest Argos position within a 30 min window. All other breaches for which a location was not recorded within 30 min of the breach were excluded. The inset shows the location of the study site in relation to Scotland, with the hashed extent representing the proposed Marine Protected Area for the Sea of Inner Hebrides.

Breaching energetics

On average, sharks required an estimated 10 to 11.5 kJ (range 3 to 22 kJ) of mechanical energy to perform a single breach, based on their metabolism-weight relationship, varying between 14 to 16 kJ for the shark 1 (range 8.5 to 22 kJ), to 10 to 11 kJ for sharks 2 and 3 (range 3 to 18 kJ). Sharks expended the same amount of estimated mechanical energy for each breach regardless of whether they breached once or several times (Wilcoxon rank sum test W=198.5, p=0.87; E_{single}= 11.52 to 11.8 kJ, E_{multi}=9.98 to 10.3 kJ), or between individual breaches within a multi-breaching event (paired t-test t=0.2, df=15, p=0.84; E_{first}= 10.29 to 11.57 kJ, E_{second}= 10.25 to 11.82 kJ). A single breach represented an estimated 0.05 to 0.13 % of daily routine metabolism, which ranged from 12.06 $MJ.day^{-1}$ (502.6 $kJ.h^{-1}$) for shark 1, to 20.8 $MJ.day^{-1}$ (868 $kJ.h^{-1}$) for sharks 2 and 20.3 $MJ.day^{-1}$ (847.4 $kJ.h^{-1}$) for shark 3 (Table 2.1). When correcting routine metabolism for the temperature ranges experienced by the sharks, routine metabolism ranged from 11.77 $MJ.day^{-1}$ for shark 1 to 22.21 $MJ.day^{-1}$ for shark 2 with breaching accounting for similar costs (Table 2.1) If plankton concentrations experienced by the tagged sharks were similar to those recorded off Plymouth reported by Sims (1999) (mean 2.41 $g.m^3$ wet weight), the total prey wet weight required to meet the sharks' average daily energy expenditure (DEE) was estimated at 2.39 $kg.day^{-1}$ for shark 1, 4.13 $kg.day^{-1}$ for sharks 2 and 4.04 $kg.day^{-1}$ for shark 3 (Table S2.3). Thus, sharks may require 2.2 to 3.2 g of copepods to fuel a single breach, with up to 6.4 g and 17.5 g necessary on days with greatest number of breaches performed by sharks 1 and 2 respectively. The time required to intake the amount of prey to meet sharks' DEE ranged from 4.8 h to 18.6 h for shark 1, 13.9 to 54 h for sharks 2 and 13.5 to 52.8 for shark 3, based on mean zooplankton density of 2.4 $g.m^3$ and mean theoretical foraging threshold of 0.62

$g.m^3$. Depending on prey concentration, it may then take shark 1 23 to 89 s and sharks 2 and 3 26 s to 1.7 min to forage enough prey to sustain an average breach.

Conversely, when using mean daily summed VeDBA, which accounts for individual variation based on accelerometry-derived measures, the proportion of DEE allocated to breaching is up to five times greater (Table 2.1). Sharks spent on average 0.26 % (sharks 2 and 3) to 0.37 % (shark 1) of their total average DEE on a breach and cumulatively up to 2 % (1.96 %), compared to 0.4 % measured using the metabolism-weight relationship. Using accelerometry data, a single breach is estimated to require between 10.9 g and 15.9 g of prey, with up to 87.5 g needed for multi-breaching events. Sharks would then require 1.9 to 2.2 min to forage enough prey to sustain an average breach, and up to 3.8 to 17.7 min for multi-breaching events. Following breaching, sharks were significantly more active for the first 15 min compared to the subsequent following hour (Table S2.4), and they did not appear to compensate for the high energetic demands of multi-breaching events by reducing their swimming speed and activity level compared to single breaches. In addition, sharks maintained their speed (Student t-test: t=0.12, df=22, p=0.90), displayed similar VeDBA (Wilcoxon rank sum test: W=207, p=014), and sustained their TBA (W=218, p=0.57) before and after breaching, regardless of whether they breached once or multiple times.

Table 2.1: Summary of energy expenditure by day (Daily Energy Expenditure, DEE), by breach and by maximum number of breaches made in a day per shark estimated from routine metabolic rate (MJ.day^{-1}) and summed VeDBA (g). The proportion of DEE needed to sustain an average breach and maximum breaches per shark is also shown as well as the routine metabolism range estimated for the temperature range experienced by the sharks and resulting corrected proportions

		Shark 1	Shark 2	Shark 3
Daily Energy Expenditure (DEE)	RM (MJ.day^{-1}) [min-max]	12.06 [11.77 – 12.57]	20.83 [15.24 – 22.21]	20.33 [19.53 – 21.51]
	Summed VeDBA (g)	$13.7e^4$	$19e^4$	$24.7e^4$
Average Breach	Mechanical power (kj)	16	11	-
	Summed VeDBA (g)	506.1	490.6	637.4
% of DEE for a single breach	RM [min-max]	0.13 [0.13 – 0.14]	0.05 [0.05 – 0.06]	-
	Summed VeDBA	0.37	0.26	0.26
Maximum breaches	Mechanical power (kJ)	32.2	88	-
	Summed VeDBA (g)	1012	3729	1385
% of DEE for maximum breach	RM [min-max]	0.27 [0.25-0.27]	0.42 [0.40-0.58]	-
	Summed VeDBA	0.74	1.96	0.56

*RM = Routine Metabolism (MJ.day-1)

Behavioural variations in breaching

Sharks 1 and 2 breached repeatedly forwards (100 % n=2 breaches, and 96.5 % n=55 breaches, respectively), whereas shark 3 varied (60 % backwards n=3 breaches, 20% forward n=1 breaches, 20 % sideways n=1 breach; Fig. 2.8). Sharks were significantly more likely to breach backwards when ascending to the surface more vertically (binomial logistic regression Z=-2.72, p<0.01). Behavioural asymmetries in rolling direction during breaches were also recorded, with sharks predominantly rolling on their right-hand side (n=45 breaches, 70.3 % of all breaches; Fig. 2.8). While the sample size of breaching events for sharks 1 and 3 was small, both sharks consistently rolled to the right. Shark 2 also tended to perform right-sided breaches, with 66.7 % of breaches (n=38) rolling to the right (Pearson chi-squared with Yates continuity correction: χ^2=8.96, df=1, p<0.01). Rolling direction was independent of whether it was day or night (χ^2=0.64, df=1, p=0.42) as well as the pitch direction (forward or backwards) (χ^2=0.46, df=1, p=0.50).

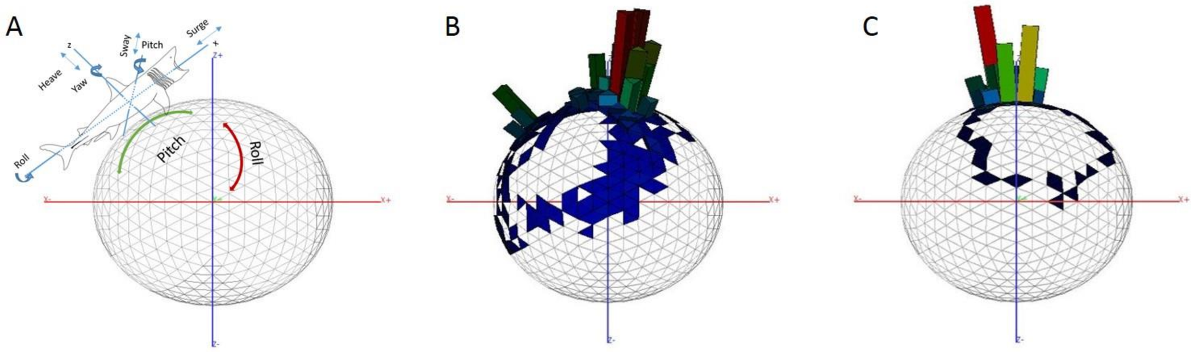


Figure 2.8: Dubai plots of shark breaching behaviour. Acceleration data are plotted in a 3-dimensional histogram where the height of the resulting bars represent the amount of time sharks spent in a particular posture in each facet of the sphere (A). In the central Dubai plot (B), posture of all five breaches made by shark 3 were overlaid. The taller histogram bars at the “north pole” of the plot indicate the longer time spent swimming horizontally before and after the breach. In comparison, the short-lived backwards breaches are represented by the smaller histogram bars on the left of the sphere, with the consistent right-sided rolling behaviour highlighted by the shortest blue bars crossing the “equator” facing the reader. Conversely, the far right plot (C) represents a single breach performed by shark 2 rolling on its right side, as indicated by the short blue histogram bars on the opposite face of the sphere.

Time-activity budget

All sharks allocated the majority of their time to swimming slowly (mean 86.1 % ± 13.6, range 71.8 to 98.8 %), and a minority to more powerful swimming (1.2 % to 28.2 %, Table 2.2). Breaching represented a fraction of the tracking period (<0.001 % for all sharks), equivalent to 1.8 min of the overlapping deployment (3 days 17.5 hours) and 11.2 min of for the full deployment (31 days 19 hours) respectively for shark 2, in comparison to an average of 3 days 5 hours 6 min of slow swimming.

Table 2.2: Ethogram of basking sharks behaviour displaying the duration and proportion of time allocated to breaching, strong swimming and slow swimming for both the total duration of the tag deployment and the contemporaneous tracking period (09:31:00 2 Aug 2017 – 03:00:00 7 Aug).

	Shark 1		**Shark 2**		**Shark 3**	
	Full deployment 4.8 days	Overlapping deployment 3.7 days	Full deployment 31.8 days	Overlapping deployment 3.7 days	Full deployment 5.5 days	Overlapping deployment 3.7 days
Breaching	<0.001 % 0.4 min	<0.001 % 0.1 min	<0.001 % 11.2 min	<0.001 % 1.8 min	<0.001 % 0.9 min	<0.001 % 0.6 min
Strong Swimming	5.1 % 5.9 h	1.2 % 1 h	4.1 % 31.3 h	12.1% 10.9 h	25.3 % 33.2 h	28.2 % 25.2
Slow Swimming	94.9 % 108.4385	98.8 % 88.4 h	95.9 % 731.5 h	87.8 % 78.6 h	74.7 % 97.8 h	71.8 % 64.3 h

Discussion

I present the first direct records of complete breaching events by basking sharks, showing that basking sharks can breach multiple times in surprisingly short succession, and that they do so both during the night and day. On average, sharks breached twice a day, swimming up from approximately twenty metres depth, and experienced g forces of up to 20 g at the peak of breaching, approximately four times those experienced by sprinting cheetahs (Wilson et al. 2013) and comparable to galloping horses (Burla et al. 2014). To perform such feat, sharks increased their rate of energy expenditure by some 30 to 50 times, suggesting breaching should have an important, but as yet unclear, function.

Relationship to previous work

Basking shark breaching events appear to have similarities to other marine ambush predators, such as oceanic whitetip sharks that ascend from 160 m deep at 4 $m.s^{-1}$ to catch prey (Papastamatiou et al. 2018a) and even to great white sharks that can breach at speeds of 5 $m.s^{-1}$ (Johnston et al. 2018), while smaller mako sharks have been found to breach as fast as 8.2 $m.s^{-1}$ derived from video data (Halsey & Iosilevskii 2020). While the basking sharks initiated their ascent to the surface at different depths, they consistently returned to the same depths as they started at, usually at a slower speed. A portion of a breach by a basking shark has been reported previously – Johnston et al. (2018) presented an accelerometry record of a breach by an 8-metre basking shark from 28 metres at 5.1 $m.s^{-1}$ off Malin Head, Ireland, but unfortunately no data were available following the single breach or during the descent following breaching.

How expensive is breaching?

In the present study, breaching was estimated to be more than 30 times more energetically demanding than routine swimming. Sharks expended similar amount of energy for both single and multiple breaches, with consecutive breaches also requiring a consistent amount of power. This is in line with the idea that any type of courtship display that is brief or performed infrequently has low energy cost, no matter how impressive the behaviour (Clark 2012). The cost of breaching is however six times lower those estimated in Johnston et al. (2018). This may be because sharks in the present study were smaller (5 and 6 m), breached at slower speeds, which gradually increased towards the surface (rather than the constant speed reported in Johnston et al. (2018)), and started breaching from a shallower depth (19 m compared with 28 m in Johnston et al. (2018)), or just because the single breach off Ireland was atypical. Resting metabolic rate (RMR) typically increases with mass (Clarke & Johnston 1999, Gillooly et al. 2001, Killen et al. 2010), with larger individuals being able to generate higher maximum levels of energy output (Biro & Stamp 2010). Since a positive correlation exists between RMR and sustained energy output such as daily energy expenditure (Biro & Stamp 2010), then larger sharks with greater RMR can invest more energy in costly behaviours such as courtship or aggressive defence of mates (Kotiaho et al. 1998, Hunt et al. 2004, Low 2005, Olsson et al. 2009, Clark 2009, Clark 2012). Future work may reveal more insight into the dynamics of breaching between sharks of different sizes and or/sexes. Despite the large cost of breaching, it typically lasts just two minutes from start to finish, constituting 0.34 % of time over a 24-hour period.

Similarly, sharks sustained comparable activity levels after multi-breaching events compared to single breaches, maintaining their speed and energy expenditure, suggesting that sharks did not require recovery periods from breaching. As ram ventilating species, basking sharks may need to maintain a minimum speed to optimise water flow across the gills to meet oxygen requirements (Jacoby et al. 2015). Equally, while feeding events could not be identified with the accelerometry data, sharks may have been actively foraging following highly demanding breaches to make up for energy spent. Sharks daily routine metabolism was estimated at 12.1 MJ.day^{-1} for shark 1, 20.8 MJ.day^{-1} for sharks 2 and 20.3 MJ.day^{-1} for shark 3, requiring 4.8 to over 24 hours of filter feeding per day to meet their estimated daily energy requirements, depending on prey concentration. Because VeDBA is capable of discerning greater resolution in movement, the estimated cost of breaching is five times larger than estimated using generalise equations, when using VeDBA-derived energetics, breaching was found to make up 5 times more of the sharks DEE, for example meaning that a basking shark would have to forage for 18 min to breach six times in one day (the maximum number of breaches performed in a day), compared with 3.5

minutes from generalised equations. These values should, however, be taken conservatively since (i) the prey densities used to estimate foraging times were not recorded *in situ* and may not be representative of the actual prey abundance since zooplankton vary both spatially and temporally throughout the water column and (ii) the energetic values were measured for movement-derived energy expenditure and do not include basal metabolic rate or thermic effect of activity (Gleiss et al. 2011). While predictive models have recently been established between dynamic body acceleration and oxygen consumption to predict field metabolic rates (Wright et al. 2014, Lear et al. 2017, Byrnes et al. 2020), these are skewed towards a smaller species, and require knowledge of the study species' temperature coefficient Q_{10} to be included in laboratory calibration to validate accuracy of the models (Lear et al. 2017). Allometric scaling of metabolic rate is therefore often used to estimate the energy requirement of larger species (Stemmens et al. 2013, Payne et al. 2015) where respirometry studies are logistically challenging. To date, the largest shark studied via respirometry, a 126 kg Greenland shark (*Somniosus* microcephalus) remains six to nine times smaller than the basking sharks in the present study (Ste-Marie et al. 2020). Estimates for large species typically rely on interspecific mass or temperature scaling derived from species orders of magnitude smaller or with different temperature sensitivities (Lowe et al. 2001, Lear et al. 2017, Luongo et al. 2018, Watanabe et al. 2019a, Ste-Marie et al. 2020), undoubtedly leading to inaccuracies in extrapolated estimates (Payne et al. 2015). Therefore both the VeDBA and mass-metabolic DEE estimates and associated foraging times of the basking sharks in the present study should be taken conservatively.

Diel patterns of breaching

Breaches by basking sharks in the present study occurred throughout the diel phase, with 40 % occurring at night. Breaching has not, to our knowledge, been described to take place during darkness before, although survey effort and detectability are low at night. In the Shetland Islands, 95 % of basking shark breaches were observed during daylight hours before 12pm (Hayes et al. 2018). Similarly for cetaceans, aerial behaviour were most frequently reported in the morning for spinner dolphins (De Carli et al. 2018) and in the afternoon for humpbacks (Félix 2004) and sperm whales (Waters & Whitehead 1990). Tagging technologies can therefore provide new insights into biologically important behaviours that would otherwise be missed when limited to visual observations during daylight hours, particularly for non-air breathing species.

The timing of breaching events varied between sharks, but since tags remained on two of the sharks for a short duration recording two and five breaches respectively, it is difficult to infer particular diel preferences in breaching behaviour. Nonetheless, all three sharks did breach at night, suggesting that breaching is unlikely to be a visual signal. While sharks are thought to perceive contrast, very little is known about elasmobranch motion vision (Hart & Collin 2015), particularly for deep diving species such as basking sharks. Furthermore, if/and/or breaching was a visual cue, it would require the receptors of the signal to observe the breach near the surface. Gore et al. (2018) and Hayes et al. (2018) found that the majority of breaches recorded were performed by solitary sharks compared to those observed in groups of more than two individuals at the surface. In the present study, the presence of conspecifics during breaching events was unknown, however sharks tended to initiate breaching around 20 m before returning to similar depth, suggesting that the number of sharks observed at the surface during breaching events is not a reliable indicator of the number of individuals receiving the signal. In humpback whales, breaching may represent a visual signal when carried out within the visual range of the receiver but primarily plays a central role in communication owing to the loud splash produced by breaching individuals (Dunlop et al. 2010).

Possible functions of breaches

In cetaceans, different aerial behaviours have been found to play different roles. Bottlenose dolphins select types of aerial behaviours to signal to close conspecifics without advertising intent to competitors (Lusseau 2006), while different leaps in spinner dolphins may increase foraging efficiency and social bonding or function as a signal to group members to switch to a more active state

(Pearson 2017). For humpback whales, the role of different surface behaviour may change depending on the social and environmental context (Kavanagh et al. 2017). The flapping of pectoral fins, peduncle and fluke were used more for close-range or within group communication, whereas breaching occurred more frequently in windier conditions and may have played a role in communication between distant groups of whales.

Unlike marine mammals and many teleosts, sharks lack structures such as swim bladders that convert acoustic pressure and sense sound using particle motion including acceleration, velocity and displacement (Gardiner et al. 2012, Nedelec et al. 2016). Therefore, sharks are less likely to rely on the auditory component of breaching compared to the induced hydrodynamic stimuli of particle motion. The lateral line of sharks is used to detect vibration of prey, predators and conspecifics through the water, and is most sensitive to low frequencies (Braun & Sand 2013) such as those produced by breaching. As the lateral line is a short-distance mechanosensory structure responding to close-range stimuli (Braun & Sand 2013, Hart & Collin 2015), sharks may use other sensory perceptions when breaching, detecting the electrical potential generated by conspecifics through electroreception (Kalmijn 1982). Although basking sharks exhibit some of the lowest ampullae of Lorenzini abundance of any shark species examined to date (Kajiura et al. 2010), they are able to detect the low electric signal of zooplankton prey so may be more attuned to sensing conspecifics emitting greater electrical intensity (Kempster & Collin 2011) since electroreception has been found to facilitate social behaviours (Hart & Collin 2015). Some elasmobranchs use electric sensors during courtship to localise and detect receptive and/or non-receptive conspecifics (Sisneros & Tricas 2002). Since two of the sharks were identified as female, breaching could possibly convey readiness to mate or rejection of undesirable males (Tomaru et al. 1995).

Sharks could also convey their size to other individuals, with larger sharks generating greater particle oscillation. In other species, breaching has been linked to display of strength, intimidation and male competition during courtship

(Félix 2004, Pacheco et al. 2013, and Maricato et al. 2017). Since the local prey densities recorded off the Isles of Coll and Tiree would require the sharks to forage for an unrealistic amount of time to meet their daily energetic demands, it is possible that aggregations may not primarily be linked to foraging, with sharks using the opportunity to locate and court mates. While it is worth considering that the depth at which zooplankton were sampled may not be representative of average prey densities, breaching events have been recorded in areas where basking sharks displayed courtship-like behaviours during aggregations such as close following, parallel and echelon swimming (Wilson 2004, Gore et al. 2019). Breaching may then possibly also be associated with courtship.

Although the aforementioned functions of breaching are largely speculative, it is most likely that this behaviour is triggered by a number of stimuli and plays a range of different roles such as parasite removal. Spinner dolphins have been found to use aerial behaviour to dislodge remoras (Fish et al. 2006, Weihs et al. 2007), while blacktip sharks and humpback whales breach to remove sharksuckers (Ritter & Brunnschweiler 2003) and barnacles (Félix et al. 2006) respectively. Gore et al. (2018) observed lampreys attached on a third of basking sharks in the same study site, but were found to still be attached following breaching events that may offer one explanation for multiple consecutive breaches.

Lateralisation

Variation was found in the side preference of rolling and direction of breaching behaviour, with a directional bias towards right-sided rolls for 2 of the 3 sharks. This is the first evidence to our knowledge of behavioural lateralisation in basking sharks, albeit at the individual level. Laterality, referring to the preference of using a specific limb or direction of movement that is consistent across events (Canning et al. 2011) has been reported in number of vertebrate taxa, most notably in marine mammals (Wells et al. 2006, Kot et al. 2014, Tyler-Julian et al. 2016, Platto et al. 2017). Lateralisation of aerial displays has been observed in cetaceans, with right-sided biases in lunging reported in a number of species (Canning et al. 2011, Kot et al. 2014, Karenina et al. 2016). Breaching on the other hand was not found to display laterality at the population-level in both humpback whales (Clapham et al. 1995) and orcas (Karenina et al. 2016). These differences in biases are thought to be attributed to sensory lateralisation. In contrast with breaching, lunging is associated with foraging behaviour, requiring attention to and sensory perception of prey stimulus (Karenina et al. 2016), supporting a number of studies highlighting right-sided preference in feeding behaviour in cetaceans (Clapham et al. 1995, Woodward & Winn 2006, Vaughn et al. 2010, Kot et al. 2014). However, Clapham et al. (1995) and Karenina et al. (2016) did not investigate individual-level differences in breaching lateralisation, which could have displayed similar variations as the basking sharks.

Lateralisation has also been reported in fish in relation to aggression (Ariyomo & Watt 2013), communication (Fine et al. 1996), foraging (Takeuchi & Hori 2008), anti-predatory behaviour (Bisazza et al. 2010), reducing the cost of transport (Payne et al. 2016, Royer et al. 2020) and in response to climate change (Vila Pouca et al. 2018), although most research has focused on teleost (Bisazza & Brown 2011). While gaps in knowledge regarding laterality in elasmobranchs prevail, recent studies by Byrnes et al. (2016a, 2016b) investigated the possible relationship between lateralisation and personality traits in Port Jackson sharks in wild and captive conditions. Despite not finding correlations between lateralisation and boldness that may have been attributed to small sample size or lack of biologically relevant stimuli, lateralisation was found on the individual level. Females displayed greater lateralisation which may be associated with the ability to process multiple stimuli during mating. Another possible explanation for the variation observed in both rolling side preferences and pitch direction of breaches (forward or backwards) in our study could be linked to differences in the function of varying breaches. A significant relationship was found between the angle of ascent and the direction of breaching, with sharks more likely to breach backwards when swimming more vertically towards the surface.

The potential effects of the tag attachment on the sharks' behaviour must also be considered. External tags have been reported to alter behaviour and decrease swimming capacities of several marine vertebrates (Hoolihan et al. 2011, Walker et al. 2012), with tail slapping, rapid swimming and breaching recorded in cetaceans following suction-cup attachment (Hanson & Baird 1998, Hooker et al. 2001; Blomqvist and Amundin 2004). However the degree to which they are affecting individuals are highly context and species dependent (Gleiss et al. 2009, Jepsen et al. 2015, Omeyer et al. 2019). While not all tag-induced behavioural changes have a fitness consequence (Walker et al. 2012), due to the considerable energetic cost associated with breaching, the potential influence of the tags on basking shark breaching behaviour should not be overlooked. In the present study, although the sharks were found to breach predominantly on their right-hand side, tags were deployed on the left side of the base of the caudal fin, suggesting that the sharks were not purposefully landing on the right to generate the force to remove the tag.

Further work is required to investigate behavioural lateralisation in elasmobranchs in the wild at both the individual and population level as well as sex biased variation (Finger et al. 2016, Byrnes et al. 2017b). Accelerometry is an invaluable tool to investigate variation in behaviours that would otherwise be difficult to observe in non-air breathing species. The use of g-spheres can provide not only compelling representation of accelerometry output which may not be obvious in two-dimensional plots, but also highlight intraspecific behavioural differences or similarities in behaviour types between species (Wilson et al. 2016). For example, future research investigating whether white shark exhibit similar lateralisation trends in breaching, and possible links with personality (Jacoby et al. 2014, Towner et al. 2016). Future work looking into the use of animal-borne acoustic proximity receiver that record interaction between sharks (Guttridge et al. 2010) in combination with accelerometry could provide new insight into not only the social networks of basking sharks at aggregation but also whether sharks may breach when in proximity of conspecifics. While the acceleration signature of breaching is unique, further validation of rare or poorly observed behaviours need ground-truthing through video footage to provide a more complete time-activity budget, highlight sexual differences as well as provide behavioural context to particular observations.

While the current study described breaching behaviour and highlighted possible evidence of lateralisation, these results must be interpreted with caution. Estimates derived from accelerometry data alone are unlikely to be sufficiently accurate to describe changes in animal posture owing to the difficulties in separating the gravity component of acceleration (the static acceleration used to measure pitch and roll) and dynamic acceleration (Noda et al. 2014). Furthermore, conventional methods for deriving static acceleration use frequency-based filtering method (Sato et al. 2003) or running mean smoothing windows (Wilson et al. 2006, Shepard et al. 2008, the current study) which tend to be applied to all the accelerometry data, resulting in over- or underestimated changes in posture (Noda et al. 2012). This becomes particularly apparent during unsteady, accelerated movement such as feeding events or fast-start behaviour, where the errors in estimating true posture become increasingly large (Noda et al. 2012, Brugarolas et al. 2013, Noda et al. 2014). Changes in posture and body orientation such as pitch and rolling behaviour displayed by basking sharks during breaching are unlikely to faithfully describe the true attitude of the sharks. As the animals surge forward, the forward acceleration increases, resembling a change in static acceleration. Such limitations may be overcome by combining accelerometers with additional movement sensors such as gyroscopes. These inertia sensors accurately reconstruct gravity-based acceleration and 3-dimensional movement at high temporal resolution, providing great potential for describing the kinematics of short-lived, high intensity behaviours like breaching (Noda et al. 2014, Kawabata et al. 2014, Jeantet et al. 2020). Future work integrating gyroscopes could derive additional characteristics such as angular velocity and movement direction to further describe fine-scale behaviour.

Location of breaches

All breaches for which geographical positioning were obtained occurred in August off the coast of Coll and Tiree, within the boundaries of the proposed Marine Protected Area. If breaching is related to courtship display, the present study provides further evidence of the importance of the Sea of Hebrides for basking sharks and echoes previous findings of high area use from satellite tracking (Doherty et al. 2017b), public sighting data (Southall et al. 2005, Witt et al. 2012), and boat survey (Southall et al. 2005, Speedie et al. 2009, Gore et al. 2016, Gore et al. 2019). Protecting areas supporting key life stages is particularly important for the recovery of endangered migratory species where protection throughout their ecological range is impossible (Hooker et al. 2011, Schofield et al. 2013, Magris et al. 2014) and little is known about their reproductive cycles (Matthews 1950, Sims et al. 2000). MPAs are likely to be more effective, maximise protection and serve their purpose if there is underlining knowledge of spatial use and encompass several important behaviours (Speed et al. 2010, Hooker et al. 2011, Doherty et al. 2017b). The proposed MPA has the potential to provide protection not only for suitable habitat for key foraging site but also other life-history events.

Chapter 3: No Place Like Home? Investigating the effects of translocation on juvenile green turtles (*Chelonia mydas*) using multi-sensor biologging tags

Abstract

Translocation, the intentional human-mediated movement of organisms from one area to another, is occasionally used for endangered sea turtles as a conservation tool to mitigate against anthropogenic threat. However, little is understood on the effects of translocation on turtles. Most studies to date have focused on adult nesting females reporting strong site fidelity regardless of distance or time in captivity. Comparatively, knowledge about juvenile turtles' ability to rehome and the behavioural and energetic costs associated with translocation is lacking. In the present study, juvenile green turtles (*Chelonia mydas*) were tracked with GPS and multi-sensor biologging tags to investigate behavioural changes and movement-related energy expenditure following a 4 km translocation from their feeding grounds in the Bahamas. Turtles rehomed in as little as 15 hours within hundreds of meters of their capture location, displaying directed swimming after a circuitous orientation phase. Compared to resident turtles tracked at their foraging site, translocated turtles allocated twice as much time to energetically demanding behaviours, reducing periods of resting and foraging and did not display diurnal patterns behaviour. Understanding the effects of translocation on a species is crucial for informing management practices. The excellent homing abilities of turtles and associated energetic costs expected to increase with displacement distance undermine the efforts to mitigate threats by translocating turtles. Translocation may therefore only offer a short-term conservation solution.

Introduction

Globally, marine ecosystems are at risk from increasing anthropogenic impact, with the oceans affected by multiple stressors such as climate change, overfishing, pollution and habitat degradation (Halpern et al. 2008, Halpern et al. 2015). To tackle these threats, mitigation strategies have included designations of protected areas (Selig et al. 2014), modification of fishing gear (Senko et al. 2014), spatio-temporal restrictions such as time-area closures (Hoos et al. 2019) or limiting dredging events to environmental windows once species have migrated (Dickerson et al. 2007). By law, governmental departments and agencies are required to take reasonable precautions to ensure the activities they fund or carry out do not jeopardise the existence of, or destroy critical habitats of threatened and endangered species (Endangered Species Act of 1973). Therefore, when no other mitigation solutions are possible, necessary measures are required to minimise injury and mortality to species during operations, such as translocation. Translocation, involving the intentional human-mediated movement of a living organism from one area to release at another (IUCN 2013), has been used as a conservation method to assist with repopulating endangered species (Norris et al. 2017), to increase genetic diversity (Johnson et al. 2010), restore ecological integrity (Hayward et al. 2007), remove nuisance species (Robinson et al. 2008, Fernando et al. 2012, Devan-Song et al. 2016), and to protect populations from degraded habitats (Barham et al. 2006). However, the effectiveness of this method has been variable (Griffith et al. 1989, Batson et al. 2015, Wolfe et al. 2018), and appears to have been more successful in terrestrial environments (Lepeigneul et al. 2014) than the marine realm (Hindell 1997, Read et al. 2007, Oro et al 2011), where little to no barriers hinder animal movement (Olden et al. 2011, Knox & Monk 2014). For this reason, over two thirds of the species translocated in the marine environment have been sessile (e.g. coral, Boch et al. 2019, eelgrass, Cabaço et al. 2010), and less than a quarter of translocation projects involve species at risk of extinction (vertebrates, invertebrates and plants (Swan et al. 2016)).

Since the 1980s, all seven species of sea turtles have been listed by the IUCN Red List as threatened with extinction, following centuries of overexploitation (Jackson et al. 2001, McClenachan et al. 2006), fisheries bycatch (Wallace et al. 2010), pollution (Kamrowski et al. 2012, Nelms & Duncan 2015), habitat degradation (Mitchelmore & Collier 2017, Whittock et al. 2017) and climate change (Hawkes et al. 2009). Translocation has been used as a potential conservation tool following injury (fisheries interaction, vessel strike), natural and anthropogenic disasters (extreme weather, oil spills) and habitat loss (dredging events) (Innis et al. 2019, Barham et al. 2006, Bargo et al. 2005, Dickerson et al. 2007). Since 1992, turtles have been translocated away from hopper dredging sites in the United States as a mitigation method recommended by the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries, to minimise risk of injury or bycatch during dredging operations, particularly in areas of high sea turtle concentration (Dickerson et al. 2007). However, most translocation studies have been experimental and focused on nesting adult females because they are more tractable to catch as they move slowly on land (Luschi et al. 1996, Hays et al. 2001, Akesson et al. 2003, Girard et al. 2006, Mencacci et al. 2010, Benhamou et al. 2011). Translocation may be a problem though, as turtles have been found to return to original capture sites relatively quickly (e.g. 4.5 days following translocation of 150 km, Enstipp et al. 2016), even after several decades (Mestre et al. 2014) and thus may still be exposed to the same threats (Joyce 1982, Standora et al. 1994). Adult turtles are highly mobile and exhibit strong site fidelity (Broderick et al. 2007, Tucker 2010, Christiansen et al. 2017) and are therefore likely to return nesting beaches (Benhamou et al. 2011), or foraging grounds (Shimada et al. 2016a) following translocation.

By comparison, the extent to which juvenile turtles can rehome following translocation is far more poorly understood (Avens et al. 2003, Avens & Lohmann 2004) due to tracking tags being too large for smaller turtles (Shillinger et al. 2012, Mansfield et al. 2012), despite them being equally threatened by anthropogenic activities (Santos et al. 2015). Following a pelagic life stage, juvenile turtles undergo an ontogenetic habitat shift (Arthur et al. 2008), to neritic developmental habitats that should have greater resource abundance and quality (Christiansen et al. 2017), and refuge from predators (Heithaus et al. 2008, Hart et al. 2010). Varying by species, juvenile turtles may maintain strong site fidelity to a home range, defined as an undefended space occupied by an organism during its daily activities (Powell 2000). In addition, juvenile sea turtles occupying waters in temperate latitudes often display seasonal migration, overwintering in warmer waters (Fukuoka et al. 2015, Williard et al. 2017), indicating that homing behaviour may not be restricted to adults. Knowledge of the location of reliable foraging and resting sites, as well as refuge from predators, should play an important role in survival during juveniles turtles' vulnerable life stage, and contribute towards turtles' biological and reproductive fitness (Shimada et al. 2016c).

Previous research in a range of vertebrates has highlighted that translocation can decrease survival (Villaseñor et al. 2013) and reproduction (Devan-Song et al. 2016), and increase stress (Dickens et al. 2010, Heiken et al. 2016) or bring about unexpected behavioural responses (Heidinger et al. 2009). Little is known in general about the effects of translocation on turtles, but at least 13 studies to date have suggested they are likely to return home following translocation (Table S3.1). Enstipp et al. (2016) suggested that a single adult female green turtle (*Chelonia mydas*) released 150 km away from its nesting site, and tracked back to its foraging ground, likely had to maintain three times the standard metabolic rate of resting at their foraging site before translocation (over 2300 additional kJ expended per day), swimming continuously over four days without resting. Life stage and size likely play an important role in the effectiveness of translocation (Letty et al. 2007), and translocation is likely to have greater costs in juvenile turtles since more energy is budgeted towards somatic growth and reproductive development (Okuyama et al. 2013, Patricio et al. 2014). While turtles may benefit in the short-term from removal from danger, the energetic impact of translocation on juvenile turtles needs to be measured.

The advances and miniaturisation of animal tracking technologies over the past 20 years have provided invaluable insight into movement (Hochscheid 2014, Christiansen et al. 2016, Mansfield et al. 2014, Mansfield et al. 2017), physiology (Okuyama et al. 2014), ecology (Lamont & Iverson et al 2018, Fukuoka et al. 2019) and behaviour (Okuyama et al. 2013, Jeantet et al. 2018) of juvenile turtles. High resolution, animal-borne, multi-channel tags offer exceptionally fine scale (i.e. sub-second) recording of environmental and biological parameters such as temperature, depth, speed, and acceleration (Wilson et al. 2008, Walker et al. 2015). Dynamic Body Acceleration, which is derived from measurements of raw body acceleration, can be used to estimate energy expenditure (Okuyama et al. 2014, Enstipp et al. 2016) and to discriminate between different types of activities (Jeantet et al. 2018), such as feeding (Okuyama et al. 2009) or social interactions (Jeantet et al. 2018). Populations of juvenile green sea turtles (*Chelonia mydas*) in southern Eleuthera, The Bahamas, have been subject to long-term monitoring by mark-recapture since 2012, with individual turtles being caught up to 17 times over a period of years, indicating high site fidelity to their resident tidal creek. A recent study by Gary (2017) conducted in one of the creeks of Eleuthera documented the smallest home ranges of juvenile green turtles reported to date (mean 0.64 km^2 ± 0.24 s.d.), making it an ideal site to investigate the site fidelity and homing behaviour of juvenile green turtles.

The present study used accelerometry combined with temperature depth measurements and GPS tracking to compare behaviour and energetic expenditure between control and translocated juvenile green turtles in The Bahamas, to estimate the additional energy expenditure incurred by juvenile turtles following translocation. Specifically, the study investigated:

- How quickly do turtles rehome and do they return via the shortest routes?
- What is the estimated energetic cost of homing?
- How do swimming and navigational behaviours differ?
- What is the duration required for behaviours and energy expenditure to regain similar patterns as foraging turtles?

Methods

The study was conducted in two adjacent creeks located four kilometres apart in southern Eleuthera, The Bahamas: Poison Creek (24°48'53.9"N, 76°11'50.9"W) and Starved Creek (24°48'54.4"N, 76°11'09.9"). The creeks are low lying ecosystems formed from scouring of calcareous rock substrate by tidal water and result in small bays or passages with limited freshwater input (Bjorndal et al. 2000). Both creeks are inhabited year-round by juvenile green turtles and were selected based on previous long-term population monitoring conducted since

2012.

Habitat characterisation

In order to characterise the habitats through which juvenile green turtles moved, benthic cover was characterised in both creeks between March and April 2017. Depth and percentage cover of macroalgae, seagrass species *Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii* and sediment type was recorded within a 50 x 50 cm quadrat across a 100 x 100 m grid generated in ArcGIS covering both creeks and the separating stretch of coastline. Areas of high and low density of macroalgae and *Thalassia testudinum* were identified using Getis-Ord Gi* statics in ArcGIS to analyse spatial variation in resource distribution between both creeks. The hotspot analysis finds clusters of areas with significantly high or low coverage of macroalgae *or Thalassia testudinum* compared with the entire study site. To account for spatial autocorrelation and determine the distance parameters in the density analysis, a Global Moran's I test was used (Scott & Janikas 2010). Percentage cover of both macroalgae and *Thalassia testudinum* were interpolated to produce a smoothed surface through ordinary kriging using the ArcGIS Geostatistical Analysist Toolbox. Depth data were corrected for low tide and interpolated to produce a bathymetry map of the study area.

Turtle capture and logger deployment

All turtle research was approved by the Bahamian Department of Marine resources under permits MAMR/FIS/17 and MAMR/FIS/34A and followed the Cape Eleuthera Institute guidelines. A total of sixteen juvenile green sea turtles (*Chelonia mydas*), were caught between 30 March and 17 June 2017. Once located, turtles were approached quietly and captured in within 3 min to reduce disturbance and associated handling stress. Capture location was recorded for each turtle and newly captured turtles were tagged with metal Inconel flipper tags. For each individual, morphometric measurements were taken, including body mass (mean: 15.2 kg ± 5.6 kg, range: 7 to 22.5 kg), using spring balance accurate to the closest 0.5 kg, straight carapace length (SCL, mean: 469 ± 59 mm range: 384 to 547 mm) with Vernier callipers to the closest 0.1 cm, and curved carapace length (CCL, mean: 498 ± 64 mm range: 401 to 580 mm) with a tape measure (Table S3.2). Four turtles were caught in Poison Creek and 12 were caught in Starved Creek, of which six (n = 3 Poison Creek, n = 3 Starved Creek) were not translocated, and instead tracked from their initial capture location, and considered ‘control’ treatments. Two of these turtles (turtle1 and turtle 2) were subsequently recaptured and used as controls again two months later (and renamed turtle 12 and turtle 13 respectively), before being translocated to Poison Creek to track their homing behaviour (and renamed turtle 14 and turtle 15). An additional ten turtles were tracked after being translocated 4 km to the adjacent creek (Table 3.1). Due to a smaller population of turtles in Poison Creek, only one of the translocated turtles was tracked from Poison Creek while the other nine were tracked from Starved Creek. Thus, in total there were 20 turtle tracks recorded, from 16 unique individuals, of which two were tracked three times each (Fig. 3.1).

Table 3.1: Table summarising the technology deployed (accelerometers and GPS tags) and the number of tags retrieved from juvenile green turtles translocated or used as controls by release site (Starved Creek or Poison Creek).

Capture location	**Starved Creek**		**Poison Creek**		**Total**
Treatment	**Control**	**Translocated**	**Control**	**Translocated**	
Nb. turtles	5	11	3	1	20
Accelerometer tagged	5	7	3	1	16
Functioning accelerometers retrieved	3	4	3	0	10
GPS tagged	5	11	3	1	20
Functioning GPSs retrieved	3	9	2	1	15
Functioning combo set	1	3	2	0	6

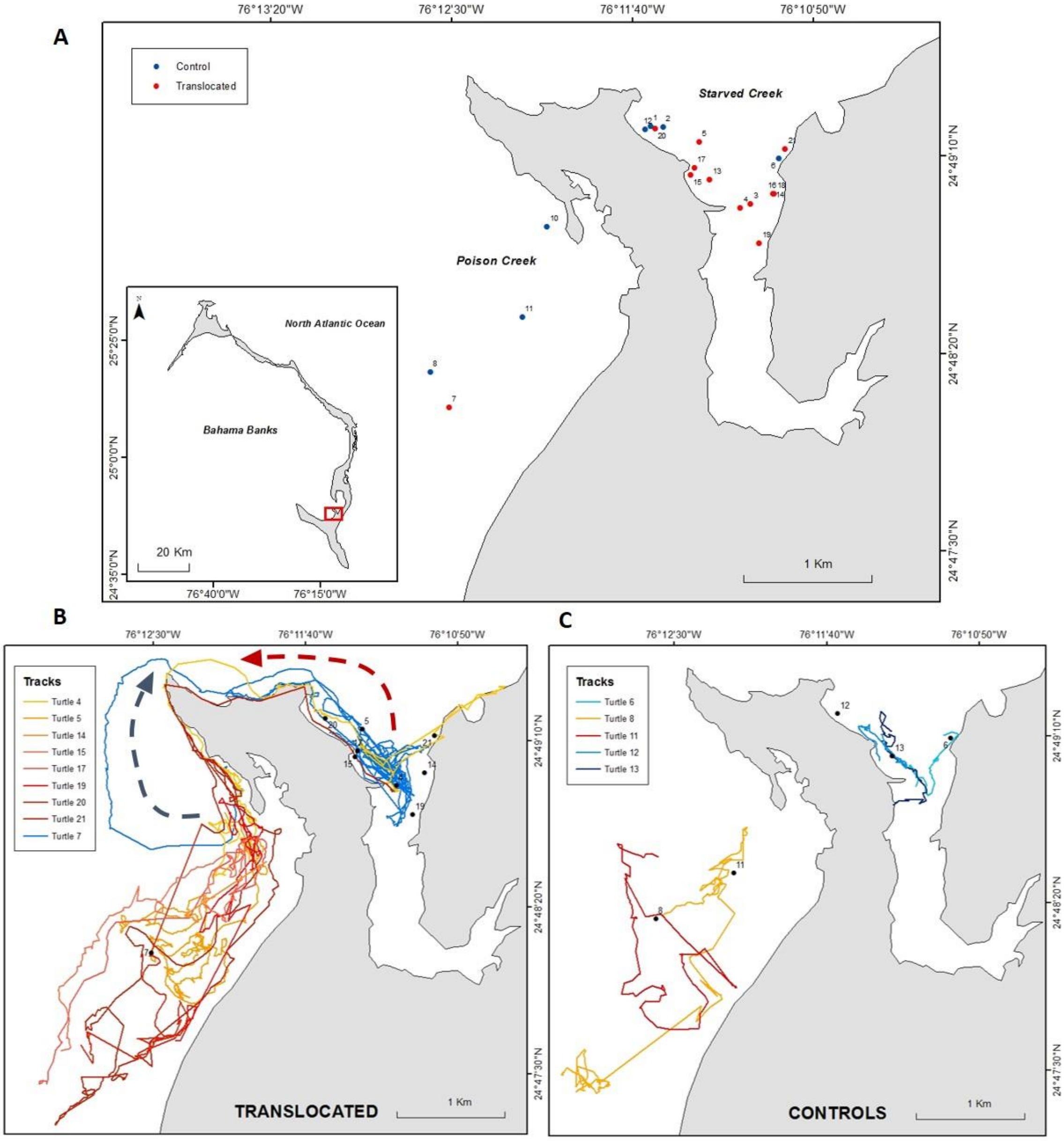


Figure 3.1: Maps showing the study sites, Poison and Starved Creeks, in relation to Eleuthera Island in The Bahamas (inset in **A**). (**A**) Capture locations of all 20 turtles in relation to their home creek. (**B**) Tracks of nine translocated turtles tagged with GPS trackers, with turtles translocated to Poison Creek from Starved Creek (direction of the red arrow) represented in varying shades of red (n = 8), and the single turtle translocated to Starved Creek from Poison Creek (direction of the blue arrow), in blue. Complete homing tracks of three turtles (Turtle 4: yellow, Turtle 7: blue and Turtle 21: dark red) visible around the headland separating both creeks. (**C**) Tracks of five control turtles in their home creeks.

Sixteen of the 20 tracks were recorded using OpenTags dataloggers (OpenTags motion dataloggers, Loggerhead Instrument, FL, USA, 10.5 x 4.7 x 2.2 cm, 110g in air, https://www.loggerhead.com), which recorded accelerometry and magnetometry at 8 Hz on three orthogonal planes corresponding to the dorso-ventral, anterior-posterior and lateral axes. OpenTags also recorded depth (to 0.5 m resolution) and temperature (to 0.5 ˚C resolution) at 1 Hz (Shiomi et al 2010, Hart et al. 2016, Enstipp et al 2016). Loggers were fitted on the turtles' second vertebral scute, which was sanded and then sterilised with 70 % alcohol solution to ensure a clean surface for tag adhesion. The tag was attached in an anterior-posterior direction using two-part epoxy which was left to dry for an hour and a half. Turtles were shaded and cooled with water on the boat throughout the attachment process to minimise stress. Turtle movements were tracked using Trackimo 3G GPS Trackers (Trackimo, NY, USA, 4.5 x 4 x 1.8 cm, 40 g in air https://trackimo.com), which allowed live tracking of the turtles every minute via the 3G network. GPS units were waterproofed using Plasti Dip (Performix Brand, Blaine, MN, USA) and housed in a custom-designed buoyant casing made from two GoPro Floaty packs, and a hydrodynamic nose from reinforced polystyrene, sealed with adhesive band and electrical tape. The GPS antenna must be kept at the sea surface to collect location data, thus the final package, which measured 5x4x10 cm, was attached to the turtle via a 4-metre tether line of (20 lb) test monofilament fishing line tied to a small (5 mm diameter) sterilised drill hole on the trailing edge of the left and right 4th marginal scute from the tail end (see also Gary 2017). The tag package floated at the sea surface behind the turtle with the line strength chosen so as to break off in case of ensnarement and reduce the risk of entanglement. The attachment procedure took less than five minutes. Turtles were additionally marked with short coloured flagging tape, attached to the flipper tags, for easier identification from a boat following release. To reduce the possible use of visual cues for rehoming as well as visual disturbance, turtles' eyes were covered during translocation. Following release, turtles were monitored from a small boat until they were no longer visible. The position of tagged turtles was usually transmitted every 30 to 60 minutes throughout the tracking period via the local GSM network, but if no movement was recorded for an hour, or the tag moved at unusual speed or trajectory (which likely indicated that the tag had been shed and was drifting in a current), the last known location of the turtle/tag was visited as soon as possible after sunrise. Turtles were recaptured and tags were retrieved once turtles had successfully rehomed, or if the transmitted battery voltage indicated the tag had died. In the case where translocated turtles did not home before the GPS battery was exhausted, we attempted to find and recapture the turtles as soon after sunrise and over subsequent days, weather permitting to remove the tags and release turtles back to their capture location.

Track analysis

Tracking metrics such as distance, time, speed and angle between locations were calculated using custom script in R. Tracking data were apportioned into day and night using sunrise and sunset times for the study site (https://www.wunderground.com/weather/bs/rock-sound). Since turtles were translocated to the adjacent creeks around a headland, homing behaviour was segmented into three geographical areas (hereafter referred to as ‘homing phases’), (i) release site to headland, (ii) headland and (iii) headland to capture location, where the end of each segment represented the goal direction for homing. Homing behaviour was evaluated using two metrics: (i) orientation efficiency, estimating the swimming direction in relation to the homeward direction and (ii) angular dispersion, measuring how direct the route taken was. The Orientation Efficiency *O* of the turtles’ homing path was estimated by measuring the cosines of the angular differences between the turtle’s heading (orientation angle θ, calculated using “bearing” function in R) and the goal direction ϒ for each s step of the with orientation θ, with the starting coordinates (x0, y0) and ending at locations (xs, ys) as described in Girard et al. (2006):

$$O = \sum_{i=1}^{s} \cos(\theta_i - \Upsilon_{i-1})/s$$

For turtles that were tracked back to the release site, the Orientation Efficiency *O* was estimated for each homing phase, and averaged over all three sections for the overall total Orientation Efficiency. An additional Rayleigh test for uniformity was calculated to assess statistical significance of turtles’ heading in relation to the final location for each homing phase. The angular dispersion *r* is a modification of a straightness index, describing tortuosity of the turtles' track, where 0 describes a track that is comprised of random angles (and may never reach a goal), and 1 indicates a ballistic, straight line. Angular dispersion was calculated for each turtle following (Estevez & Christman 2006) as the turning angle θ (in radians) ~ at 1 min time sampling frequency:

$x_k = \frac{1}{k \sum_{i-1}^{1} \cos(\theta_i)}$ and $y_k = \frac{1}{k \sum_{i-1}^{1} \sin(\theta_i)}$

And

$r = \sqrt{x_k^2 + y_k^2}$

Angular dispersion was calculated for (i) the entire track length and (ii) each of the three homing phases for the translocated turtles. To investigate site fidelity of the translocated turtles, a home range was estimated for 12 turtles that were captured three or more times as part of the Cape Eleuthera Institute's long-term monitoring programme. Minimum Convex Polygons (MCP) were calculated in ArcGIS for each turtle using capture locations from 2014-2019.

Accelerometry and behavioural analysis

Accelerometry data were first calibrated to take into account small differences in the placement of the tags on each turtle. First, data were calibrated to one unit of gravity (9.8 m.s^{-1}) by rotating the tags through known angles in all three spatial planes using the 'tagtools' package in R (https://github.com/stacyderuiter/TagTools). Then, the turtles' body pitch and roll were extracted from the raw accelerometry data, with positive and negative angles indicative of an upward and downward pointing direction, respectively. Temperature and depth data were linearly interpolated to match the accelerometry and magnetometry 8 Hz sampling frequency. Temperature and depth data were omitted for four turtles due to sensor malfunction. Accelerometry data comprises two components, (i) low-frequency static acceleration and (ii) high-frequency dynamic acceleration. The static component relates to the inclination of the tag with respect to the earth's gravitational field (which is analogous to the turtle's body posture), and was obtained by individually smoothing each of the three acceleration channels with a running mean of three seconds (Wilson et al. 2006, Shepard et al. 2008). These smoothed values were then subtracted from the raw data for the corresponding axis, leaving three-dimensional dynamic acceleration, relating to the changes in velocity owing to the patterns of the animal’s movement (Gleiss et al. 2011). The three-dimensional dynamic acceleration was then used to make a summary metric describing effort, VeDBA (Vectorial Body Dynamic Acceleration), calculated as follows:

$$VeDBA = \sqrt{(A_x^2 + A_y^2 + A_z^2)}$$

VeDBA is considered a proxy for the rate of energy expenditure, when tag orientation varies over time (Qasem et al. 2012, Wright et al. 2014). A spectrogram of the lateral acceleration (x-axis) was generated in Ethographer ver. 2.04 (Sakamoto et al. 2009) in Igor Pro (Igor Pro 8, WaveMetrics Inc., Lake Oswego, USA), by continuous wavelet transformation using the Marlet wavelet function, with a minimum cycle of 0.125 seconds and maximum cycle of 1 second (Sakamoto et al. 2009). Dominant Stroke Frequency (DSF) and Flipper Beat Amplitude (FBA) was calculated at a frequency of 1 Hz using the Peak Tracer function. The resulting values were linearly interpolated to provide a value at 8 Hz. The three accelerometry metrics (VeDBA, DSF and FBA) were compared between day and night, using sunrise and sunset times for the study site to partition the data (https://www.wunderground.com/weather/bs/rock-sound). The number of surfacing events were extracted from the depth data of six turtles using the findpeak function in R. The surface threshold was characterised at 0.20 m, and dive duration was calculated as the time between surfacing events, with a minimum threshold of 20 s between surfacing events. Of the 10 retrieved multi-channel tags, seven experienced erroneous pressure readings at low tide due to the extreme shallow nature of the creeks, so depth data was excluded from the analysis. Since most turtles that rehomed (n=5) did so within two days, the diel differences and daily mean swimming metrics (VeDBA, including daily summed VeDBA, DSF, FBA, surfacing events and dive duration) were compared for the first 0 to 24 h and 25 to 48 hours following release to test how translocation may affect behaviour and energy expenditure using paired sampled t-tests, or Wilcoxon signed rank tests when transformation was not possible. Summed VeDBA was calculated as the total VeDBA over a 24 hour period, and was used as a proxy for the daily amount of movement related energy expended by the turtles between the first two days following release.

Activity Seascape

Activity seascapes were described for six turtles that had functioning sets of both accelerometry and tracking data, where the summed VeDBA over a one-minute window was calculated for each GPS location, and then averaged for all locations within each 100 m grid in ArcGIS (Papastamatiou et al. 2018b). The minimum amount of time spent by turtles in each 100 m grid was also estimated by the time elapsed between consecutive GPS locations within the cell, and expressed as a proportion of the entire tracking duration. Each turtles' activity seascape was visualised by plotting in a four-dimensional scatter plot using the function "scatter3D" using the R packages "knitr" and "plot3D".

Time-activity budget analysis

To determine the time-activity budget of juvenile green turtles, accelerometry data were separated in to four categories: (i) strong swimming, (ii) slower swimming, (iii) resting, and (iv) other behaviours which could not be validated through visual inspection of the raw lateral acceleration (x-axis) and using k-means clustering based on flipper beat frequency and amplitude in Ethographer. The mean signal amplitude for each behaviour was 0.06 Hz for strong swimming, 0.03 Hz for slower swimming, 0.01 Hz for resting, and 0.04 Hz for other behaviours. Behavioural differences between translocated and control turtles were compared for the first 48 hours following release using a paired t-test or Wilcoxon signed rank test when transformation was not possible.

Results

Of the 16 OpenTags deployed, 10 were recovered from the turtles providing access to a cumulative 75.2 days of data (mean 7.5 ± 7.4 days), ranging from 0.3

to 18.4 days. Turtle 18 was excluded from the analysis due to tag failure, which recorded only six hours of data. Fifteen of the 20 GPS tags provided positional data for an average deployment of 17.5 hours ± 20.4 (range: 0.5 to 85.8 hours).

Homing movements

Of the 12 translocated turtles, seven (58 %) returned to their home creek and were recaptured within 683 m of their original capture location (± 629 s.d., range 99 to 1828 m, Fig. 3.1). Homing duration varied between individuals (Table 3.2), ranging from under 15 hours for turtle 4, to at least 8 months for turtle 17. One turtle (turtle 5) was still in its translocated creek two days following release, after which it was recaptured and moved back to the vicinity of its capture location as the GPS battery was exhausted. Turtle 17 was recaptured as part of the long-term monitoring programme in its translocated creek in September 2017 three months after translocation, but was then recaptured in February 2018 in the vicinity of its original capture location in Starved Creek and was sighted nearby at the end of March 2018. Turtle 17 therefore remained in its translocation site for at least 3 months, and as much as 8 months, before returning back to its initial capture location. The remaining four translocated turtles have not been recaptured since translocation in either their home or translocated creek. Since surveys of the creeks occur infrequently, it may be that turtles have remained in their translocated location, or have rehomed but have not yet been recaptured.

Turtles may also have moved along the coastline in the opposite direction and settled elsewhere, or may also have been predated by tiger sharks that are present in the area. Starved Creek had significantly greater macroalgae density compared to Poison creek, (Fig. 3.2B), and juvenile green turtles have been anecdotally observed to feed on macroalgae, although it is likely not a main component of their diet (Gary, unpublished data). Percentage cover of *Thalassia testudinum* was similar between both creeks, with high densities concentrated in small patches at the entrance of both Starved and Poison Creeks, as well as the tip of headland separating both creeks (Fig. 3.2A), which suggests that creeks were similar in resource availability. The distance between original turtle capture and later recapture sites was similar for control turtles (mean 756 m ± 493 s.d., range 153 to 1707 m) and translocated turtles recaptured following tracking (mean 683 m ± 629 s.d., range 99 to 1828 m; one-tailed t-test, t=0.24, df=9.26, p=0.82). Turtle 5 was recaptured 3.5 km away from the original capture site two days after release, but was excluded from analyses as it did not rehome. Turtles were tracked for an average distance of 9.73 km (± 8.72 s.d., range 1.49 to 33.22 km), with control turtles being tracked for 13.90 km (± 10.12 s.d., range 4.25 to 24.71 km) and translocated turtles 17.31 km (± 18.35 s.d., range 4.13 to 63.32, Table 3.1).

Table 3.2: Summary of tag deployment and homing behaviour by turtle and treatment. NAs refer to either GPS or accelerometer tags which failed and no data was retrievable. Turtle track length is divided into the total travelled distance (*D*) calculated as the sum of the straight line distances between GPS locations, while the beeline refers to the straightest line between the release location and the last GPS point. Homing behaviour metrics include the Straightness Index (S.I), Angular dispersion (*r*), and the Orientation Efficiency (*O*).

Turtle	Treatment	Homed	Tag duration		Track Length (km)	*r*	*O*
			Accel. (days)	GPS (h)			
T1	Control	-	16.75	NA	-	-	-
T2	Control	-	1.04	NA	-	-	-
T3	Translocated	?	?	NA	-	-	-
T4	Translocated	Yes	9.23	18.44	10.7	0.04	-0.65
T5	Translocated	No	1.83	21.82	15.8	0.01	-2.23
T6	Control	-	2.11	11.97	1.9	0.54	1.83
T7	Translocated	Yes	NA	63.32	33.2	0.01	-0.91
T8	Control	-	2.87	24.72	11.6	0.1	0.8
T10	Control	-	4.91	NA	-	-	-
T11	Control	-	17.84	24.17	7.1	0.58	1.47
T12	Control	-	NA	4.25	2.3	0.09	-2.63
T13	Control	-	?	4.38	2.5	0.13	-0.17
T14	Translocated	Yes	NA	5.45	1.5	0.14	-3.96
T15	Translocated	?	?	4.13	6.4	0.11	-0.69
T16	Translocated	?	No tag	NA	-	-	-
T17	Translocated	Yes	No tag	6.03	5.8	0.05	-1.25
T18	Translocated	Yes	0.23	NA	-	-	-
T19	Translocated	Yes	18.4	10.67	7.2	0.04	-3.18
T20	Translocated	?	No tag	8.92	7.3	0.04	0.24
T21	Translocated	Yes	No tag	16.97	19.2	0.02	0.4

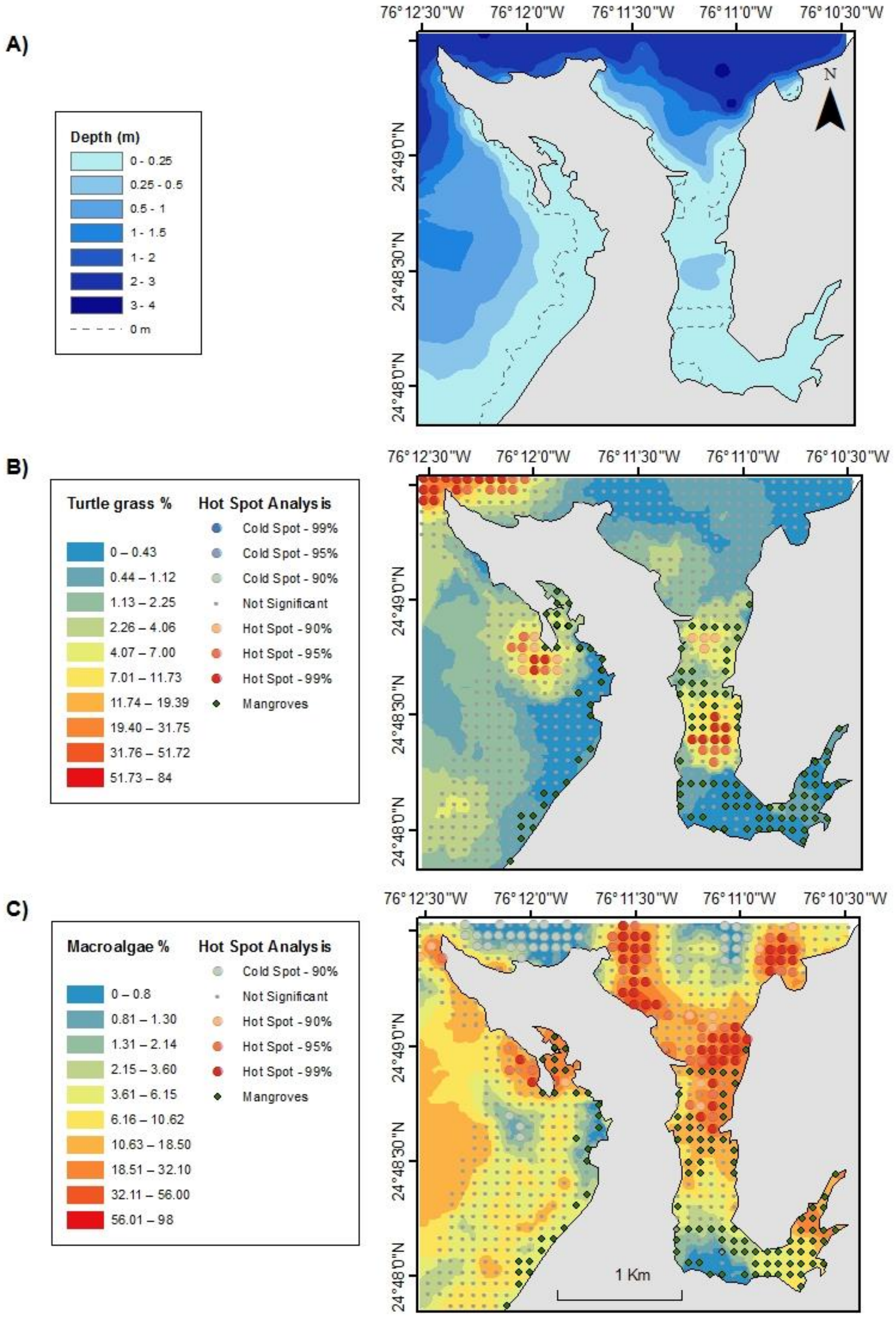


Figure 3.2: Habitat map of the study area. **(A)** Bathymetry at low tide, **(B)** percentage cover of turtle grass (*Thalassia testudinum*) and **(C)** macroalgae. Areas with significantly higher densities than surroundings (hot spots) are represented by circles in shades of red increasing with confidence interval while areas with significantly lower densities than surroundings are represented with circles of colder shades.

Directionality and Angular Dispersion

Translocated turtles had lower angular dispersion (significantly more tortuous tracks) than control turtles (Welch t-test with log transformation t=3.32, df=8.40, p<0.01, translocated: mean 0.05 ± 0.04 s.d., range 0.01 to 0.14; controls: 0.29 ± 0.25 range 0.09 to 0.58, Table 3.2). There was no significant difference in orientation efficiency between translocated and control turtles (Welch t-test t=1.70, df=7.90, p=0.13, translocated: -1.36 ± 1.49, range -3.96 to 0.4; controls: 0.26 ± 1.79, range -2.63 to 1.83), but translocated turtles tended to swim in a more sustained direction, with non-uniformly distributed heading (Rayleigh test, Table S3.3). Turtles began by travelling away from their release location following depth contours and appeared to possibly use bathymetric contours when initiating directed homewards swimming, closely following the coastline and remaining in shallow waters until reaching the tip of the headland (Fig. S3.1). This was particularly evident in the three translocated turtles that had complete homing tracks (turtles 4, 7 and 21, Fig. 3.1B). While the overall homing efficiency of their tracks were low (turtle 4: θ=-0.65, turtle 7 θ= -0.91 and turtle 21 θ= 0.4 respectively), when segmented into phases, these three turtles demonstrated significantly directed swimming (Rayleigh test, Table S3.3, Fig. 3.3A-C) towards each goal direction, with greater Orientation Efficiency and lower angular dispersion (Table 3.2). Comparatively, translocated turtle 5, which did not rehome, exhibited the most tortuous track and lowest Orientation Efficiency, travelling in the opposite direction to its capture location (*r*=0.01, *O*=-2.23 respectively; Fig. 3.3D).

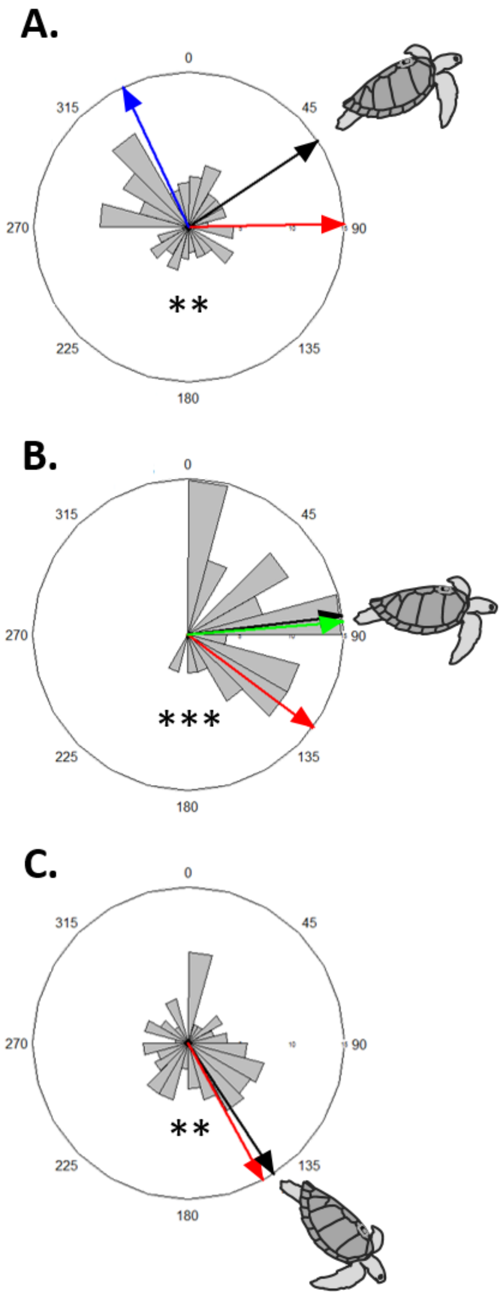
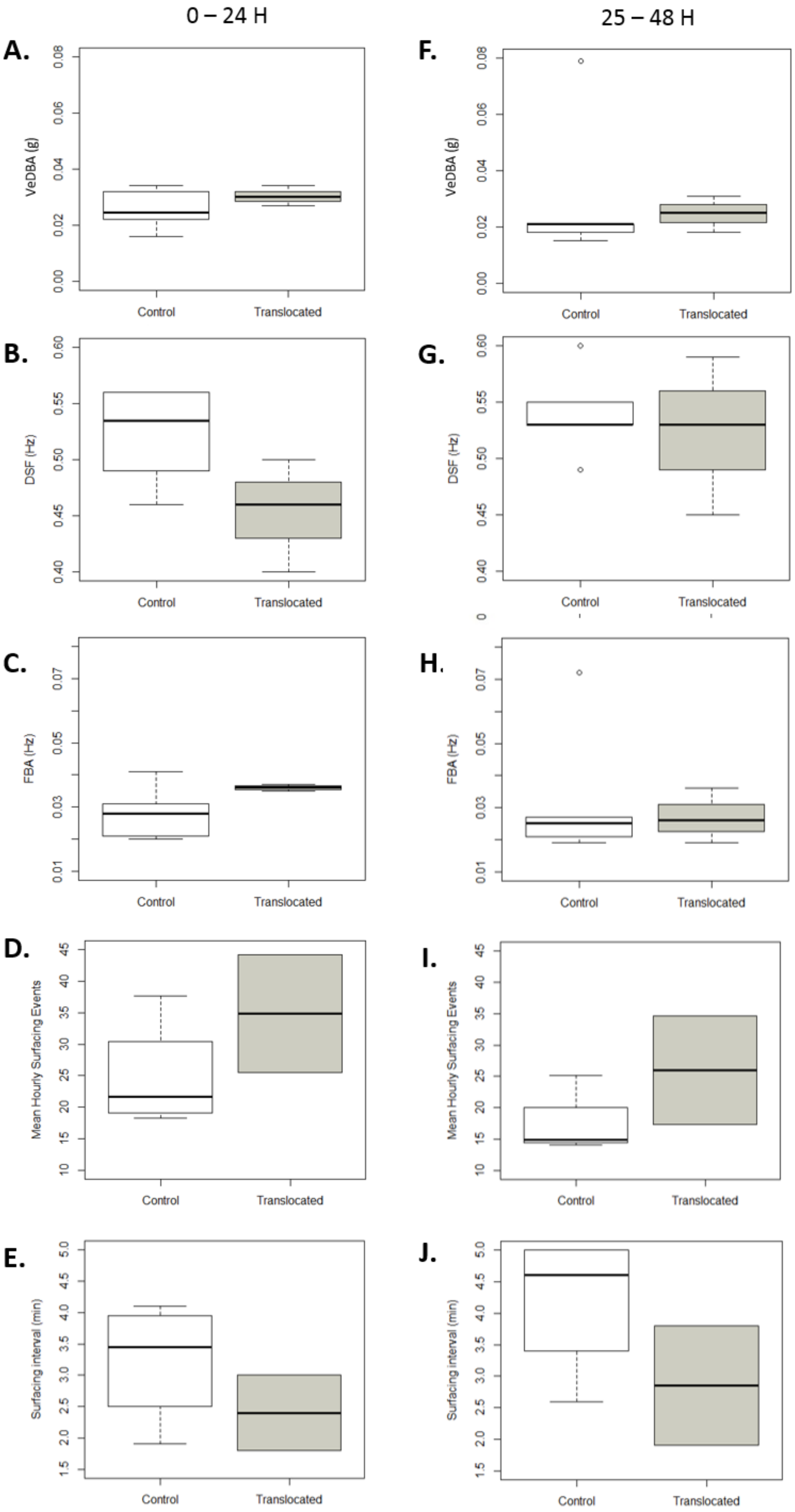


Figure 3.3: Circular histogram plots showing the heading post release for translocated turtles, where the length of the histogram bars indicate the proportion of time turtles swam in a particular direction, and black arrow shows the turtles overall mean heading. The red arrow represents the correct direction the turtle should swim as the crow flies (the homeward direction) and the blue and green arrows show the heading from the release location to the entrances of Poison and Starved creeks respectively. Turtles display directed swimming when their mean heading was similar to the goal direction with level of significance of Rayleigh test of uniformity represented by * p<0.5, ** p<0.01 and *** p<0.001. Goal direction depends on homing phase. For instance, the goal directions of a

turtle translocated to Poison Creek rehoming to Starved Creek are phase 1: towards the entrance of Poison Creek (blue arrow), phase 2: towards the entrance of Starved Creek (green arrow), phase 3: towards its capture location (red arrow). This is exhibited by turtle 4 **(A-C)** during three phases of homing. **(A)** Release location to Poison Point, **(B)** Poison Point to entrance to Starved Creek, and **(C)** Starved Creek to recapture location. (**D**) Swimming direction of a translocated turtle which did not rehome, and **(E)** a control turtle in its home range.

Accelerometry based energetic estimates

Translocated turtles expended an estimated 15 % more movement related energy than control turtles within 24 hours of release (total daily summed VeDBA: control: mean 18478 g ± 5117 s.d.; translocated: 21711 g ± 2689), had overall greater activity levels (mean VeDBA translocated: 0.031 g ± 0.01, controls: 0.026 g ± 0.01) and beat their flippers with a greater amplitude than control turtles in the first 24 hours following release (mean FBA translocated: 0.036 Hz ± 0.001 vs controls: 0.028 Hz ± 0.01, Fig. 3.4). Translocated turtles maintained similar levels of activity over the first 48 hours following release, although they were slightly more active on the first day (mean daily summed VeDBA: paired t-test t=2.75, df=2, p=0.11, day 1: 21711 g ± 2688 vs day 2: 16456 g ± 3529). While the sample size was too small to statistically test differences in diving behaviour (translocated n=2, controls n=4), translocated turtles surfaced over 40 % more frequently than control turtles during the first 48 hours following release (day 1 translocated 837 ± 317 dives vs controls 594 ± 211 dives; day 2 translocated 605 ± 269 dives vs controls 424 ± 120 dives). Translocated turtles maintained similar dive durations across the first two days post release, which were shorter compared to controls (day 1 translocated mean dive duration 2.4 min ± 0.8 s.d. vs controls 3.2 ± 1; day 2 translocated 2.9 ± 1.3 vs controls 4.2 ± 1.1 min). Similar trends were apparent when looking at translocated turtles individually. While turtle 4 was significantly more active on the first day, with greater VeDBA, surfacing more frequently and beating its flippers with a greater amplitude (Table S3.4), it slowed down and regained similar activity levels as controls on the second day after having rehomed within 15 hours. Comparatively, turtles 5 and 19 sustained high VeDBA and FBA across both days, with turtle 5 persistently orientating itself and not rehoming within the first 48 hours, maintaining high frequency of surfacing events and short dive durations (Table S3.4). Overall, control turtles also maintained similar swimming patterns over 48 hours, decreasing activity on the second day with longer resting dives (Paired sample t-test: t=8.79, df=3, $p<0.01$, day 1 3.2 min ± 1 s.d. vs day 2 4.2 ± 1.1), with the exception of turtle 11, which exhibited abnormally dynamic behaviour for 14 hours starting at 16:50 on the 24 May 2017, over 24 hours after being released, until 06:00 25 May 2017 (Fig. 3.2). Turtle 11 beat its flippers with twice the amplitude (FBA paired t-test with square root transformation t=5.67, df=23, $p<0.001$, day 1 0.031 Hz ± 0.016 vs day 2 0.072 Hz ± 0.024), and expended over twice the amount of energy relating to movement on the second day compared to the first 24 hours (day 1 24941 g vs day 2 58127 g), and almost three times the average daily summed VeDBA across the other 16 full days of tracking (mean daily summed VeDBA 21625 g ± 1604). The number of surfacing events, a proxy for respiratory frequency, increased significantly for both control and translocated turtles with increasing VeDBA, with a stronger relationship in translocated turtles than for control turtles (Least square linear regression translocated: $R^2=0.49$, F=44.41, df=46, $p<0.001$, surfacing events=3.70 + 899.48*VeDBA; controls: $R^2=0.19$, F=21.83, df=94, $p<0.001$, surfacing events=10.30 + 435.34*VeDBA). Similarly, translocated turtles exhibited a negative relationship between VeDBA and mean diving duration, which was 63 % stronger than the relationship observed in control turtles, with mean activity levels decreasing with longer diving intervals as turtles rested on the sea bed (Least square linear regression translocated: $R^2=0.38$, F=28.65, df=46, $p<0.001$, VeDBA=0.048-0.007*dive duration; controls: $R^2=0.24$, F=30.21, df=94, $p<0.001$, VeDBA=0.037-0.003*dive duration).


0 – 24 H
25 – 48 H
A.
VeDBA (g)
0.00
0.02
0.04
0.06
0.08
Control
Translocated
F.
VeDBA (g)
0.00
0.02
0.04
0.06
0.08
Control
Translocated
B.
DSF (Hz)
0.40
0.45
0.50
0.55
0.60
Control
Translocated
G.
DSF (Hz)
0.40
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FBA (Hz)
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Mean Hourly Surfacing Events
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Mean Hourly Surfacing Events
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45
Control
Translocated
E.
Surfacing interval (min)
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
Control
Translocated
J.
Surfacing interval (min)
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
Control
Translocated

Figure 3.4: Boxplots showing difference in mean VeDBA **(A, F)**, Dominant Stroke Frequency **(B, G)**, flipper beat amplitude **(C, H)**, number of surfacing events **(D, I)** and dive duration **(E, J)** between controls (white boxes) and translocated turtles (grey boxes) for the first 24 hours following release (left, **A-E**) and the subsequent 25-48 hours (right, **F-J**). Boxes show interquartile range, horizontal line shows median value, whiskers show data range and circles show statistical outliers.

Activity seascape

All turtles exhibited an initial highly dynamic phase, remaining close to the release site. These dynamic periods were interspersed with longer, less dynamic phases, which may have been resting. For example, turtle 8 visited a blue hole in a creek, in which it spent 3.4 hours, based on sudden depth changes greater than the average bathymetry of the site. In contrast, turtle 4 was actively moving throughout most of its tracking period, spending on average 1 % of its time in any 100 m x 100 m area, with the exception of two resting and/or feeding spots, identified by the turtle spending 2.4 hours in the same location, with low VeDBA. The accelerometry data indicated long stationary periods during which the turtle would come up for air before settling down to rest again (Fig. 3.5A2). The second period was once turtle 4 had made its way back to its home creek and spent over 2.6 hours possibly foraging in one particular location (Fig. 3.5), with accelerometry data indicating a low VeDBA activity that could not be clearly validated without visual observation, although habitat data and hotspot analysis highlighted an area of high *Thalassia testudinum* coverage. On the other hand, turtle 5, a translocated turtle that did not rehome, used a smaller area and spent less time in given 100 x 100 m grid cell (mean: <1 % of tracking duration), constantly swimming, expending more VeDBA per 100 m x 100 m cell than the average for all turtles (summed VeDBA turtle 5 mean 19.7 g ± 6.9 s.d. vs all turtles 17.2 g ± 4.6), highlighting behavioural variations between translocated and control turtles as well as individual turtles, which may not be obvious from tracking datasets separately.

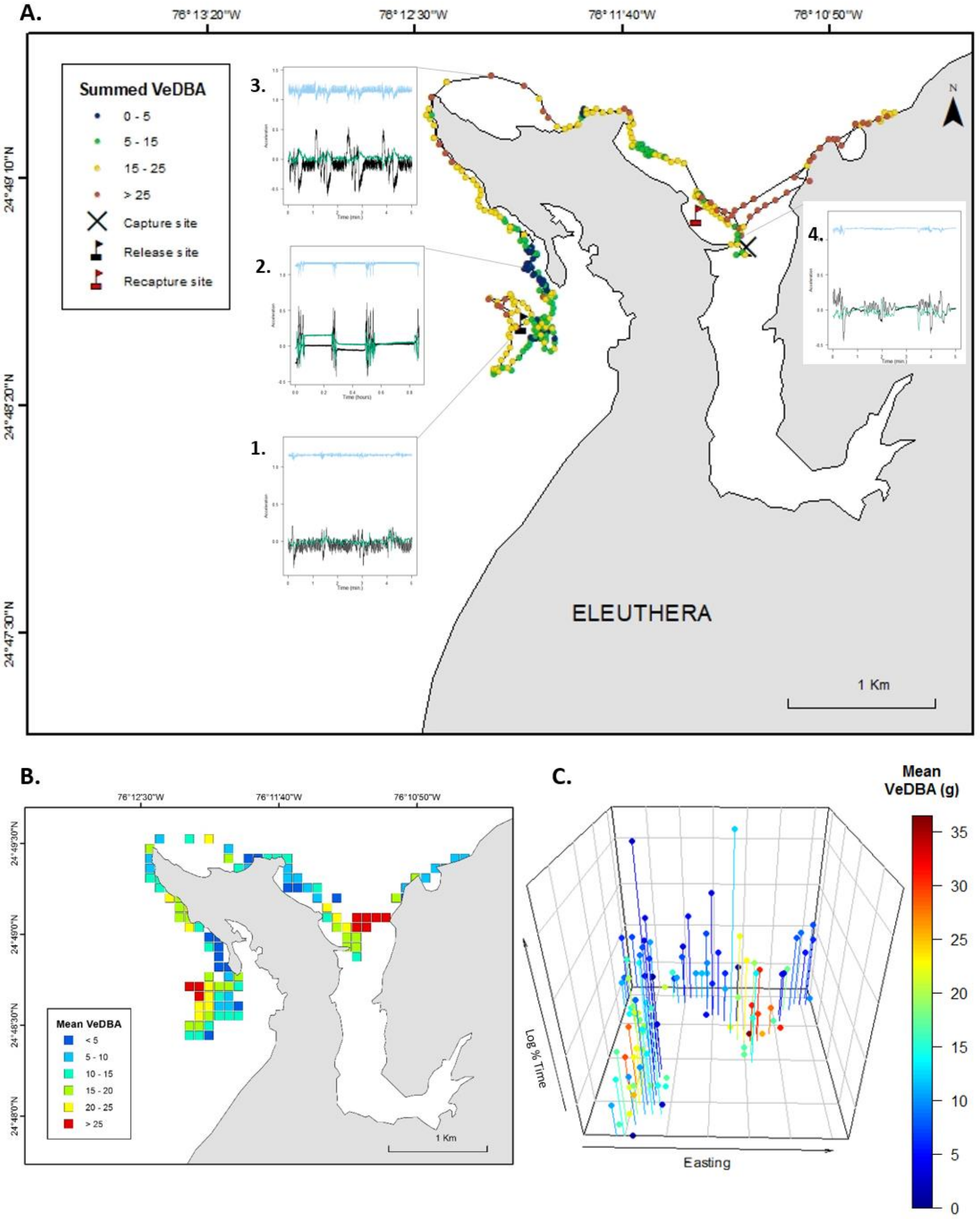

Figure 3.5: Example of activity seascape of turtle 4. **(A)** Homing tracks of turtle 4 overlaid with energy expenditure relating to movement, where colour indicates VeDBA (warmer colour showing greater activity). Example of raw accelerometry data associated to four behaviours **(A.1)** slow swimming, **(A.2)** resting, **(A.3)** fast swimming and **(A.4)** other unidentified behaviour over 5 min window (two hour window for resting behaviour in panel **(A.2)**, and their corresponding GPS location. **(B)** Activity seascape, where the colour of the grid cells increase with VeDBA intensity. **(C)** Fourth dimension to the activity seascape, where the height of vertical bars represent the log proportion of tracking duration spent by the turtle in a 100 x 100 m grid cell.

Diel behaviour

Control turtles displayed diel differences in VeDBA, dominant stroke frequency (DSF), dive duration and number of surfacing events during the first 48 hours following release, being significantly more active during the day than at night (VeDBA Wilcoxon signed rank test V=21, $p<0.05$, day 0.03 g ± 0.01 vs night 0.02 g ± 0.02; DSF Paired t-test, t=4.31, df=5, $p<0.01$, day 0.46 Hz ± 0.05 vs night 0.65 Hz ± 0.10; dive duration Paired t-test, t=3.32, df=3, p=0.04, day 3.2 min ± 0.9 vs night 4.5 min ± 1.4; surfacing events Paired t-test, t=5.07, df=3, p=0.01, day 24.1 dives ± 7.1 vs night 16.2 dives ± 6.5, Fig. 3.6). Comparatively, translocated turtles maintained similar levels of activity and flipper beat amplitude throughout both day and night during homing (VeDBA V= 6, p=0.25, FBA Paired t-test t=3.5, df=2, p=0.07, DSF t=1.13, df=2, p=0.37). While sample size for diving metrics of translocated turtles were too small to test for statistical differences (n=2), translocated turtles sustained shorter dive durations across both diel phases coupled with high number of surfacing events which decreased during the night compared to control turtles, (mean dive duration day 2.3 min ± 1.3 vs night 3.1 min ± 0.9; mean number of surfacing events day 35.7 dives ± 18 vs night 22.8 dives ± 5.9). Mean swimming metrics were similar between treatment groups for both diel phases, except for nocturnal DSF, which was significantly greater for controls than for translocated turtles (Welch t-test t=2.74, df=6, $p<0.05$, translocated 0.49 Hz ± 0.07 vs controls 0.65 Hz ± 0.10). Turtles became increasingly active after sunrise and exhibited peak VeDBA and FBA around 10:00 to 11:00 am for six of the nine tagged turtles and tailed off around dusk, however patterns of activity throughout the day varied between turtles Fig. S3.3).

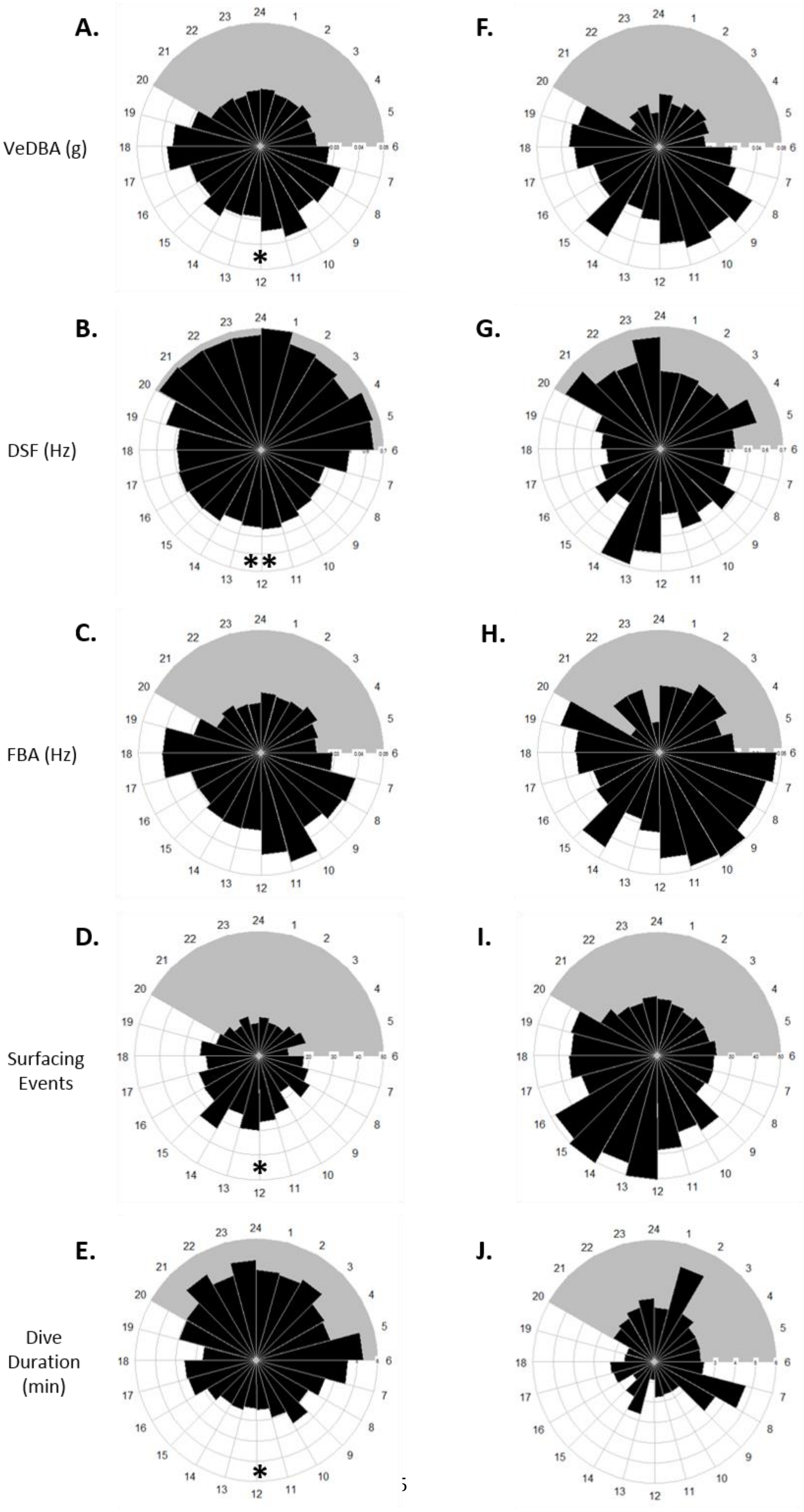A.
F.
VeDBA (g)
B.
G.
DSF (Hz)
C.
H.
FBA (Hz)
D.
I.
Surfacing Events
E.
J.
Dive Duration (min)
24
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
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Figure 3.6: Radial plots highlighting the differences in swimming metrics (VeDBA **(A, F**), dominant stroke frequency (DSF, **B, G**) flipper beat amplitude (FBA, **C, H**), number of surfacing events (**D, I**) and dive duration (**E, J**) for control (left, **A-E**) and translocated turtles (right, **F-J**) over the course of 24 hours (where midnight is at the top of each plot, and midday at the bottom). White, and shaded portions of the plot show day time and night time periods respectively. The length of each black segment denotes the mean hourly value of the corresponding metric, statistical significance is depicted by * p<0.5 and ** p<0.01.

Time Activity Budget

Control turtles maintained similar time allocation to swimming and resting over the first 48 hours of deployment, while translocated turtles spent significantly more time swimming (Welch t-test t=4.45, df=6.47, p<0.01, translocated 39.5 % ± 2.1, controls 25.8 % ± 6.9) and less time resting (t=2.87, df=6.99, p=0.02, translocated 47.5 % ± 17.4, controls 57.3 % ± 14.1) on the first day following release (Fig. 3.7). The effect of translocation on behaviour was less obvious after 24 hours, when translocated turtles resumed similar activity levels to control turtles once they had rehomed, although they spent on average 15 % less time resting than controls. Control turtle 11 displayed extremely high activity on the second day following release, expending on average four times more movement-related energy than any of the other 17 tracked days, resulting in abnormally high proportion of time allocated to fast swimming (22.9 % compared to 5.7 % ± 1.2 over rest of the tracking period). When excluding turtle 11 from analyses, translocated turtles spent twice as much time on high intensity fast swimming behaviour and almost 30 % less time resting on the second day, highlighting that effect of translocation on behaviour persisted after translocated turtles returned home.

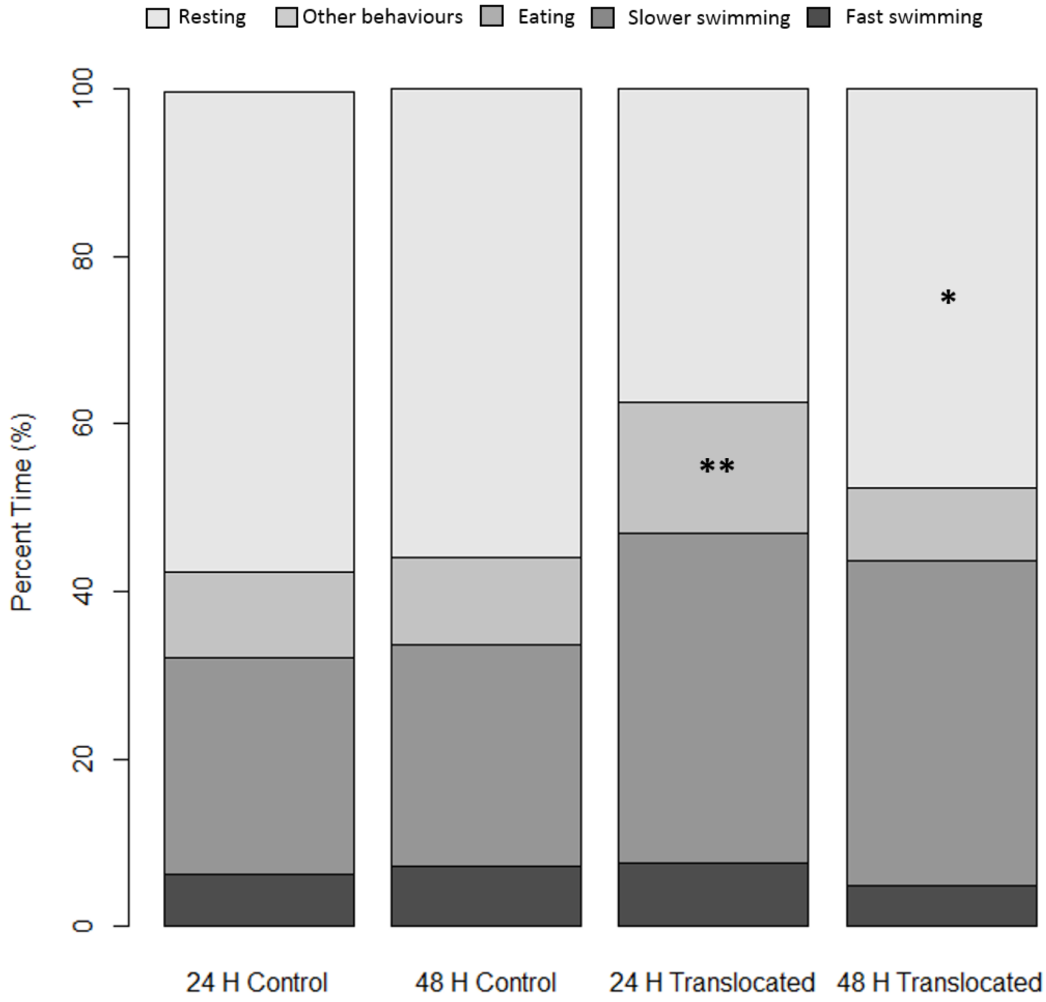


Figure 3.7: Stacked histograms showing difference in time-activity budget to five behaviours between control and translocated turtles, 24 and 48 hours after release. Bar height represents the proportion of time spent on each behaviour (fast swimming, slower swimming, eating, other and resting from dark to lighter grey). Statistical significance between days is depicted by * p<0.5 and ** p<0.01.

Discussion

This study demonstrated the strong site fidelity of juvenile green turtles to their home foraging grounds following a 4 km experimental translocation, and that rehoming following translocation has an energetic cost. Seven of twelve translocated turtles rehomed in as little as 15 hours, returning to within hundreds of meters from their initial capture site. The fine-scale resolution of the turtles' navigation behaviour following translocation, highlighted biphasic homing behaviour. Turtles began with a non-directed orientation phase, displaying tortuous tracks, followed by straighter, directed swimming towards their home range. Homing duration and behaviour varied among individuals (where translocated turtles displayed longer and more circuitous searching phase than in controls which did not orient in any particular direction following release). Similar variation in homing trajectories has been described in translocated adult sea turtles, with some individuals quickly establishing direct paths toward capture areas, while other exhibited more circuitous routes, particularly when tracked in the open ocean, before ending in a straight segment closer to target location (Luschi et al. 2001, Akesson et al. 2003, Hays et al. 2003, Luschi et al. 2007, Shimada et al. 2016b). Factors contributing to such variation might include difference in methodology (translocation distance, use of experimental magnet treatment, sampling frequency of tags), differences in the environment to which turtles were returning (continental vs island location) and differences in physiological and motivational states (nesting vs foraging) (Lohmann et al. 2008, Benhamou et al. 2011). The latter particularly appears to influence homing behaviour, where translocated post-nesting adult females were not as motivated to return to capture areas compared to those translocated during post-nesting intervals, where some tracked individuals began oceanic migration to foraging grounds instead of towards their nesting beach (Hays et al. 2003, Luschi et al. 2003, Mencacci et al. 2010). Previous studies have highlighted the ability to rehome after translocation is not limited to age class or influenced by body size, with juvenile turtles also found to return to their foraging sites following translocation (Shimada et al 2016b, Avens et al. 2003). In the present study turtles were translocated 4 km from their capture sites, however, unlike in the terrestrial environment where translocation distance can have an effect on reducing dispersal from translocation site (Hinderle et al. 2014, Milligan et al. 2018), distance does not appear to be a limiting factor in juvenile sea turtles' ability to rehome. Juveniles have rehomed following translocation over 115 km and being held in captivity for 198 days (Shimada et al 2016b), in as little time as less than 24 hours (from translocation distances of 1.5 to 4 km; Ireland 1980) and exhibited similar recapture rates at feeding grounds compared to controls (Avens et al. 2003).

Why rehome?

Juvenile green turtles generally display strong site fidelity to neritic habitats (McCellan & Read 2009, Hazel 2013, Lamont & Iverson 2018), where site selection is likely influenced by abiotic factors such as bathymetry, salinity and currents (Lamont et al. 2015) and biotic factors including predation (Heithaus et al. 2009) and prey availability (Makowski et al 2006, Lamont et al. 2015). In the present study, while the primary food source of green turtles, *Thalassia testudinum*, was similarly abundant in both creeks, macroalgae and mangrove densities were greater in Starved Creek, likely providing greater habitat complexity and refuge to turtles against predators within the shallow creek system compared to the open flats habitat of Poison Creek. The protective mangrove root systems are particularly important to juvenile turtles, which rest in shallower water at night than during daylight hours, highlighting the importance of habitat structures and how the knowledge of shelter availability influences site fidelity (Witt et al. 2011). Knowledge of the location of foraging and resting sites (Makowski et al 2006) is likely important to the survival of juveniles during a vulnerable life stage. Rather than opportunistically settling in an unfamiliar habitat where a lack of knowledge of new/poor foraging sites and shelter may be risky (Shimada et al. 2019), in the present study turtles rehomed to their familiar developmental grounds. Juvenile turtles in captivity have been recorded swimming in a homeward direction following translocation of 30 to 167 km (Avens & Lohmann 2004, Lohmann et al. 2004), highlighting not only site fidelity, but also navigational abilities developed as juveniles.

How do turtles rehome? Navigation abilities of turtles

Navigational skills are essential to a wide range of taxa, from non-migratory species (Boles & Lohmann et al. 2003, Mitamura et al. 2012, Meckley et al. 2016, Orchan et al. 2016, de Vries et al. 2017) to long-distant migrants (Gagliardo et al. 2013, Putman 2015, Lindecke et al. 2019), which rely on multisensory cues to locate their target destination (Zeil 2012, Chapman et al. 2015), most notably geomagnetic information (Begall et al. 2013, Mouritsen 2018, Lohmann & Lohmann 2019). As sea turtles mature, they learn the magnetic topography of the area in which they live in (Lohmann et al. 2007, Lohmann & Lohmann 2019). Turtles develop a magnetic compass sense, providing directional information and a mechanism to maintain heading (Lohmann & Lohmann 1993), as well as a magnetic map sense with the ability to differentiate between geomagnetic fields at their current location in relation to a target destination hundreds of kilometres away (Lohmann et al. 2004, Putman et al. 2011). This ability is referred to as 'true navigation', and has been demonstrated in sea turtles, as well as a few other species, including songbirds (Fischer et al 2001, Dennis et al. 2007, Kishkinev et al. 2015) and spiny lobsters (*Palinurus argus*), which oriented themselves towards their capture site following 12 to 37 km translocation (Boles & Lohmann 2003) by detecting geomagnetic differences. Turtles' magnetic sensitivity, as well as the spatial scale at which they are able to distinguish magnetic variations, remains unknown (Lohmann et al. 2008), particularly with respect to using magnetic navigation over short distances. In the present study, the magnetic intensity between Starved and Poison Creeks varied only by 1.4 nT compared to a variation of 1122 nT between Starved Creek and Miami, Florida, USA located 415 km away, suggesting that turtles may rely on other cues to orientate in close range. Previous studies have shown that translocated adult turtles perturbed by artificial magnetic fields were able to rehome, though taking a tortuous path, suggesting that turtles are likely to rely on a combination of mechanisms to navigate (Papi et al. 2000, Luschi et al. 2007, Benhamou et al. 2011), with homing efficiency improving with increasing number of cues used (Painter & Plochocka 2019). Polarised light and celestial cues are widely used for navigation by birds, fish, insects and mammals (Muheim et al. 2007, Heinze & Reppert 2011, Muheim 2011, Berenshtein et al. 2014, Lindecke et al. 2019), and particularly by species living in featureless landscapes such as deserts (Wehner & Müller 2006, Homberg 2015). Turtles might use such cues when swimming close to the surface to (Avens & Lohmann 2004), and/or may use directional information from wave surge motion (Wang et al. 1998, Lohmann et al. 2008). In the present study, prevailing winds and coastal currents were easterly, so turtles could have relied on wave direction, as well as wind- and waterborne chemical cues dispersed from their home creek and persisting in the sea over short distances, to orient themselves (Hays et al. 2003, Endres et al. 2016). Olfaction-mediated homing has been demonstrated in Cory's shearwaters (*Calonectris borealis*), leopard sharks (*Triakis semifasciata*) (Gagliardo et al. 2013, Nosal et al. 2016), and most notably in salmonids which, like turtles, rely on geomagnetic cues for long distance navigation, before using chemical olfactory cues from their natal stream at closer range (Bett et al. 2016, Lohmann & Lohmann 2019). Lohmann et al. (2008) and Endres et al. (2016) proposed that these cues in combination with search patterns are perhaps used by sea turtles for near range navigation, such as way-finding towards isolated features (i.e. Ascension Island). This may possibly explain the circuitous tracks displayed by the translocated turtles in the present study, which had significantly more tortuous tracks than control turtles. Orientation phases following release have been recorded in other species such as birds (Jones et al. 2003), mammals (Tsoar et al. 2011) and fish (Nosal et al. 2016). It may also be why Turtle 7, translocated to Starved Creek upwind and up-current from Poison Creek, displayed such a long (69 hours) tortuous orientation phase compared to those translocated downwind from Poison Creek. Turtles translocated on the leeward side of Ascension Island were able to return to nesting beach faster than those translocated to the wayward side of the island, consistent with the direction of wind-transported plumes (Akesson et al. 2003, Hays et al. 2003). Since only one turtle was translocated to Starved Creek, it is not possible to attribute these differences in navigation to geographical differences and the potential for the dispersal of chemical cues by prevailing currents and wind, or individual variation alone. Turtles in shallow coastal waters may be able to assess their position in relation to current-related drift by using visible fixed reference points on the seabed (Luschi et al. 1996, Girard et al. 2006, Chapman et al. 2011). After a circuitous orientation phase, translocated turtles in the present study exhibited directed swimming, following bathymetric contours and the coastline towards their natal creek. Turtles may have used a cognitive map of the benthic topography or the headland separating both sites as a familiar reference landmarks (Shimada et al. 2016a) in a similar way that homing pigeons (*Columba livia domestica*) have been found to follow familiar roads and railways on their homeward journey (Lipp et al. 2004) .

Impacts of translocation

Little work has focused on the effects of translocation on behaviour and energetics in turtles, particularly in juveniles. Translocated turtles in the present study displayed longer and more tortuous tracks as a result of translocation. Altered movement patterns (Heidinger et al. 2009, Milligan et al. 2018) and space use (Butler et al. 2005, Wolfe et al. 2018) have also been recorded in other species in response to translocation. Translocated grizzly bears (*Ursus arcto*) and tiger snakes (*Notechis scutatus*) had home ranges 3.25 and 6 times greater than control individuals, respectively (Butler et al. 2005, Milligan et al. 2018), while translocated dugite snake (*Pseudonaja affinis*) had larger activity ranges than residents (Wolfe et al. 2018). The translocated turtles in the present study allocated twice as much time to energetically demanding behaviours and maintained high activity levels throughout the night as well as the day. Atypical behaviours, or a change in time allocation to particular behaviours has been observed in translocated African elephants (*Loxodonta africana*), where translocated individuals spent 5 % less time feeding and twice as long standing than resident elephants (Pinter-Wollman et al. 2009). Relative metabolic demand has been inferred from respiratory frequency in different locomotory patterns in leatherback turtles (Reina et al. 2005), where turtles breathed more frequently during transiting dives, consistent with higher energetic demands of the swimming. Similarly, Okuyama et al. (2014) found that the number of breaths taken by juvenile green turtles tagged with head-mounted accelerometers significantly increased with Overall Dynamic Body Acceleration (ODBA). The additional time associated with swimming likely results in less time available for foraging, in addition to a potentially limited knowledge of prey availability in translocation sites. This has been observed in translocated European hedgehogs (*Erinaceus europaeus*) and African elephants (*Loxodonta africana*), which had lower body conditions than resident conspecifics, likely owing to reduced feeding activity and stress (Molony et al. 2006, Pinter-Wollman et al. 2009). While the energetic costs incurred by a homing female turtle were three times higher than the resting metabolic rate (Enstipp et al. 2016), the costs of homing is likely to be greater for juveniles, and likely to increase with translocation distance as the daily energy expenditure of adult turtles is considerably lower than those reported for free-ranging juvenile green turtles (Okuyama et al. 2014).This is due to adults storing greater amount of metabolically inert green fat compared to juveniles, resulting in adults having lower mass-specific metabolic rate (Kwan 1994, Penick et al. 1996).

Conservation Implications

When threats to a population cannot be addressed in situ, alternative approaches are often devised to mitigate threats, such as translocation (Weeks et al. 2011). The present study demonstrates that translocation is unlikely to ameliorate threats (e.g. Dickerson et al. 2007) to juvenile green sea turtles as they have excellent homing efficiency, and can return to their capture area within hours of release. Ireland (1980) reported similar findings, where turtles translocated 1.5 to 4 km away rehomed within 48 hours. Therefore, it is highly likely that turtles return to areas under threat before operations may be complete. Likewise, if translocation is used to establish a new population or increase genetic diversity of turtles in a given area (Johnson et al. 2010, Baker et al. 2011), it appears unlikely to succeed. Instead, if turtles were kept in holding facilities for the duration of the threat activity (dredging or oil spill cleaning), not only would the risks of anthropogenic activities as well as the cumulative effects of homing behaviour be reduced, turtles would likely be able to successfully rehome upon release. Choosing a release site based on species ecology and behaviour can help with reducing dispersal (Letty et al. 2007, Bradley et al. 2012, Nafus et al. 2016). These challenges, combined with the ability to rehome, has caused the failure of a number of other marine translocations, such as in sea otters (Rathbun et al 2000), Hawaiian monk seals (Baker et al 2011) and estuarine crocodiles (Read et al. 2007). Much of the existing body of literature on translocation has focused on traits that are easily assessed, such as dispersal rates or short-term survival (Pinter-Wollman et al. 2009, Villaseñor et al. 2013, Wolfe et al. 2018). To date, only one other study has used accelerometry to estimate the energetic cost of movement of translocation in turtles (Enstipp et al. 2016). With the number of wildlife translocation projects increasing globally (Seddon et al. 2007, Swan et al. 2016, Swan et al. 2018), a growing body of literature is mounting to inform best practice for successful translocations. However, research is also highlighting variation in success between and among species, and that translocation alone may not be a solution, or only provide short-term solution to a larger problem, where the conservation of whole ecosystems rather than individual species are more beneficial (Swan et al. 2016).

Chapter 4: General Discussion

This thesis advances the understanding of the spatial and behavioural ecology of two endangered species at coastal foraging sites, while highlighting the pragmatic applications of biologging technology in informing conservation.

Summary of thesis findings

Chapter 2

Using state of the art multi-sensor biologging tags, this chapter describes for the first time, and in high resolution, **direct records of breaching by three basking sharks** over 41 days in a feeding aggregation in west Scotland. A total of 67 breaches were recorded, with sharks breaching on average twice a day, both day and night. The novel data also **demonstrated for the first time that individual sharks can breach multiple times in quick succession**, up to a maximum of four consecutive breaches in 47 seconds. Breaching events were repeatable both among and between sharks, following a similar ascent rate and angle, initiating and ending the behaviour at an average depth of 20 m. Sharks breached in different directions (forward or backwards), and evidence of potential lateralisation in rolling direction was evident, with the majority of sharks rolling to their right side. Surprisingly, ascent rate, swimming speed and VeDBA were **similar between consecutive breaches** (i.e. sharks do not appear to fatigue over the course of consecutive breaches) despite high energetic demands. Foraging time required to meet sharks' daily energy expenditure ranged from 4.8 to 54 hours depending on the shark size and prey density. The cost of a single breach was estimated at 10 to 11.5 kJ of mechanical energy, requiring a foraging time of 23 sec to 1.7 minutes. These values should, however, be taken conservatively since the prey densities used to estimate foraging times were not recorded in situ, and the energetic values were derived from generalised equations and do not include the costs of basal metabolic rate or activity thermogenesis. While the **function of breaching remains unclear**, the energetic costs associated with this behaviour are over 30 times that of routine swimming, suggesting breaching likely has an important fitness purpose. Breaching events have previously been observed predominantly in solitary individuals, however since sharks initiate ascent towards the surface from an average depth of 20 m, the number of sharks recorded at the surface is not a reliable indicator of the number of individuals receiving the signal. While unlikely to rely on auditory and visual cues, sharks may use mechanosensory and electric cues to detect breaching from conspecifics, with larger sharks generating greater signals. As all the breaches for which positional data was received occurred within the proposed marine protected area, if breaching were to play a role in courtship display, this study **highlights the area as a potential mating ground** and supports previous findings of the importance of the Sea of Hebrides for basking sharks.

Chapter 3

This chapter investigated the impact of translocation on juvenile green turtle behaviour and energetics, to inform its utility as a threat mitigation solution. Turtles were translocated 4 km away, and tracked with tethered GPS tags and multi-sensor biologging tags to assess whether they rehomed and to estimate the energetic cost associated with movement. Following translocation, **turtles rehomed in as little as 15 hours**, returning to within hundreds of meters of their original capture location, demonstrating strong site fidelity. Translocated turtles displayed a long tortuous navigation phase before orienting themselves and swimming almost continuously in a homeward direction**. Translocated turtles allocated twice as much time to energetically demanding behaviours** than control (non-translocated) turtles did, and maintained high VeDBA and FBA during both night and day. Comparatively, control turtles remained near their release site, were less active and surfaced 40% less.

Control turtles exhibited distinct diurnal patterns of activity and longer resting night dives, similar to previous findings in other juvenile green turtle populations, but translocated individuals did not. Activity levels and behavioural differences were the most pronounced in the turtle that failed to rehome, expending the most energy relating to movement in apparently attempting to orient itself in its new setting, rather than settling into its release location and displaying similar behaviours to the controls at the same site. Selecting suitable habitat can be crucial for the success of translocation of some species, but in the present study the habitat at the release site was similar to turtles' capture location and most turtles still rehomed. Although translocation is occasionally used to mitigate against human activity, or in response environmental degradation, the current findings highlight that **strong site fidelity and rapid homing behaviour of turtles may undermine the effort to mitigate threats by translocating turtles**. Turtles experienced high energetic costs associated with homing behaviour which is likely to increase with translocation distance. The additional time associated with swimming resulted in less time allocated to lower intensity activities such as resting or foraging, in turn minimising the amount of energy diverted towards somatic growth and immunity which may be particularly important for vulnerable populations (e.g. a small size, or infected with fibropapilloma virus). **Homing behaviour instead perhaps exposes turtles to increased risk of human interaction** (vessel strike, bycatch) and predation through limited knowledge of local shelter. This study provides further evidence that juvenile turtles will rehome following translocation, and that translocation may therefore perhaps not be a particularly effective conservation tool.

Conservation implications

Chapter 2 could be used to assist wildlife practitioners in designating protected areas for basking sharks (Caro & Berger 2019, Wittemeyer et al. 2019), or codes of conduct for ecotourism to mitigate disturbances at a potential breeding ground (Levensen et al. 2013, Barnett et al. 2016, Murray et al. 2019). Similar research could extend to other elasmobranchs such as threatened manta rays for which breaching has also been suggested as a courtship display (Marshall & Bennett 2010, Stevens et al. 2018). Using accelerometry to elucidate the energetic requirements of basking sharks at their feeding grounds, **Chapter 2** helps to fill a knowledge gap of bioenergetics and fundamental biology surrounding an important and vulnerable group of species. These baselines provide the opportunity to investigate how basking sharks may respond to environmental change, and their long-term survival in the Anthropocene (Lawson et al. 2019).

Faced with warming sea surface temperatures and increasing oxygen minimum zones, sharks may need to divert energy from growth and reproduction towards sustaining basic metabolic rate, which increases exponentially with temperature in ectotherms (Brown et al. 2004). By understanding how human activity may possibly be affecting sharks behaviour through the use of biologging tags, mitigation can be put into place to minimise additional stressors in a changing environment.

When possible, ecosystem based approaches to conservation are likely to be of the most use in maintaining biodiversity (Swan et al. 2016, Lowerre-Barbieri et al. 2019), but if habitat is lost due to economic or environmental reasons, two options remain (i) leave animals in harm's way or (ii), translocate animals elsewhere (Nussear et al. 2012). Translocations are usually relatively ad-hoc and lack a robust evidence base, thus experimental translocations can yield novel insight into the effects of translocation (Seddon et al. 2007). **Chapter 3** informs such practice, revealing energetic costs of movement that would otherwise not be apparent through visual observations alone. This is particularly valuable in the marine realm or for inconspicuous species that prove challenging to study. The use of translocation as a conservation method may increase over the coming years (Seddon et al. 2007, Swan et al. 2016, Swan et al. 2018), tracking technology has the potential to be an ideal tool for wildlife managers to monitor animal movement, behaviour and health, particularly when combined with physiological metrics, to assess the effectiveness of translocation. Stress is likely to be inevitable during translocation (Teixeira et al. 2007, Tarszisz et al. 2014), thus the ability to understand and minimise human impact on animals through informed protocols may reduce stress-related mortality, improving the likelihood of success (Whisson et al. 2012, Lepeigneul et al. 2014, Tarszisz et al. 2014). Biologging tags can also identify species suitability for translocation which may be limited due to strong homing tendencies. Instead, when possible, resources could be allocated towards mitigating threats within the target population's home range, such as gear modification of dredging vessels (Whittock et al. 2017).

Limitations, challenges and future direction

Ground-truthing accelerometry data through visual observations helps to robustly identify the behaviour in question, particularly those that are rare or difficult to infer from inspection of the raw data alone. While this has been achieved for some species of sharks and turtles in captivity (e.g. in aquaria; Bouyoucos et al. 2018, Brewster et al. 2018, Jeantet et al. 2018, Hounslow et al. 2019), it is logistically unfeasible for large organisms such as basking sharks, and behaviours may differ from those displayed in the wild. Jeantet et al. (2018) validated over 30 behaviours in three species of sea turtles in captivity however since turtles were fed at the surface of the holding tank, accelerometry-derived feeding events in the study could not be used to classify foraging of wild turtles on seagrass. Calibration of accelerometry data in free-ranging animals can be carried out by animal-borne cameras (Watanabe et al. 2019b, Tackaberry et al. 2020, Yoshino et al. 2020), which will also provide social and environmental context to movements (Moll et al. 2007, Tremblay et al. 2014). Animal-borne cameras would be especially valuable for basking sharks, for which foraging events could not be detected from accelerometry data (they don’t appear to signal a postural change as they open their jaws to filter-feed). Jaw- or head-mounted accelerometers have accurately identified feeding events in loggerhead turtles (*Caretta caretta*), Arabian oryx (*Oryx leucoryx*), sheep (*Ovis aries*), Aldabra tortoise (*Aldabrachelys gigantea*) and common carp (*Cyprinus carpio*) (Makiguchi et al. 2012, Hochscheid et al. 2013, Wilson et al. 2020b), as well as the ability to distinguish between prey items (Okuyama et al. 2009), however this remains logistically challenging for large marine animals (which largely cannot be captured, and are thus tagged in passing), and may raise ethical concerns pertaining to increased drag in ram filter feeders. Video data would provide the opportunity to derive information on the time allocated towards foraging and energy intake to incorporate into bioenergetic models at their feeding grounds (Heaslip et al. 2012, Wanatabe et al. 2014, Machovsky-Capuska et al. 2016). Future work should incorporate measurements of prey abundance in situ such as knowledge of plankton in **Chapter 2**, and of turtle grass densities in **Chapter 3** and their known caloric content, combined with known feeding rates to shed light into the basic energetic requirements for the two vulnerable groups.

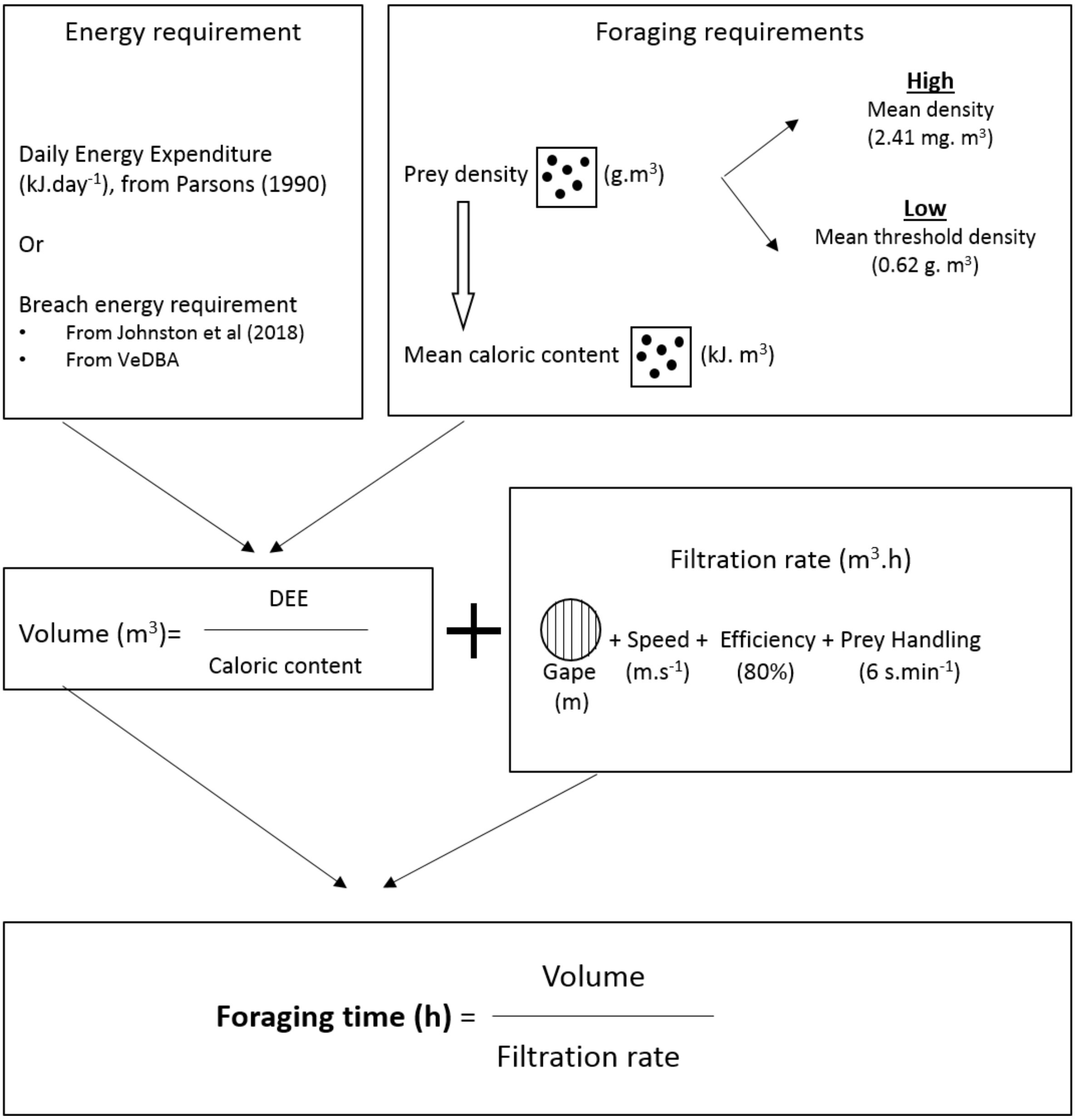
Future technological developments improving remote transmission of data would reduce the need to recapture animals to retrieval tags (Williams et al. 2020). In **Chapter 3**, data was lost from 20% (n=4) of turtles due to the inability to locate tagged individuals. Issues lay with the short battery life of the GPS units sampling at a high frequency (one position per minute). Since this study was investigating the fine scale movement patterns of turtles following translocation, fine temporal resolution was required, but deployment duration was therefore short owing to limited memory on board the tag. Longer tag deployment would allow for more accurate quantification of homing duration and insight into behaviour upon return to home range. Future studies on turtle movements within habitats with extensive structures such as coral reefs or coastal mangrove habitats such as in **Chapter 3** should consider that floating tethered tags may be lost if caught on reefs or mangrove roots. This was particularly the case for control turtles in Starved Creek which has a higher density of mangroves than Poison Creek, which shed light on how capture, handling, transport and translocation effect energy expenditure behaviour. Longer tag deployment would have provided a more comprehensive understanding of the extent of the impact of human intervention.

Despite limited sample size and tag attachment duration, consistent patterns emerged between turtles and basking sharks. **Both chapters** highlighted how the two species allocated the greatest proportion of their time to low intensity behaviours (slow swimming and resting), and quantified the movement related energetic costs of behaviours (breaching and homing behaviours respectively). Future tagging effort of basking sharks with multi-channel biologging technologies may provide insight into variation in breaching behaviour and energy expenditure, which was not possible in the current study due to a limited sample size. In particular, reciprocally logging acoustic “business card” tags would shed light on the social context of behaviours. Barkley et al. (2020) identified accelerometry-derived metrics before, during and after interaction with conspecific Greenland sharks (*Somniosus microcephalus*). Replicating this study with respect to breaching would help to validate whether the behaviour is socially driven. Location of breaching events appeared to be dispersed around the coast of the Isles of Coll and Tiree, but additional data could highlight breaching hotspots. Basking sharks form conspicuous aggregations worldwide (Compagno 1984, Witt et al. 2012, Crowe et al. 2018), therefore tagging in other locations would provide further insight into the energetic expenditure at differing foraging sites as well as the preponderance of breaching events within these sites, and how they may differ in frequency, distribution and occurrence. Variations in particular behaviours have been recorded for different populations of a same species across geographical locations, such as hunting techniques in Orcas (*Orcinus orca*) (Guinet et al. 1991, Ford et al. 1998, Visser et al. 2008, Wright et al. 2017). Increasing the tag deployment period to have a broader temporal coverage of the summer feeding aggregation may provide insight into the onset of breaching, and whether the timing of the behaviour may suggest potential courtship. Variation in foraging behaviour may also be detected across the feeding season with longer tag deployment, filling the knowledge gap on how basking sharks may change in body condition and possibly influence the timing of their migration (Brodersen et al. 2008, Dickerson 2018, Anderson et al. 2019). Battery life and memory capacity of biologging tags hampers long deployment durations, especially when sampling at high frequency in order to detect rare behaviours such as breaching. Latest accelerometer tags can now process data on board to log bouts of pre-determined behaviours (e.g. standing, walking and lying down, Le Roux et al. 2017), maximising tag memory and battery, increasing deployment duration (Le Roux et al. 2017). The use of such tags has the potential to revolutionise the long-term study of species that would otherwise be difficult or impossible to observe.

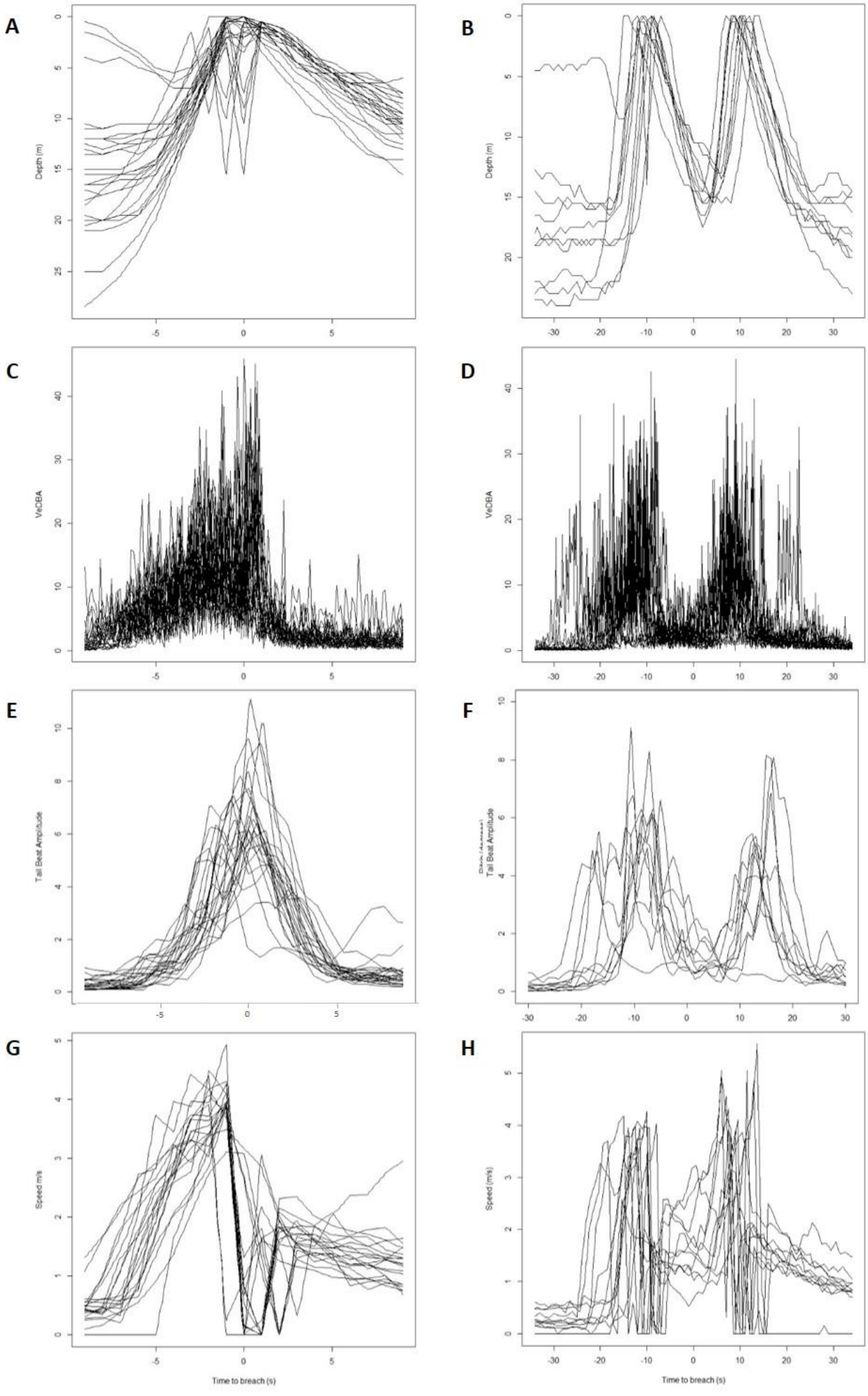
While biologging tags provide a wealth of data at an unprecedented scale, challenges arise in processing and analysing large complex datasets, especially when attempting to visualise data to display biologically important patterns (Whitney et al. 2018). Developments in multidimensional visualisation methods and analyses techniques such as three-dimensional histograms and machine learning algorithms have revolutionised big data exploration and interpretation (Li et al. 2016, Wilson et al. 2016, Williams et al. 2017, Brewster et al. 2018, Ali et al. 2019, Wang et al. 2019, Wilson et al. 2020b), and can be combined with environmental and spatial variables to provide greater context to movement (Papastamatiou et al. 2018, Williams et al. 2020). Integrating accelerometry-derived metrics such as basking shark postural data into 3D histograms emphasised variations and lateralisation of breaching behaviour, while turtle VeDBA combined with tracking data highlighted activity phases of homing behaviour and activity seascape. Analysing body movement in tandem with head orientation and rotation using a novel “orientation sphere” (O sphere) visualisation approach has helped to quantify feeding, navigation and vigilance behaviour in loggerhead turtles and Arabian oryx (Wilson et al. 2020b). Using a multi-faceted approach to analysing accelerometry would be a pragmatic solution for future studies as well as re-analysing previously collected data comparing similar behaviours in other marine species where particular patterns may not be as apparent using two dimensional representation alone (Whitney et al. 2018, Williams et al. 2020). With a wealth of existing biologging data, there is a need for developing and using centralised global sharing platforms to identify areas of research where efforts have been duplicated and highlight knowledge gaps both geographically and in terms of taxa (Hussey et al. 2015, Dwyer et al. 2015, Lennox et al. 2017, Williams et al. 2020).The interdisciplinary collaboration between ecologists, engineers, computer scientists and mathematicians from the initial experimental design phase to analysis will continue to maximise the output of biologging technology as well as improve and facilitate their use in conservation (Walsh et al. 2015, Wszola et al. 2017).

In this thesis, complex accelerometry data was analysed and interpreted using novel visualisation methods to highlighting the pragmatic application of biologging technologies in marine conservation. Similar approaches may be used to identify important life history events through accelerometry as well as inform conservation practitioners and decision makers on whether marine translocation is sustainable.

Appendices



Supplementary Figure 2.1: A schematic diagram of how the foraging time required to meet daily energy expenditure and breaches was calculated based on filtration rates and prey densities. Foraging times were estimated for both high and low prey densities based on zooplankton samples collected off Plymouth and the Isles of Coll and Tiree respectively.


A
B
C
D
E
F
G
H
Depth (m)
VeDBA
Tail Beat Amplitude
Speed m/s
Speed (m/s)
Time to breach (s)
Time to breach (s)
0
5
10
15
20
25
-5
-30
-20
-10
30
40

Supplementary Figure 2.2: Line plots showing the overlay of depth (**A, B**), VeDBA (**C, D**), tail beat amplitude (**E, F**) and speed (**G, H**) profiles for single and double breaching events. Each breach is shown as a black line recording 28 single breaches (**A, C, E and G**) over a 20 s window and 13 double breaches (**B, D, F and H**) over a 70 s window. Note the peak in each metric corresponds with the moment the sharks break the surface.

Supplementary Table 2.1: Summary table of statistical tests comparing swimming metrics between the ascent of single breaches and the first breach of multi-breaching events, using paired t-test or Wilcoxon rank sum test.

	Depth (m)	Duration (s)	Speed (m.s^{-1})	VeDBA (g)	TBA (Hz)	Pitch – mean (degrees)	Pitch – max (degrees)	Roll- max (degrees)
Total Ascent	W=279 p=0.34 X_s=20.13 ±9.59 X_m=22.15 ±11.04	W=240 p=0.97 X_s=52.32 ±74.20 X_m=70.47 ±121.27	W=165.5 p=0.77 X_s=1.50 ±1.10 X_m=1.65 ±1.18	W=288 p=0.25 X_s=5.99 ±4.42 X_m=7.57 ±4.99	W=270.5 p=0.45 X_s=1.18 ±1.13 X_m=1.33 ±1.03	W=232.5 p=0.91 X_s=22.88 ±13.36 X_m=21.46 ±10.52	W=196 p=0.34 X_s=77.36 ±8.67 X_m=74.84 ±9.64	W=232.5 p=0.91 Xs=160.27 ±18.50 X_m=157.78 ±22.82
Peak Ascent	t=1.21 df=33 p=0.24 X_s=14.56 ±5.59 X_m=16.69 ±5.79	t=0.74 df=30 p=0.47 X_s=5.96 ±1.57 X_m=6.35 ±1.81	W=208 p=0.67 X_s=2.61 ±0.55 X_m=2.64 ±0.53	t=0.77 df=22 p=0.45 X_s=10.69 ±1.37 X_m=11.18 ±2.42	W=288.5 p=0.24 X_s=1.16 ±1.25 X_m=1.63 ±1.23	W=194.5 p=0.31 X_s=39.93 ±13.42 X_m=38.40 ±15.48	W=196 p=0.34 X_s=77.36 ±8.67 X_m=74.84 ±9.64	W=232.5 p=0.91 Xs=160.27 ±18.50 X_m=157.78 ±22.82

Supplementary Table 2.2: Summary table of statistical tests comparing swimming metrics between the ascent of the first and second breach of multi-breaching events, using paired sampled t-tests or Wilcoxon signed-rank tests. P values are given showing the difference in swimming metrics of the total ascent phase of the first breach differ from the ascent of the second breach, but not all metrics for the peak ascent phase.

	Depth (m)	Duration (s)	Speed ($m.s^{-1}$)	VeDBA (g)	TBA (Hz)	Pitch – mean (degrees)	Pitch – max (degrees)	Roll- max (degrees)
Total Ascent	V=139 **p<0.01 **** X_1=22.15 ±11.04 X_2=13.85 ±2.61	V=147.5 **p<0.001***** X_1=70.47 ±121.27 X_2=6.53 ±4.26	V=6 **p<0.01**** X_1=1.65 ±1.18 X_2=2.85 ±0.46	V=35 **p=0.05 *** X_1=7.57 ±4.99 X_2=9.83 ±3.31	t=2.74 df=16 **p=0.01**** X_1=1.33 ±1.03 X_2=1.90 ±0.58	t=3.48 df=16 **p<0.001***** X_1=21.46 ±10.52 X_2=32.63 ±5.77	V=114 p=0.08 X_1=74.84 ±9.64 X_2=72.79 ±9.52	V=57 p=0.38 X_1=157.78 ±22.87 X_2=161.23 ±25.98
Peak Ascent	V=122.5 **p=0.03** * X_1=16.69±5.79 X_2=13.83±2.61	V=58.5 p=0.13 X_1=6.35 ±1.80 X_2=5.94±3.11	t=1.58 df=15 p=0.14 X_1=7.23 ±2.42 X_2=8.40 ±2.59	V=103 p=0.22 X_1=11.17 ± 2.42 X_2=10.04 ± 3.10	V=33 **p=0.04 *** X_1=1.63 ±2.07 X_2=2.07 ±0.85	V=127, p=0.93 X_1=38.40 ±15.48, X_2= 38.21 ±12.80	V=114 p=0.08 X_1=74.84 ±9.64 X_2=72.79 ±9.52	V=57 p=0.38 X_1=157.78 ±22.87 X_2=161.23 ±25.98

Square transformation for Peak ascent speed

Supplementary Table 2.3: Summary of the foraging time (h) and amount of prey (kg.day^{-1}) required to meet the Daily Energy Expenditure (DEE) (kJ.day^{-1}) of each shark, corrected for the average temperature as well as the temperature range (min. and max) experienced during tag deployment. Foraging times were estimated for both the mean (2.41 g.m^3) and threshold (0.62 g.m^3) prey densities.

	Threshold	Temperature (˚C)	DEE (kJ.day^{-1})	Prey (kg.day$^{-1)}$	Time (h)	
					Thresh. dens (0.62 g.m^{-3})	Mean dens. (2.41 g.m^3)
Shark 1	Mean	14.3	12061.35	2.39	18.61	4.79
	Min	14	11774.61	2.34	18.17	4.67
	Max	15	12757.84	2.53	19.69	5.07
Shark 2	Mean	14.6	20832.54	4.13	54.04	13.90
	Min	10.7	15237.14	3.02	39.52	10.17
	Max	15.4	22212.97	4.41	57.62	14.82
Shark 3	Mean	14.3	20337.29	4.04	52.75	13.54
	Min	13.8	19537.9	3.88	50.68	12.99
	Max	15	21511.69	4.27	55.80	14.47

Supplementary Table 2.4: Summary statistics for the difference in recovery period between 15 min following a breach and an hour later. The mean depth, speed, VeDBA and TBA was calculated over a 15 min window after the end of the descent of the last breach (X_{15}) and compared to a subsequent 15 min window an hour after the breach (X_{60}) using Wilcoxon signed rank tests. P values highlight no difference in recovery periods.

	Depth (m)	Speed ($m.s^{-1}$)	VeDBA (g)	TBA (Hz)
Test	V=451	V=405	V=657	V=1096
p-value	p=0.46	p=0.62	p=0.12	p=0.50
mean ± sd	X_{15}=18.67 ± 8.14 X_{60}=19.70 ± 9	X_{15}=0.19 ± 0.13 X_{15}=0.18 ± 0.14	X_{15}=0.32 ± 0.19 X_{15}=0.28 ± 0.12	X_{15}=0.08 ± 0.04 X_{60}=0.08 ± 0.05

Supplementary Table 3.1: Summary table of translocation studies on sea turtles. The number of rehomed turtles and the duration of the rehoming journey is indicated when available.

Reference	Species	Age class	Distance	Duration
Ireland 1980	10 green turtles	Juveniles	1.5 – 4 km	N=6 rehomed within 24 hours N=1 rehomed within 2 days
Luschi et al. 1996	4 green turtles	Adult post-nesting females N=1 translocated	Experiment 1: 11 km Experiment 2: 284 km	Exp 1: 7.7 hours Exp 2: 7 days
Luschi et al. 2001	18 green turtles	Adult nesting females	215 ± 172 km Range: 60-450 km	N=10 rehomed in 12 ± 13 days Range: 2-45 days N=8 moved towards Brazil
Akesson et al. 2003	Same data as Luschi et al 2001			
Avens et al. 2003	405 Loggerhead turtles	Juveniles N=207 translocated of which n=28 radio tracked	15-20 km	17% (n=35) recaptured in home range within the same year (similar recapture proportion as controls) N=9 <1 week N=16 <2 weeks

				Of tracked turtles n=4 successful tracks, homed in 3-5 days
Hays et al. 2003	6 green turtles	Adult nesting females	50 km	N=5 rehomed 9 ± 11 days Range:1-27 days N=1 failed to find Ascension island and headed toward Brazil
Luschi et al. 2003	5 loggerhead turtles	Adult post-nesting females	1175 ± 572 km Range: 1148-2193 km	N=2 returned to feeding ground within 46 and 61 days N=1 tracked for 143 days but authors unsure of location home grounds N=2 oceanic wandering
Girard et al. 2006	3 green turtles	Adult nesting females	158 ± 75 km Range: 115-245 km	31 ± 25 days Range: 13-59 days
Luschi et al. 2007	20 green turtles	Adult nesting females N=13 pre-	100-120 km	N=19 returned within 2-29

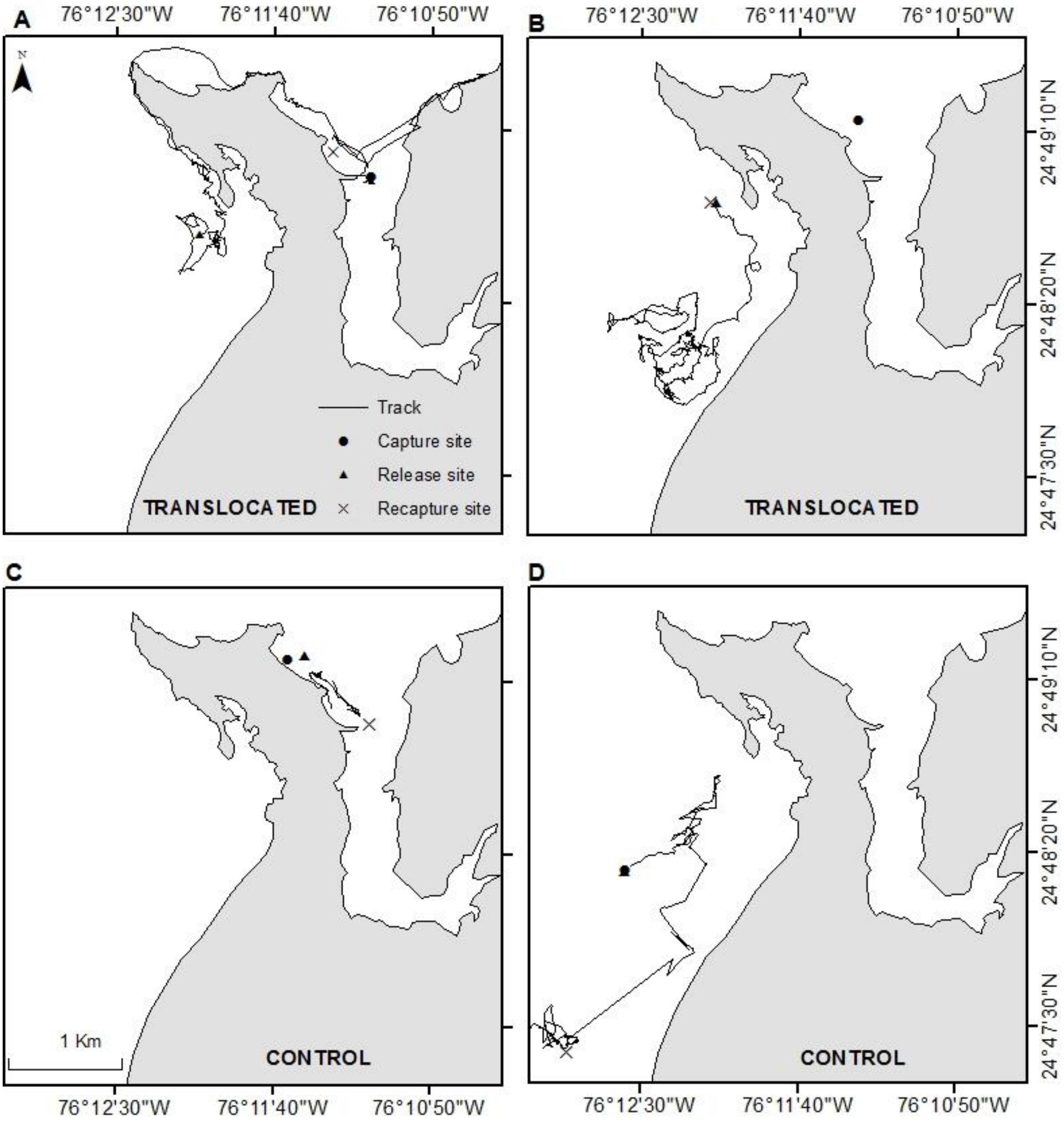
		nesting N=7 post-nesting Controls: n=7 Magnet-treated (MT): n=6 Magnet-attached (MH): n=7		days N=1 tracked to 140 km westward of nesting beach
Benhamou et al. 2011	24 green turtles	Adult nesting females	190-200 km	Controls: 10 ± 2 days Magnet-treated: 14 ±4 days Magnet-attached: 21 ± 7 days
Shimada et al. 2016a	22 green turtles	Adult females and males	Mean ± SD = 18.0 ± 4.6 km Range: 8 to 28.1 km	NA
Shimada et al. 2016b	79 green turtles 30 loggerhead turtles 2 olive ridley turtles 1 hawksbill turtle (n=58 translocated, CM=43, CC=13, LO=2)	Adult (n=92) and juvenile (n=21) turtles of both sexes Translocated Adults: 48 Translocated Juveniles:10	Adults: 19.6 ± 13.5 km Range 7.7 to 100.9 km Juveniles: 68.7 ± 132.6 km Range 6.6 to 432.1 km	Green turtles mean: 1.95 days Range: 0.36-21.15 days Loggerheads: 3.03 days Range 1.06-4.35 days
Enstipp et al. 2016	1 green turtles	Adult female post-nesting	150 km	4.5 days

Supplementary Table 3.2: Summary table of turtle straight carapace length (SCL), curved carapace length (CCL), curved carapace width (CCW) and weight.

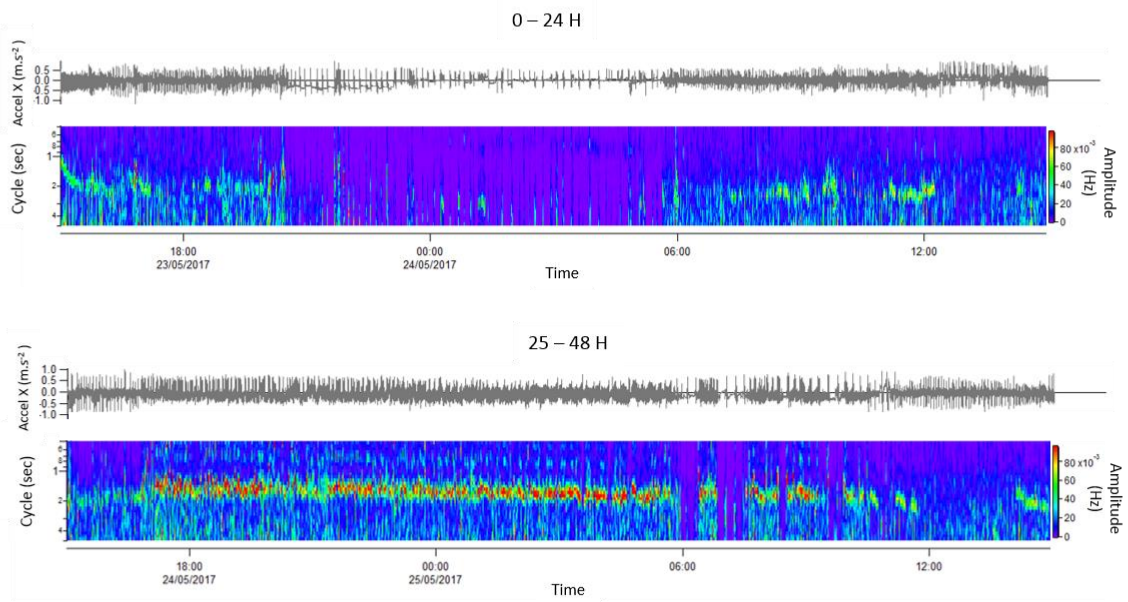
Turtle	Treatment	SCL (mm)	CCL (mm)	CCW (mm)	Weight (kg)
T1	Control	539	576	518	22.5
T2	Control	490	522	468	18
T3	Translocated	523	549	463	19
T4	Translocated	523	552	483	19
T5	Translocated	438	456	403	11.5
T6	Control	547	580	507	21.5
T7	Translocated	385	401	360	7.5
T8	Control	408	435	398	8.5
T10	Control	407	434	392	8.5
T11	Control	396	415	351	10.5
T12	Control	491	523	469	18
T13	Control	541	577	520	22.5
T14	Translocated	491	523	469	18
T15	Translocated	541	577	520	22.5
T16	Translocated	486	522	462	18
T17	Translocated	387	410	348	8.5
T18	Translocated	434	467	419	11
T19	Translocated	454	483	411	12.5
T20	Translocated	384	414	342	7
T21	Translocated	512	543	492	19
Total mean ± sd		469 ± 59	498 ± 64	440 ± 61	15.2 ± 5.6
Translocated mean ± sd		470 ± 60	498 ± 64	437 ± 61	15 ± 5.5
Control mean ± sd		467 ± 63	498 ± 69	445 ± 66	15.5 ± 6.2

Supplementary Table 3.3: Summary table of statistical significance of Rayleigh test of uniformity for turtles' swimming direction for the entire tracking length and for each phase of homing behaviour

Turtle	Treatment	Total track	Release site to headland	Headland	Headland to capture location
T4	Translocated	t=0.23 p=0.79	t=0.20 **p<0.01**	t=0.6 **p<0.001**	t=0.19 **p<0.01**
T5	Translocated	t=0.02 p=0.73	-	-	-
T6	Control	t=0.06 p=0.39	-	-	-
T7	Translocated	t=0.11 **p<0.001**	t=0.19 **p<0.001**	t=0.75 **p<0.001**	t=0.36 **p<0.001**
T8	Control	t=0.17 **p<0.001**	-	-	-
T11	Control	t=0.12 p=0.18	-	-	-
T12	Control	t=0.18 **p<0.001**	-	-	-
T13	Control	t=0.16 **p<0.1**	-	-	-
T14	Translocated	t=0.37 **p<0.001**	-	-	-
T15	Translocated	t=0.24 **p<0.001**	-	-	-
T17	Translocated	t=0.49 **p<0.001**	-	-	-
T19	Translocated	t=0.29 **p<0.001**	-	-	-
T20	Translocated	t=0.28 **p<0.001**	-	-	-
T21	Translocated	t=0.28 **p<0.001**	t=0.25 **p<0.001**	t=0.87 **p<0.01**	t=0.72 **p<0.001**



Supplementary Figure 3.1: Maps showcasing four types of tracking behaviours, with circles representing turtles' capture location, triangles the release site and crosses where turtles were recaptured following tag deployment. (**A & B**) Tracks of turtles translocated to Poison Creek, with (**A**) rehoming to Starved Creek, and (**B**) remaining in Poison Creek. (**C**) Control turtle tracked in Starved Creek and (**D**) control turtle tracked in Poison Creek.



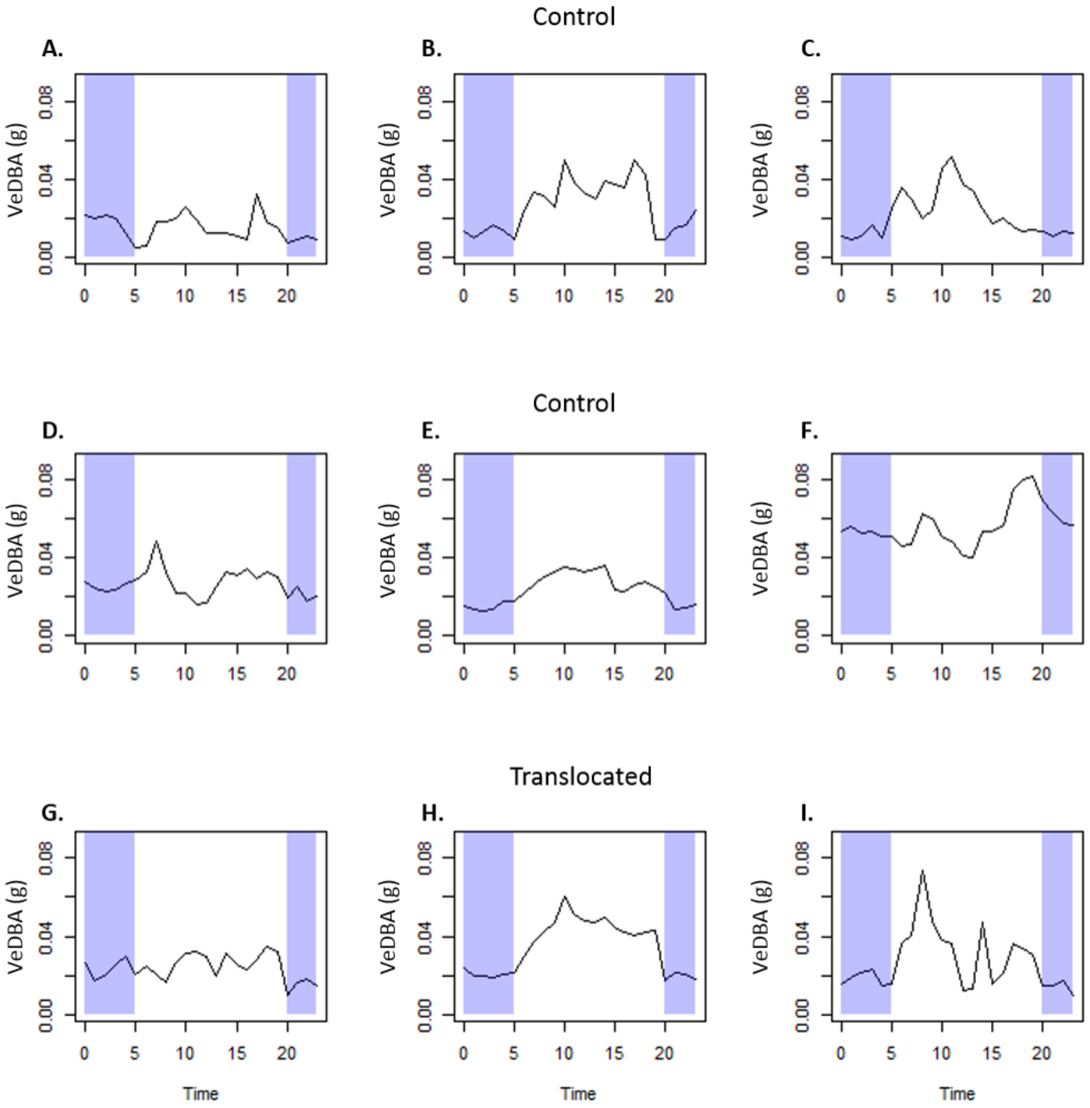
Supplementary Figure 3.2: Spectrogram showing the heave (X) axis of accelerometry collected from turtle 11's first and second day of tracking following deployment, where the intensity of the colour corresponds to the amplitude of the signal. While turtle 11 displayed clear diel patterns of activity during the first 24 hours, whereupon signal amplitude was low between sunset and sunrise times (20:00 – 06:00), abnormal swimming behaviour with high signal amplitude observed between 16:50 24th May 2017 – 06:00 25th May 2017.

Supplementary Table 3.4: Summary table of mean VeDBA, Dominant Stroke Frequency (DSF) and Flipper Beat Amplitude (FBA) between the first 24 hours and 25-48 hours after release for each turtle. Statistical differences are highlighted in bold. X1 mean for first 24 h, X2 for 25-48 hours.

Turtle	Treatment	VeDBA (g)	DSF (Hz)	FBA (Hz)	Dive Number	Dive duration (min)
T1	Control	Wilcoxon signed rank test V=160, p=0.79 X1=0.02 ± 0.01 X2=0.01± 0.01	Wilcoxon signed rank test V=191 p=0.25 X1=0.69 ± 0.30 X2=0.60 ± 0.26	Wilcoxon signed rank test V=165 p=0.68 X1=0.02 ± 0.02 X2=0.03 ± 0.01	Paired t-test log transform t=2.2, df=23, **p=0.03** X1=20 ±10.3 X2= 14.8 ± 7	Paired t-test log transform t=2.2, df=23, **p=0.04** X1=3.8 ± 1.9 X2=5 ± 2.4
T2	Control	X1=0.03 ± 0.01	X1=0.54 ± 0.20	X1=0.03 ± 0.02	NA	NA
T4	Translocated	Paired t-test t=3.65, df=23, **p<0.01** X1=0.03 ± 0.01 X2=0.02 ± 0.08	Paired t-test Log transform t=0.54, df=23, p=0.6 X1=0.50 ± 0.17 X2=0.53 ± 0.21	Paired t-test t=3.43, df=23, **p<0.01** X1=0.04 ± 0.02 X2=0.02 ±0.01	Log transform T=2.41, df=23, **p=0.02** X1=25.5 ± 12.6 X2=17.3 ± 5.7	Square root transform T=2.18, df=23, **p=0.04** X1=3 ± 1.7 X2=3.8 ± 1
T5	Translocated	t=0.36, df=20, p=0.72	V=82, p=0.26	t=0.63, df=20, p=0.53	Log transform t=1.94, df=23, p=0.07	t=0.80, df=23, p=43

		X1=0.03 ± 0.01 X2=0.03 ± 0.01	X1=0.40 ± 0.1 X2=0.45 ± 0.17	X1=0.04 ± 0.01 X2=0.04 ± 0.01	X1=44.2 ± 26.5 X2=34.6 ± 12.2	X1=1.8 ± 0.9 X2=1.9 ± 0.7
T6	Control	V=173, p=0.53 X1=0.02 ± 0.01 X2=0.02 ± 0.01	t=0.25,df=23 p=0.80 X1=0.53 ± 0.09 X2=0.53 ± 0.18	V=153, p=0.94 X1=0.02 ± 0.02 X2=0.02 ± 0.02	t=1.65, df=23, p=0.11 X1=18.2 ±9.2 X2=14.9 ± 8.9	t=1.80, df=23, p=0.09 X1= 4.1 ± 1.9 X2=5 ± 2
T8	Control	t=5.88, **p<0.001** X1=0.03 ± 0.01 X2=0.02 ± 0.01	V=53, **p<0.01** X1=0.46 ± 0.12 X2=0.53 ± 0.14	Square root transform t=3.75, **p<0.001** X1=0.04 ± 0.02 X2=0.03 ± 0.01	Log transform t=3.49, df=28, **p<0.01** X1=37.6 ± 19.5 X2=25.1 ± 7.1	t=3.27, df=23, **p<0.01** X1=1.9 ± 0.8 X2=2.6 ± 0.7
T10	Control	V=125 p=0.49 X1=0.02 ± 0.01 X2=0.02 ± 0.01	Square root transform t=0.24, df=23, p=0.81 X1=0.49 ± 0.10 X2=0.49 ± 0.14	Square root transform t=1.04, df=23, p=0.31 X1=0.02 ± 0.01 X2=0.02 ± 0.01	Log transform t=4.30, df=23, **p<0.001** X1=23.2 ± 12.6 X2=15.9 ± 5.4	t=4.9, df=23, **p<0.001** X1=3.1 ± 1.2 X2=4.2 ± 1.2
T11	Control	V=12, **p<0.001**	V=147, p=0.94	Square root transform T=5.67,		

		X1=0.03 ± 0.02 X2=0.08 ± 0.03	X1=0.56 ± 0.1 X2=0.55 ± 0.1	df=23, **$p<0.001$** X1=0.03 ± 0.02 X2=0.07 ± 0.02	NA	NA
T19	Translocated	V=194, $p=0.22$ X1=0.03 ±0.02 X2=0.03 ±0.01	V=100, $p=0.16$ X1=0.46 ±0.02 X2=0.59 ± 0.02	V=231, **$p<0.05$** X1= 0.04 ± 0.02 X2=0.03 ± 0.03	NA	NA



Supplementary Figure 3.3: Line plot showing variation in hourly mean VeDBA of all nine turtles tracked with OpenTags for the first 48 hours following release, where **A-F** are control turtles and **G-I** translocated turtles. The shaded areas correspond to the nocturnal period, and clear background to daylight hours. Turtles became active following sunrise and displayed peak activity levels in the middle of the day before decreasing at dusk.

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