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Using acoustic and satellite tracking data to better understand the factors associated with marine mammal habitat use and movements within urban coastal environments: dugongs in Moreton Bay, Queensland

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Dugong. Illustration by D Zeh in watercolour, 2022.

Dedication

This thesis is dedicated to my fiancée Deborah Moran who put off her own career plans for years to support my devoting all my time to writing. Deborah also postponed our wedding several times so that our life together would not be caught up in thesis activity. These years were filled with months apart for which I had failed to plan. Deborah, you have my undying gratitude for your love, patience, and support. I am so grateful you stuck it out. Now let's get the wedding moving!

Statement of the Contribution of Others¹

Thesis Chapter	Publication on which based	Role of each author
1	General Introduction	Zeh wrote the chapter with the assistance of Marsh in editing.
2	Methods based on chapters 3 - 6	Zeh wrote the chapter with the assistance of Marsh in editing. Heupel and Marsh co- designed the study and gained the funding. Babcock and Pillans contributed to the acoustic array design and initial deployment in season 1 and uploaded the acoustic data in season 1. Townsend deployed the acoustic array for seasons 2-3 and uploaded the acoustic data. Limpus led the team that undertook dugong capture and release for seasons 1-3. Zeh was a member of the fieldwork team and prepared the acoustic and satellite transmitters and built the harnesses. Powell helped redesign the harness attachment used for Season 2 and 3. Limpus retrieved satellite transmitters for re-use
3	Zeh DR, Heupel MR, Limpus CJ, Hamann M, Fuentes MMPB, Babcock RC, Pillans RD, Townsend KA, Marsh H. 2015. Is acoustic tracking appropriate for air-breathing marine animals? Dugongs as a case study. Journal of Experimental Marine Biology and Ecology 464 :1-10.	Zeh wrote the chapter. Marsh, Heupel, and Hamann assisted Zeh in analysing and interpreting data. Fuentes contributed costing scenarios. All authors contributed to the editing.
4	Zeh DR, Heupel MR, Hamann M, Limpus CJ, Marsh H. 2016. Quick Fix GPS technology highlights risk to marine animals moving between protected areas. Endangered Species Research 30 :37-44.	Zeh wrote the chapter. Marsh, Heupel, and Hamann assisted Zeh in analysing and interpreting data and editing.

¹ The full names of the persons mentioned in this table are provided in the Acknowledgements below

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6	Zeh DR, Heupel MR, Hamann M, Jones R, Limpus CJ, Marsh H. 2018. Evidence of behavioural thermoregulation by dugongs at the high latitude limit to their range in eastern Australia. Journal of Experimental Marine Biology and Ecology 508:27-34	Zeh analysed satellite and acoustic data in coordination with Marsh and Heupel and wrote the chapter with the assistance of Marsh, Heupel, Hamann and Limpus. Jones also assisted Zeh with statistical analysis.
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Abstract

Information on the space use of marine mammals is critical to the design of effective management interventions because increasing numbers of marine mammals are listed as threatened. Acoustic telemetry has revolutionised the tracking of many aquatic species because it enables their movements to be studied in three dimensions irrespective of whether they return to the surface to breathe. Although acoustic tracking has become the method of choice for marine species that rarely or never come to the surface, such as such as sharks, rays and teleosts, it has rarely been used for marine mammals, which are surface breathers. As acoustic telemetry becomes more widely practiced, receiver arrays are being deployed in increasing numbers of locations to provide data on the movements of individual organisms, especially coastal species but questions remain about whether these arrays could also be used to study the movements and habitat use of co-occurring marine mammals.

Sirenians should be better-suited to acoustic technology than most other coastal marine mammals because their hearing frequency does not overlap the acoustic transmitter frequencies. Within the sirenia, the methods should be best suited to the Vulnerable dugong, which make much more use of 3-dimensional space than any of the three species of manatees.

This thesis explored the potential of acoustic technology to track dugong movements and habitat use by comparing for the first time, acoustic and GPS/satellite technologies to track dugongs in an urban coastal environment. Its substantive original contribution to knowledge is proof of concept that acoustic technology is potentially an important addition to the marine mammal tracking toolbox, especially in coastal areas with one or more acoustic arrays.

I used data from GPS-satellite and acoustic technologies to determine the efficacy of satellite and acoustic telemetry to document the 2- and 3-dimensional space use of dugongs in the vicinity of an acoustic array in a high density dugong area established in the Eastern Banks-South Passage area of Moreton Bay, near Brisbane Australia. I fitted 30 dugongs (29 individuals; one repeat fitting) with GPS and acoustic transmitters over three years and compared the benefits and limitations of each approach from the perspectives of animal welfare, information on 2- and 3-dimensional space use, tracking duration, and cost. I concluded that both technologies generally provided comparable information on 2- dimiensional space use in the vicinity of the array, but that acoustic telemetry enabled individual dugongs to be tracked for longer and provided superior data on their 3-

dimensional space use. GPS technology was superior to acoustic technology for studying long-range movements such as those beyond the spatial footprint of the receiver array. I concluded that the relative merits of the two technologies depend on the research question in the context of the species of interest, the location of the study, and whether the study site has an established acoustic array.

My research provided new insights into dugong behaviour, demonstrating that behaviour in three dimensions is as individualistic as in two dimensions and raising questions about the reason for two animals, both females, spending considerable periods at depths of >10 m in Moreton Bay where seagrass has only been detected to 7m. I also found further evidence for dugongs using behavioural thermoregulation in winter at the high latitude limits of their range by taking advantages of the tides to move between the seagrass banks of Moreton Bay to warmer oceanic waters outside the bay where seagrass has not been detected. Additional results from GPS/satellite data suggested a coastal movement corridor for dugongs between Moreton Bay and Hervey Bay. These results indicate the need for place-based dugong management to consider areas beyond seagrass communities.

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Chapter 1

General Introduction

1.1 Marine mammal distributions, movements, and habitat use

Marine mammals today are highly valued as charismatic megafauna although many species were hunted for meat and oils nearly to extinction (Mazzoldi et al. 2019). Nonetheless, increasing numbers of species are listed on the IUCN Red List of Threatened Species (IUCN 2020). Information on the unknown or undocumented space use of marine mammals can support conservation and management efforts and is important for designing effective management interventions but such information is challenging to obtain. Implementing the results into policy changes depends on whether the results can be explained in terms that fit the existing conservation issues and whether policymakers are focusing on those particular issues (Hays et al. 2019).

Many marine mammals move extensively, and most species are difficult to track because they spend most of their time underwater, except for minimal exposure while breathing. Satellite tracking has proven effective for collecting movement data for many species of marine mammals, including dugongs (*Dugong dugon*, Müller 1776), but can have limitations of bandwidth (to transmit all the available data to the satellite), battery life, and initial expense (Chung et al. 2021). In this chapter, I compare how acoustic and satellite technologies have been utilised to collect the data required for movement and habitat analyses for the management of marine fauna of conservation concern. I then explain the potential for acoustic tracking to inform dugong conservation management and how acoustic technology is well suited to trial with dugongs, providing the rationale for the objectives of my research. I conclude by outlining the structure of this thesis.

Marine mammals are a diverse group of megafauna that live all or most of their lives near or in the ocean or freshwater bodies of water. There are over 130 marine mammal species, grouped into four categories: cetaceans (order: Cetartiodactyla: whales, porpoises, and dolphins), pinnipeds (order: Pinnipedia: seals, sea lions, walruses), sirenians (order: Sirenia: dugongs and manatees), and marine fissipeds (order: Carnivora: polar bears, sea otters) (Committee on Taxonomy 2020; Hoyt 2018).

Many of these species are now on the IUCN Red List (IUCN 2021) as a result of threats from a growing list of anthropometric causes (Nelms et al. 2021). While many threats and their causes can be identified individually, their cumulative impacts on ecological and

physiological processes are difficult to quantify (Breitburg and Riedel 2005). For example, chemical pollutants typically have long-term consequences in addition to the immediate impacts of accidents like oil spills (Takeshita et al. 2017). Nevertheless, identifying the threats with the most significant immediate and long-term impacts can help prioritise appropriate mitigation.

Avila et al. (2018) analysed over 1780 publications (covering 1991 to 2016 and 121 species) and concluded that, in over 50% of marine mammal core habitats, the threats affecting the greatest number of species (> 60% of those reviewed) originate from direct human activities including incidental catch from fisheries (bycatch), direct harvesting (whaling and hunting), vessel strikes and tourism. Specific technological tools are being developed to mitigate problems like vessel strikes through careful monitoring of ships and the affected species (Cope et al. 2020). However, there are many additional threats (described as anthropogenic trauma by Bárcenas de la Cruz et al. 2018) causing long-term damage to marine mammal populations that are unlikely to be addressed by technological solutions and require other approaches to modify human behaviour towards marine mammals.

The habitats of many marine mammals, especially coastal species, are frequently disturbed by recreational and commercial fishing, recreational boating, shipping, and urban growth (Anderson 2001; Reijnders et al. 2009). Additionally, the many sources of resultant noise pollution in the ocean today are of serious concern because of the habitat disturbance that these sources create with resultant displacement of marine mammals. Ship and watercraft noise can interrupt their acoustic behaviour (e.g., communication) and reduce foraging success by interfering with their capacity to locate prey (for species that catch mobile prey for food) or prevent animals from reaching their feeding areas (for species like dugongs that feed on stationary forage) (Di lorio and Clark 2010; Erbe et al. 2019; Tyack 2009). Impulsive noise from geophysical research such as that caused by seismic air guns and high-intensity sonar, and the loud, low-frequency sounds created by pile-driving associated with the construction of off-shore wind farms can also cause behavioural responses in marine mammals as well as masking the sounds they use to communicate. The magnitude of these impacts, which may cause auditory damage or death (Parsons 2017; Schrope 2002), depends on substrate, the depth of the water and the distance between the sound source and the marine mammal (Bröker 2019; Erbe et al. 2016; Hastie et al. 2019). Tracking the movements of affected marine mammals provides information that can inform planners and managers of the likely consequences of such activities which, in turn, may help to minimise their impact.

The gradual increase of ocean temperatures as a result of climate change is another substantial environmental threat to marine mammals (Anderson 2001; de Vere et al. 2018; Sousa et al. 2019). Some marine mammals may be able to adjust to variations in ocean temperature via thermoregulation but will still likely be affected indirectly by changes to the life cycles and abundance of their prey/food and habitat degradation. These changes can lead to significant impacts on populations (Evans et al. 2010; Simmonds and Eliott 2009) including restricting movements as for terrestrial mammals (Tucker et al. 2018). For polar marine species that are highly dependent on sea ice and exhibit strong site fidelity, increasing ocean temperatures accelerate the loss of sea ice and are already threatening their survival but other species with larger, migratory populations may be more resilient to change (i.e., more resistant to disease and stress; see Moore and Reeves 2018). Most affected species are difficult to observe. Thus, tracks of their movements combined with remotely sensed environmental data can provide insights on the abilities of different species to adjust to changing conditions.

Some species of marine mammals are more vulnerable to climate change than others. Albouy et al. (2020) compared the characteristics of the 20 marine mammals most vulnerable to increasing temperatures under three greenhouse gas emission scenarios. The dugong was included in this highly vulnerable group because it exhibits a unique combination of functional traits, based on its taxonomic distinctiveness, strictly marine habitats, and dependence on seagrass communities. Although conservation managers typically have little direct influence on mitigating climate change, reducing other anthropometric impacts on the movements and habitat use of marine mammals such as the dugong can increase their resilience to climate change.

The likelihood of population maintenance is enhanced by understanding how a population uses key habitats; not only what the animals do and where they go, but understanding and, if possible, separating the influence of environmental variables (e.g., temperature) and spatial characteristics (e.g., distance or neighbourhood abundance) on the animals' ecology (Currie 2007). Food preferences and avoidance of competition (or predation) are normally important factors in habitat use (Evans et al. 2010) and influence the movements of individuals. Documenting various types of movement, particularly dispersal, migration, home range and eruption (irregular movement into areas not usually occupied) is important for habitat management (Morrison et al. 2006). The conservation value of tracking marine mammals depends on whether the resultant knowledge can be applied to the conservation planning and management of threats to threatened species. Fraser et al. (2018) analysed 13,349 movement ecology papers published between 1990 and 2014 across animal taxa and found

that explicit connections to conservation and management were made in 35% (n = 4,672) of these papers, including status assessments and recovery plans (n = 72 documents) for 12 endangered mobile species. This analysis demonstrated that when the results of movement ecology are available, the research informs conservation planning about a third of the time.

The range of questions that can be addressed through tracking include understanding which abiotic factors are associated with the movements and spatiotemporal distribution of species (Bailey et al. 2019). Such factors include how migration patterns might change due to global warming, identifying the major drivers of long-distance movements, how risk from predators changes when home ranges change, identifying hot spots on a global scale and how the analysis of movement data translates into the development of conservation policy (Hays et al. 2019; Hays et al. 2016). Successful marine mammal conservation requires managing human influences on many species found in the marine environment and is enhanced by understanding of their behavioural ecology.

Evaluating the impact of human activities on a species' habitat and nearby areas and identifying areas of conflict (e.g., from commercial and recreational boat traffic, coastal zone development, oil and gas surveys, wind farms) informs the determination of whether mitigation is possible or necessary (Ayram et al. 2017). An early step in such evaluation is to understand the species' population by identifying the critical and differentiating characteristics of the habitat use and movements of individuals within that population. The boundaries of core habitats can be defined by following individual movements and identifying home ranges (Vander Wal and Rodgers 2012; Wilson et al. 2017), including pinpointing the differences between populations that succeed in one area from those declining in other areas. Repeated observation of identifiable individuals can also establish how many individuals are in a population and the trend in their abundance, what areas make up their home ranges and the behavioural variations driving how the species uses the habitat (Wells 2009). The resulting knowledge base aids management decisions on whether to protect a large area or a chain of smaller areas (Di Sciara et al. 2016).

Natural features are used to identify individual marine mammals based on colour patterns, scars, and notches in specific body areas (e.g., flukes, dorsal fins with flank, Wells 2009). Catalogues of photographs are used to identify and re-identify individuals. This technique has been particularly useful for cetacean species that are not readily tracked (Hammond et al. 1990) using other techniques.

The mark-recapture method is central to estimating the abundance, survival rates, and/or behaviour of many large cetacean species including blue whales (*Balaenoptera musculus*) (surfacing and diving characteristics in Sri Lankan waters, de Vos et al. 2013), humpback whales (*Megaptera novaeangliae*) and killer whales (IWC 1990), as well as many smaller coastal species such as bottlenose dolphins, (*Tursiops truncatus*). The basic dataset is the number of times identified individuals have been spotted (or not) during one or more surveys, most often via photo-identification (Hammond et al. 1990). The analysis of the sighting data can shed light on human-animal interactions. For example, using photo identification as the base for a boat-based mark-recapture dolphin survey, Allen et al. (2017) showed that some individual dolphins (*Tursiops truncatus*) associate with fishing trawlers to forage, information useful for investigating the impacts of bycatch.

The successful use of photographic records requires repeated visual sightings of individuals. The difficulty in following marine mammals when the target animals spend so much of their time underwater limits the information on space use that can be obtained from mark-recapture studies. In addition, this approach is challenging for species that move huge distances over oceanic environments. As a result, other tagging methods have been developed to follow species throughout the difficult marine environment. Some tags are relatively simple in design, although their application can be complicated due to the difficulty of handling the animal and identification after release. For example, titanium turtle tags have been attached to dugongs (Beck and Clark 2012) but these tags cannot be read without recapture (Lanyon et al. 2002). A similar problem arises with miniaturised passive integrated transponder (PIT) tags, which can provide unique identification but can only be detected within 15 cm making them useful for identifying a dead or captured animal but not useful for surveys (Beck and Clark 2012).

The use of DNA profiles to uniquely identify individuals of various species and to determine family structures within populations (Hammond 2009) has become an established tool in marine mammal research since the 1990s and overcomes some of the disadvantages discussed above. DNA tissue samples can be collected while an animal is restrained, but for species that are impractical to capture, samples can be taken using a hollow-tipped arrow fired from a crossbow or airgun (see Barrett-Lennard et al. 1996).

The advantage of DNA profile analysis is that movement between habitats can be established along with family structure. Cope et al. (2015) profiled 1002 dugongs in four locations in Queensland yielding 525 parent-offspring relationships. 30% of parents captured in Moreton Bay and Great Sandy Straits had at least one offspring that was sampled in a

different location indicating that movements between these locations, which are about 300 km apart, are much more frequent than indicated by the satellite tracking of a small number of individuals.

While ID methods are important for identifying individuals, most marine species are difficult to observe when moving through the water, so researchers go to tracking hardware to gather movement data. Tracking analyses typically focus on movements of the target species along with habitat preferences and habitat use irrespective of whether the movements are local, regional, or greater. To track a marine mammal that frequently travels relatively short distances, a common tracking method is to attach a VHF (very high frequency) radio transmitter to the animal with the researcher (who may be nearby but not necessarily with sighting distance) following the movements using a receiver and taking frequent location data points using a GPS (global positioning system) receiver. For large marine mammals that travel longer distances, scientists have collected fine-scale data on their movements over relatively short time spans using equipment attached via suction cups or using pronged darts. In a comparison, suction cups attachment was usually less than 24 hours; stainless steel dart attachment lasted over a month in tests on blue and humpback whales (Szesciorka et al. 2016). Suction cup tags have recently been used for short-term detailed studies of dugong diving behaviour (Cleguer et al. in prep) but these tags detach after a few days. Transmitters and other data collection devices are also glued on pinnipeds since the epoxies can cure during haul-out.

For some marine mammals making longer movements that make following impractical or for following movements over a longer period, the researcher may attach a unit consisting of a PTT (platform transmitter terminal) with an integral GPS unit that transmits location data at regular intervals to an ARGOS satellite for processing and download (hereafter referred to as satellite-GPS). Satellite-GPS units can collect data for months without the researcher being present. With either option, transmitters can be set at different frequencies to allow for several animals to be tracked simultaneously. Technology improvements from PTT manufacturers have enabled the collection of location data with greater accuracy and precision while requiring increasingly shorter time at the water surface to transmit a complete signal. For example, PTTs with Quick Fix Pseudoranging (QFP, Telonics Inc, Arizona USA) can calculate positions in as little as 5 seconds. Fastloc (Wildtrack Telemetry Systems Ltd, Leeds, UK) can pinpoint locations in milliseconds of GPS signal. Both these technologies are particularly suited for marine mammal tracking applications.

Examples of studies using satellite-GPS technology on marine mammals are plentiful. In addition, analysis of tracking data can help understand the environmental factors associated with the animals' movements and provide information on overlaps and/or conflicts between species and individuals within species, and between species and human activities. Jiménez-López et al. (2019) followed 11 fin whales (Balaenoptera physalus) in the Gulf of California, Mexico using ARGOS satellite tags and collected tracking data for up to six months. The resulting models showed the location of preferred habitats and areas important to seasonal migrations. Double et al. (2014) tracked Pygmy blue whales (Balaenoptera musculus brevicauda) moving between Australia and Indonesia using ARGOS satellite tags with a customised attachment device. The whales mostly travelled within 100 km of the Australian coast, identifying a migration corridor. Baird et al. (2012). attached ARGOS satellite tags to false killer whales (*Pseudorca crassidens*) from two different populations using titanium anchors and supplemented the data with photo ID data. The whales' core habitat was described from the satellite data, but further analysis showed that habitat use overlapped with longline fisheries and that the two populations, thought to be well-separated, occasionally overlapped.

Newer technologies have been adapted for tracking as they have become available. For example, tracking using cell phone technology was applied to a conflict stemming from the overlap of grey seal (*Halichoerus grypus*) distribution and local fisheries operating in the Celtic Shelf and Irish Sea (Cronin et al. 2016). Many fishermen believed that their catch was negatively impacted by the presence of grey seals and pushed for them to be culled. In this case, the analysis from a tracking technology based on GPS phone tags showed that direct competition was relatively low, suggesting that culling grey seals was unnecessary (Cronin et al. 2016). In the Hawaiian Islands, data from GPS phone tags supported the identification of the home ranges and diving patterns of individuals from different monk seal (*Neomonachus schauinslandi*) sub-populations. Monk seals residing within the main Hawaiian Islands spent less time foraging at sea (less effort) but still had higher pup survival rates and pups that were in better condition than seals in other Hawaiian Island areas (Wilson et al. 2017).

The time-depth recorder or TDR is an important tool that has been developed to illuminate diving and underwater movements. Time-depth recorders can record temperature measurements allowing the relationship between the animal and its environment to be directly measured rather than inferred through remotely sensed data (Evans et al. 2013). Time-depth recorders are often used to in conjunction with satellite tracking to obtain detailed information on underwater activities linked to the location of the marine mammals as

Hagihara (2015) demonstrated during her dugong research. Tracey et al. (2014) and Udyawer et al. (2019) also used the combination of time-depth recorders and satellite tracking to create three-dimensional (3D) activity spaces illustrating dugong dive behaviour in Hervey Bay, Queensland, Australia and the Gulf of Carpentaria, Northern Territory, Australia, respectively.

Such combinations of technologies have enabled a richer understanding of the underwater movements of marine mammals. GPS-GSM phone tags used with ARGOS satellite or VHF transmitters have produced data for species that frequently haul out. Lactating California sea lions (*Zalophus californianus*) were tracked using a combination of satellite transmitters, time-depth recorders, and radio (VHF) transmitters (Briscoe et al. 2018; Kuhn and Costa 2014). Results illustrated that the distribution of place-constrained species could be clarified by examining habitat selection based on prey availability augmented by remote-sensed environmental variables. Bailey et al. (2014) combined VHF and ARGOS satellite with GPS-phone telemetry to study harbour seals (*Phoca vitulina*). Habitat preference (defined as the ratio of the use of a habitat area over the availability of that habitat (Aarts et al. 2008) was significantly associated with water depth, seabed slope, distance to nearest haul-out site, and sediment type.

Researchers have also applied passive acoustic monitoring methods (recording natural sounds, not originating from an acoustic transmitter) to determine location, assess abundance, and/or to follow migration of marine mammals that frequently communicate, or use sounds underwater (e.g., the gray whale (*Eschrictius robustus*), Burnham and Duffus 2019). The distribution of dugong groups was defined via data accumulated from acoustic (passive) observations in Japan and Thailand (Ichikawa et al. 2012; Ichikawa et al. 2004; Ichikawa et al. 2009).

1.2 Acoustic Tracking

Acoustic transmitters attached to the target species and transmitting signals received by fixed-mounted underwater receivers have been used efficiently to track many marine animals (especially fish, sharks, and rays) that are rarely seen at the water's surface. The transmitters are light weight (acoustic 9-16 g vs PTT 1.2–2.6 kg) and much less expensive than satellite tags (acoustic ~\$900 vs PTT ~\$3000). Active acoustic tracking requires an array of acoustic receivers that can collect signals from many different transmitters across species, enabling the cost of the receivers, receiver deployment, and subsequent data collection to be socialised among many projects. Acoustic transmitters have been attached to a variety of species in several ways: surgically implanted inside the abdominal cavities of

blacktip sharks (*Carcharhinus limbatus*) (Heupel et al. 2012) and Australian lungfish (*Neoceratodus forsteri*) (Roberts et al. 2017); attached to a titanium dart secured to a reef manta ray (*Manta alfredi*) by a diver using a sling spear (Braun et al. 2015); attached via a suction cup to a humpback whale (*Megaptera novaeangliae*) using a tagging pole (Baumgartner et al. 2008); using a tagging pole from a small boat (Dewar et al. 2018) to insert the tag anchor below the dorsal fin of a basking shark (*Cetorhinus maximus*); fired from a cross-bow into the blubber of a right whale (*Eubalaena glacialis*) in a combination acoustic/VHF transmitter assembly (Winn et al. 1995), and fastened to a harness secured around the tailstock of a dugong (Marsh et al. 2011, and as described in Chapter 2). Using the acoustic detection data, custom R scripts can calculate approximate 2- and 3D underwater activity spaces and create graphics to illustrate them (Simpfendorfer et al. 2008; Simpfendorfer et al. 2012; Udyawer et al. 2015).

Active acoustic tracking has been used much less for marine mammals than for bony fish and sharks. This is at least partially because of the overlap of the typical tag frequency of 69 kHz (Vemco 2012) with the hearing frequencies of some species of marine mammals, potentially interfering with or modifying the animal's behaviour or otherwise affecting the results. For example, bottlenose dolphins hear tones with a frequency up to 160 kHz so it would be likely that the dolphins could hear the 69 kHz transmitter. The same is likely to be true for most other odontocetes. The hearing range of sirenians however, is between 1-18 kHz (Anderson and Barclay 1995). Dugongs, for example, communicate using chirps, trills, and barks, all lower than 18 kHz (Parsons et al. 2013) which is much lower than the typical acoustic transmitter frequency of 69 kHz (see Fig. 1.1 below for comparisons). Nonetheless, to date researchers have not used acoustic tracking to follow dugong movements, possibly because acoustic arrays are not widely available in the dugong's vast Indo-Pacific range even though arrays have been established at several locations in the coastal waters of their range in Australia.



Figure 1.1: Comparison of marine animals' hearing ranges with the frequency of the acoustic transmitter. Thin lines represent animal hearing ranges and thick lines represent vocalisation ranges. (¹Stirling et al. (1987), *Odobenus rosmarus rosmarus*; ²Hanggi and Schusterman (1994), *Phoca vitulina*; ³Anderson and Barclay (1995), *Dugong dugon*; ⁴Gerstein et al. (1999), *Trichechus manatus*; ⁵Wartzok and Ketten (1999), *Zalophus californianus*; ⁶Kastelein et al. (2002), *Odobenus rosmarus divergens*; ⁷Kastelein et al. (2003), *Stenella coeruleoalba*; ⁸Southall et al. (2003), *Mirounga angustirostris*; ⁹Bartol and Ketten (2006), *Chelonia mydas*; ¹⁰Popov et al. (2007), *Tursiops truncatus*; ¹¹Sayigh et al. (2007), *Tursiops truncatus*; ¹²Nachtigall et al. (2008), *Lagenorhynchus albirostris*; ¹³Dow Piniak et al. (2012), *Dermochelys coriacea*; ¹⁴Gaspard III et al. (2012), *Trichechus manatus latirostris*; ¹⁵Martin et al. (2012), *Caretta caretta*, ¹⁶Reichmuth et al. (2013), *Zalophus californianus*; ¹⁷Ferrara et al. (2014), *Dermochelys coriacea*; ¹⁸Gridley et al. (2014), *Tursiops aduncus*). The frequency of the acoustic transmitter is 69 kHz (shown by a dashed line).

1.3 Dugongs

Dugongs have specialised food and habitat requirements that make them vulnerable to environmental changes astheir bodies evolved to efficiently digest seagrass and to thermoregulate their body temperatures (Marshall et al. 2020). Dugongs are the only strictly herbivorous marine mammal (Marsh et al. 1999) and seagrass community specialist (Marsh et al. 2018). Although seagrass is their primary food source, their diet also occasionally includes algae (Whiting 2008) and invertebrates (Marsh et al. 2011). Dugongs mainly occur in coastal waters such as shallow protected bays and mangrove channels (Heinsohn et al. 1977) and leeward of large inshore islands (Marsh et al. 2011). Dugong distribution is highly correlated with seagrass distribution and water temperature in the Indo-West Pacific (Chilvers et al. 2005; Marsh et al. 2011). Dugong skin has a poor thermal conductance, which allows heat to be lost to the surrounding water (Marsh et al. 2011). Because of the potential for heat loss, many dugongs appear to move away from water temperatures less than 18.8°C (Marsh et al. 2011). Northern Australian coastal waters from Moreton Bay, Queensland to Shark Bay, Western Australia support a significant proportion of the world's dugongs (Marsh et al. 2011). The Great Barrier Reef in Queensland and Shark Bay, Western Australia are included in the Natural Heritage List (Turnbull 2007) and the World Heritage List (UNESCO 2021). Their globally significant dugong populations are one of the reasons for such listings.



Figure 1.2: Map showing dugong distribution, status, and populations sizes in Australia in 2021 (Marsh 2022). Drawn by Adella Edwards.

Dugongs living along the urban Queensland coast from Cooktown to the southern boundary of the Great Barrier Reef Marine Park (15° 27'S to 27°28'S) are declining (Marsh 2022; see Fig. 1.2). They are exposed to pressures resulting from the activities of the local human populations causing habitat loss. Seagrass habitat is in decline in most of the world's bioregions, with losses most frequently attributed to coastal development and declining water quality (Dunic et al. 2021; Waycott et al. 2009). Reports of seagrass losses attributable to climate change are growing (IPCC 2019). The IPCC (2019) has high confidence that the range of seagrass has contracted at low latitudes since the 1970s in response to global warming, principally due to marine heatwaves. Other direct major threats are from gill netting

and subsistence hunting, shipping, and recreational boating. (Grech and Marsh 2008; Heinsohn and Spain 1974; Marsh et al. 2011; Marsh et al. 2019). Low rates of production and slow life histories have been shown to be high risk predictors for marine animals like the dugong (Davidson et al. 2012). In response to these stressors and threats, the dugong is protected under several laws and conventions.

The dugong is listed as 'Vulnerable to extinction' on the IUCN Red List of Threatened Species (Marsh and Sobtzick 2015), on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and Appendix II of the Convention on Migratory Species (CMS 2021) with its subsidiary Dugong Memorandum of Understanding (Dugong MOU). As a signatory to both conventions and the Dugong MOU, Australia has international obligations to conserve dugongs in its waters. To this end, dugongs have been listed as marine and migratory species and classified as a Matter of National Environmental Significance under the *Environment Protection and Biodiversity Conservation Act* 1999 (EPBC Act). Australia has further international responsibilities as a signatory to the World Heritage Convention. As explained above, the Great Barrier Reef is listed as a World Heritage Site. Its Outstanding Universal Value includes its major feeding grounds for one of the world's largest dugong populations (see Criterion (x), UNESCO 1981). Dugongs are listed in Queensland as Vulnerable under the *Nature Conservation Act* 1992 and listed as a protected species under the Great Barrier Reef Marine Park Regulations 1983.

The extent to which dugong numbers have declined has not been quantified for any country within its range but researchers have shown that the areas inhabited by dugong populations are fragmented and shrinking (Marsh and Sobtzick 2015). Trends in abundance in most regional areas including Australia (see Fig. 1.2) have not been established, in part because an unknown number of dugongs undertake large-scale movements of up to several hundred kilometres (Marsh et al. 2002). Along the urban coast of the southern GBR region in Queensland, however, long-term aerial surveys indicate that the dugong population has declined (Marsh et al. 2011). Nonetheless, these surveys indicate that dugong populations in the large bays of southeast Queensland (Hervey Bay and Moreton Bay) are slowly increasing (Fig. 1.2) Marsh and Rankin, unpublished).

Although many dugong habitats in eastern Queensland have been protected from incidental fishing by spatial closures (Dobbs et al. 2008; Fernandes et al. 2010; Marsh 2000), several important habitats are adjacent to current major ports, greatly increasing the risk of exposure to a host of high-density human activities that may not exist in less developed areas,

especially if the rate of human population increase is rapid in the port areas (Marsh et al. 2011). Throughout their range, dugongs regularly use seagrass habitats in the vicinity of busy port areas including Singapore, one of the largest and busiest ports in the world (Marsh et al. 2011). In the Great Barrier Reef region, dugongs use seagrass habitats close to the ports of Gladstone and Townsville (Marsh et al. 2011). In southeast Queensland, dugongs live in the vicinity of the Port of Brisbane in Moreton Bay, an area growing in population and supporting significant recreational and commercial activities (Chilvers et al. 2005; Marsh et al. 2002). Moreton Bay supports the largest population of dugongs adjacent to a major metropolitan centre in the world (Marsh et al. 2002), possibly greater than 1000 individuals (Lanyon et al. 2019a) with population estimates based on aerial surveys of around 600 animals (Lanyon et al. 2019a; Sobtzick et al. 2017).

Pressures on Moreton Bay dugongs are increasing as the human population increases: 12 of 26 deaths from boat collisions recorded in Queensland between 2000 and 2015 were identified as being within Moreton Bay (Marsh et al. 2011; Meager 2016; Meager and Limpus 2012). The total number of dugongs killed by boats in Queensland including Moreton Bay is unclear but is likely to be higher than reported because the causes of deaths of 738 dugongs during the same 16 year period could not be determined (Meager 2016; Meager and Limpus 2012). Although dugongs used to be frequently caught in shark nets set for protection of bathers (Marsh et al. 2005; Marsh et al. 1999), far fewer have been caught in recent decades (Meager et al. 2013): 39 dugongs were recorded drowned in shark nets from 1989 to 2011 (catch data obtained from the Queensland Shark Control Program, Queensland Department of Agriculture and Fisheries). Local pollution (particularly nutrient runoff which contributes to poor water quality in western Moreton Bay) and dredging are factors associated with seagrass degradation. Nutrient runoff is exacerbated by weather events such as floods and the trajectory of a seagrass beds depends on its capacity to recover between successive events in a disturbance cycle (O'Brien et al. 2018). The severity of such weather events in predicted to increase with climate change exacerbating the ongoing loss of seagrass communities further impacting dugongs (Marsh et al. 2022).

Managers face significant challenges in protecting dugongs from anthropogenic impacts in areas of high human use. Detailed knowledge of local habitat and seagrass use by dugongs is particularly important in such areas. I consider that human activities that affect populations of dugongs and other threatened marine wildlife should be managed more intensively in high human-use areas to reduce the potential for reproductive isolation of populations that remain in the dwindling number of coastal wild places. Details about dugong movements and habitat use can be used to help reduce two areas of uncertainty present in marine management: the

uncertainty of population risk and uncertainty of anthropogenic effects (Botsford and Parma 2005). For example, mapping dugong movements has provided insight into the location of seagrass meadows (Hays et al. 2018; Marsh et al. 1997; Taylor and Rasheed 2011).

Both the habitats and activities of coastal species are often influenced by tidal movements. Movements from a bay to oceanic waters can be assisted using an outgoing tide and returning on an incoming tide, thus saving energy. Tidal movements affect dugongs more than most other marine mammals because the dugongs' food source (seagrass) is rooted to the bottom. During low tides, seagrasses may be inaccessible to dugongs (see Marsh et al. 2011), a situation very different to most marine predators, which can swim after their prey when the tide changes.

Tracking dugong movements presents similar challenges to many other medium-sized marine mammals, the first being individual identification, which is crucial to the tracking process. The problem of individual identification without capture is more challenging than the identification of the Florida manatee (Trichechus manatus). Hundreds of Florida manatees are struck each year by boat propellers; surviving animals retain permanent propeller scars including marks on their bodies, notches in their flippers or tail flukes suitable for photoidentification which requires at least one permanent unique feature (Bassett et al. 2020; Beck and Clark 2012; Beck and Langtimm 2002; Langtimm et al. 2004). Once the individuals have been uniquely identified, photographic records are collected in printed or electronic catalogues and matched via automated software (e.g., IMatch software, see Barton and Reynolds III 2008; Westphal 2020). This method has not been widely applied to dugongs because the incidence of vessel strike scars on dugongs is much lower than for Florida manatees (Marsh et al. 2011). All weather paint sticks (crayons), have occasionally been used short-term but they only last a few days (see Lanyon et al. 2002). Freeze-branding may last over 10 years (Beck and Clark 2012) but is labour-intensive and may raise animal welfare concerns. Lanyon et al. (2002) began a mark-recapture program in southeast Queensland, principally Moreton Bay, attaching a long-term dorsal PIT tag, a titanium turtle tag, fluke notch and temporary paint stick mark to individual dugongs. Skin biopsies were taken for DNA marker analysis and faecal samples analysed for reproductive hormone presence. The program continues and over 120 dugongs are currently either captured or skin-biopsied each year (Lanyon et al. 2019b).

Many dugongs have been tracked using satellite tags since 1986 (Marsh and Rathbun 1990), each animal showing great variability in movement patterns (Marsh et al. 2011). Dugongs frequently undertake large-scale movements (LSMs, greater than 15 km) and

Sheppard (2008) noted that 44 of 70 dugongs tracked made one or more LSM, yet some animals remained with 10 km of the capture point for over a year. In the Torres Strait, Cleguer et al. (2016) tracked six dugongs and noted one made an LSM of 74 km but in tracking 12 dugongs in New Caledonia, all but one made an LSM, the longest being nearly 73 km (Cleguer et al. 2020).

As mentioned above, in comparison with satellite tagging, the submersible data-logging acoustic receiver is an inexpensive tool for long-term monitoring of aquatic animals and may provide an alternative method to satellite tags (Simpfendorfer et al. 2002). Acoustic receiver arrays have already been placed in many locations world-wide, particularly near ports in Australia and North America with proposals to improve an integrated array system for Europe (Abecasis et al. 2018; Reubens et al. 2019). The arrays have been used to record the presence of fish species (McKinzie et al. 2014; Roberts et al. 2017), sharks (Heupel and Simpfendorfer 2014; Revier et al. 2014; Shipley et al. 2018), manta rays (Braun et al. 2015; Couturier et al. 2018), and sea turtles (Brodie et al. 2018). Acoustic receivers can record the presence of hundreds of different animals from a range of local species tagged with acoustic transmitters (CoML 2010) and may provide better accuracy than satellite tags since tracking does not depend upon a satellite capturing the GPS signal. Successful use of acoustic tags in areas having acoustic arrays in place could produce habitat use and movement information comparable to ARGOS/GPS tags and should, therefore, be applicable to any areas where acoustic arrays have been installed. Acoustic and satellite-GPS tracking technologies have been used together to track manta ray movements (Braun et al. 2015) but have not been explored for the dugong.

This thesis explores the potential of acoustic technology to track dugong movements and compares this technology with satellite-GPS technology for the first time with the following objectives:

Main objective: To investigate use of satellite and acoustic technologies to study dugong movements and habitat use in an urban coastal environment by:

- Comparing the relative advantages and disadvantages of using passive acoustic tracking and satellite-GPS tracking to quantify the movement and residency patterns of dugongs in the urban environment of Moreton Bay.
- b. Using satellite-GPS tracking to investigate the use of movement corridors in large-scale dugong movements between Moreton Bay and Hervey Bay.
- c. Using acoustic tracking to understand dugong 3D habitat use in a feeding ground and adjacent areas in Moreton Bay.

d. Using satellite-GPS tracking and acoustic tracking to quantify the movements of dugongs between their feeding grounds in eastern Moreton Bay and adjacent oceanic waters to explore whether these movements could be interpreted as behavioural thermoregulation.

This thesis is organised into seven chapters as follows:

Chapter 1 (this chapter): **Introduction**: The background rationale for the thesis and its objectives with an outline of its structure.

Chapter 2: Study site and general methods: A description of the study site and methods that are common to each of the four data chapters.

Chapter 3: Comparing the relative advantages and disadvantages of using automated acoustic tracking and ARGOS/GPS tracking to quantify the movement and residency patterns of dugongs in the urban environment of Moreton Bay (Sub-objective A). This chapter is based on Zeh, D.R., Heupel, M.R., Limpus, C.J., Hamann, M., Fuentes, M.M.P.B., Babcock, R.C., Pillans, R.D., Townsend, K.A. and Marsh, H. 2015. Is acoustic tracking appropriate for air-breathing marine animals? Dugongs as a case study. *Journal of Experimental Marine Biology and Ecology*, 464 1-10. doi:10.1016/j.jembe.2014.11.013.

Chapter 4: Using ARGOS/GPS tracking to investigate the use of movement corridors in large-scale dugong movements between Moreton Bay and Hervey Bay (Subobjective B). This chapter is based on Zeh, D.R., Heupel, M.R., Hamann, M., Limpus, C.J., Marsh, H. 2016. Quick Fix GPS technology highlights risk to marine animals moving between protected areas. *Endangered Species Research*. 30: 37–44, doi: 10.3354/esr00725.

Chapter 5: Using acoustic tracking to understand dugong 3D habitat use in a feeding ground and adjacent areas in Moreton Bay (Sub-objective C). This chapter, which explores the potential of acoustic tags to provide insights into the local scale 2D and 3D activity space use of dugongs, will be prepared for publication in a journal such as *Marine Mammal Science* after I have submitted this thesis for examination.

Chapter 6: Using ARGOS/GPS tracking and acoustic tracking to quantify the movements of dugongs between their feeding grounds in eastern Moreton Bay and adjacent oceanic waters to explore whether these movements could be interpreted as

behavioural thermoregulation (Sub-objective D). This chapter is based on Zeh, D.R, Michelle R. Heupel, M.R., Hamann, M., Jones, R. E., Limpus, C.L., and Marsh, H. 2018. Evidence of behavioural thermoregulation by dugongs at the high latitude limit to their range in eastern Australia, *Journal of Experimental Marine Biology and Ecology* 508: 27-34.

Chapter 7: General Discussion: A summary of how the objectives of the thesis have been achieved, what the findings mean and recommendations for further research.

The structure of this thesis is visualised in the diagram below; the information about each chapter reflects the relevant objective addressed in the chapter. This diagram will be repeated on the title page of each chapter to assist the reader understand how each chapter fits into the overall structure of the thesis.



Chapter 2

Study site and general methods common to Chapters 3 – 6

In this chapter, I describe the Moreton Bay study site and the methods common to Chapters 3-6. My description of Moreton Bay includes the local marine mammal species and details about seagrass beds, water depth, and the conservation measures in place within the Moreton Bay Marine Park. The tracking hardware used is described including how acoustic receivers were deployed in an array, and how data were collected. Technical specifications and capabilities of the acoustic and satellite-GPS receivers and transmitters and corresponding data analyses are included.



2.1 Study site: Eastern Banks, Moreton Bay

Moreton Bay, Queensland is one of the largest estuarine bays in Australia and is adjacent to Brisbane, the third largest city in Australia with a population of over two million people and the nation's third largest cargo port (Australian Government 2015). Apart from the port area, the entire bay, including three nautical miles seaward, comprise the Moreton Bay Marine Park, a multiple use protected area (see inset, Fig. 2.1). Maximum water depth in the Park is about 30 m in shipping channels with most depths less than 12 m. (Roelfsema et al. 2009). The bay supports extensive stands of mangroves and variable benthic habitat types include extensive sand banks and seagrass beds, mud banks and deeper coastal waters. Many seagrass areas can be less than 2 m deep at low tide and some areas are exposed at low tide. Thirteen species of marine mammals have been sighted in or nearby the Moreton Bay Marine Park including dugongs, Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), Indo-Pacific humpback dolphin (*Sousa chinensis*), humpback whales (*Megaptera novaeangliae*) and other cetaceans (Chilvers et al. 2005).

The Moreton Bay Marine Park incorporates a range of no-take, limited activity, and Go Slow Zones. The last are intended to lower the incidence of damage inflicted on marine mammals, sea turtles and seagrass from vessel strikes. Direct injury to dugongs and sea turtles has been well-documented (Groom et al. 2004; Hazel and Gyuris 2006; Hazel et al. 2007; Maitland et al. 2006). Dugongs can also be indirectly affected when propeller strikes destroy the seagrass rhizospheres causing depletion of internal nutrient stores (Sweatman et al. 2017). Seagrass can be damaged by the recreational and commercial harvest of polychaete worms, which are used by fishermen for bait (Skilleter et al. 2006) as well as coastal development, dredging, urban and industrial runoff (Coles et al. 2007) and intense storms and cyclones (See Marsh et al. 2018 for a discussion of the complex life interactions of dugongs with seagrasses).

Within the Moreton Bay Marine Park, the Eastern Banks–South Passage area, adjacent to Moreton and North Stradbroke islands, is dominated by seagrass, especially in shallow water regions. The area has been identified as an important dugong habitat area because large numbers of dugongs have been recorded there consistently (Chilvers et al. 2005; Grech et al. 2011; Heinsohn et al. 1978; Lanyon 2003; Marsh et al. 1999; Preen 1992).


Figure 2.1: Map of Moreton Bay study area showing the distribution of seagrass and the locations of the acoustic receivers making up the acoustic array. The array covered most of the Eastern Banks seagrass areas where the dugongs were captured and outfitted with satellite tags and acoustic transmitters. The significance of the 800 m buffer around each acoustic receiver is to roughly approximate how close a dugong must be to the receiver for the acoustic transmitter signal to be recorded. The inset highlights the study area in relation to the Moreton Bay Marine Park.

2.2 Acoustic array

In areas up and down the east coast of Australia, the Integrated Marine Observing System (IMOS) has installed acoustic receivers under the aegis of its Animal Tracking Facility. These IMOS installations are structured to collect long-term data collection and serve as a backbone for national acoustic tracking efforts (Harcourt et al. 2009). The IMOS database holds recorded data on more than 117 species including dugongs (Hoenner et al. 2018).

The Eastern Banks–South Passage area in the Moreton Bay Marine Park was chosen as the project study site because of the large number of dugongs present (Lanyon et al. 2019a, Marsh et al. 2002, Sobtzick et al. 2017), and an array of 28 acoustic receivers (VR2W, Vemco, Nova Scotia, Canada) was strategically placed within this area covering 170 km² of this high-density dugong habitat (see Fig. 2.1). The acoustic receivers were predominately located in the Eastern Banks due to the density of dugongs there and arranged so that dugongs feeding in the high-quality seagrass would likely pass close enough to a receiver that the transmitted signal could be recorded. Acoustic receivers were deployed on paving slabs with metal poles, auger anchors or float and anchor systems depending on depth and current (see Fig. 2.2). The acoustic receivers placed in the Moreton Bay study area were archival, storing the data in memory within the device until it was recovered, and the data were uploaded manually.



Figure 2.2: Illustration of tracking equipment. Acoustic receivers were deployed on paving slabs with metal poles (shown), auger anchors, or float-and-anchor systems, depending on depth and current. The float shown in the illustration was attached to the metal pole to help divers find the receiver for data upload. GPS positions were transmitted hourly from the satellite tag to an ARGOS satellite. An acoustic signal was transmitted every 45-90 seconds and received by one or more acoustic receivers whenever the transmitter was within range. Acoustic and GPS data could be simultaneously collected if the dugong was near the surface. Illustration by D Zeh.

2.3 Tracking hardware attachment

The tracking hardware was externally attached to each dugong tailstock (see Fig. 2.2 and Fig. 2.3) using a version of the harness described by (Marsh and Rathbun 1990). The harness in place during my first field season was found to have a fault with the release system and was replaced in the second season with an improved harness based on a design used for tracking manatees (J. Powell, pers. comm.). Additional minimal changes to the harness design were made in the third season to lessen the time taken to attach the harness. Each harness incorporated a corrodible link to release the harness and tether after several months. Timing of release was dependent upon the salinity and temperature of the bay and marine areas, which influenced the corrosion rate of the metal corrodible link (Klinesmith et al. 2007; Zakowski et al. 2014).



Figure 2.3: Attachment of tailstock harness. The tailstock harness was pre-assembled with the tracking hardware to allow the attachment to be done in as short a time as possible. The assembly was finalised when the dugong was restrained by securing the harness into the bracket. The acoustic transmitter was attached to the harness strap inside the rubber tubing and recorded the depth and temperature of the water at that site. The time-depth recorder was attached to the tether just above the harness assembly bracket. All tracking hardware was turned-on and checked for proper operation prior to attaching the harness to the dugong. Illustration by D Zeh.

2.4 Acoustic transmitters and receivers

An acoustic transmitter (V16TP, Vemco, Nova Scotia, Canada) was attached directly to the tailstock harness (see Box 2.1 and Fig. 2.3). The transmitter had an estimated battery life of 824 days (The manufacturer currently estimates battery life at ~3.5 years; Vemco 2021). Each transmitter emitted a unique ID code, depth (m) and temperature (°C) at 69 kHz at a pseudo-random interval every 45–90 seconds to avoid signal collision with other deployed transmitters. Dugongs do not hear this frequency, as it is outside their hearing range (see Fig. 3.5 in Chapter 3) although it would likely be a consideration for other marine animals and other research projects using acoustic technology (Bowles et al. 2010). Transmitter signals could be detected if a tagged dugong was within ~800 m of the array of 28 receivers. The detection range was calibrated based on data collected from moored sentinel tags in the study area (M. Heupel, unpublished data).



Photos: Vemco

Box 2.1: Acoustic equipment specifics.

The VR2W receiver (Vemco, Nova Scotia, Canada) shown at left uses replaceable lithium batteries with a projected battery life of 15 months and weighs 1190 g. The unit is tethered via a screw anchor or tied to an upright standard attached to a concreted base. See Fig. 2.2.

The small V16TP transmitter (Vemco, Nova Scotia, Canada) shown at left (inset), uses lithium batteries within its sealed unit with a projected battery life of ~3.5 yrs. The unit weighs 36 g.

2.5 Acoustic array deployment and maintenance

The initial array was deployed in March 2012. At the end of the field season, the data were uploaded in November 2012 and the array was removed by CSIRO in December 2012 for deployment elsewhere. New receivers were redeployed at the same locations in April 2013 (based on GPS locations taken in 2012) and data were uploaded in May, August, and December 2013 and in April 2014. To upload the data, each receiver was removed and replaced as near as possible to its original deployment location.



Box 2.2: Satellite-GPS tag (PTT) specifics. The Telonics Gen 4 Marine Unit (Telonics Inc, USA) shown at left is a platform transmitter terminal (PTT) in a sealed housing with built-in GPS. Four "C" size lithium batteries are held within the lower clear housing and stabilise the unit upright in the water. The antenna is at the top next to a salt-water switch which turns off the unit when the switch is submerged. The unit weighs 1300 g and has a maximum battery life of 2 years.

2.6 ARGOS/GPS

The satellite-GPS tag was attached to the harness via a three-metre plastic nylon tether (see Box 2.2) which was designed to break under stress if the tether were to become snagged using a weak link. The tag was a platform transmitter terminal (PTT) consisting of a sealed housing holding a GPS unit with Quick Fix Pseudoranging (QFP) technology (Gen 4 Marine Unit, Telonics Inc, USA) for capturing a latitude/longitude position and transmitting the

position to an ARGOS satellite. The PTTs were programmed to emit each dugong's GPS position hourly.

2.7 Method of attaching tracking hardware

All dugongs were captured opportunistically in seagrass habitats on the eastern banks during blocks of dedicated fieldwork in 2012, 2013 and 2014 using the rodeo method developed by Marsh and Rathbun (1990) and refined by Lanyon et al. (2002). Mothers and calves were specifically avoided. For each dugong, total body length was measured (cm) in a straight line from snout to fluke notch, sex was noted, and a titanium ID tag attached as standard protocol (see Limpus 1992). Dugongs were classified as adults, sub-adults, and juveniles based on direct line measurement of body length (see Lanyon (2003) and Burgess et al. (2012) for size categories). The dugong monitoring and restraint protocols followed Lanyon et al. (2002). The veterinary protocol developed by Dr Mark Flint (pers. comm.) was strictly followed to ensure that the targeted dugongs were in good condition before, during and after the GPS-satellite tags were deployed. Dugongs were handled in accordance with Marine Parks and James Cook University Animal Ethics permits (see Ethics, front pages, v).

2.8 Acoustic detection analysis

Passive acoustic tracking does not provide GPS location data for individuals since the data consist of receiver-based detections. To compare between methods, acoustic data were processed to provide positional locations for individuals using a centre-of-activity approach (Simpfendorfer et al. 2002) that produced weighted-mean locations from detections captured by at least three receivers simultaneously in each three-hour time bin. Dugong positions were calculated based on a weighted mean of the number of detections at each receiver within each period. The period was set to 3 h for all individuals in post-processing. Acoustic receiver data were uploaded approximately every 3–4 months.

With an appropriate arrangement of acoustic receivers, an estimated mean-position may be calculated at a much finer scale than simply the presence within the receiver range (Simpfendorfer et al. 2002). Activity space calculations based on the mean-position would be expected to be comparable to activity spaces calculated using GPS tracking points since both were based on the probability of an animal using the area. While the individual GPS locations (in 2D) were likely be more accurate than the mean-position data, the two datasets were expected to yield similar activity space results due to the scale of the study area.

2.9 GPS location analysis

GPS location data for each dugong were downloaded daily from the ARGOS website and compiled from the time the telemetered dugong was released until its transmitter was detached or stopped transmitting. Immediate post-capture locations were not removed from the data set as studies of the behaviour of dugongs fitted with time-depth recorders (TDRs) indicated no behavioural changes after capture and handling (Hagihara et al. 2011). The specific tag detachment time was determined by the clear difference between the pre- and post-detachment tracks which enabled accurate estimation of the overall GPS transmitter deployment time and aided in tag equipment recovery. While the tag and harness were attached, the track pattern was visibly irregular but after detachment, the track was obviously smoother as the detached transmitter floated adrift with the current. This difference in tracks enabled the overall GPS transmitter deployment time to be estimated accurately. The hourly GPS location data used to analyse movements between Moreton Bay and the regions outside the bay near South Passage (Fig. 2.1) were filtered but not binned to capture all available movements. All tracking data were truncated at the estimated detachment date, to ensure that activity spaces excluded drift data.

Raw GPS data were read into a custom database written in open-source PostgreSQL and initially filtered to keep only data necessary for further processing in R (R Core Team, 2014) and to add columns for further calculations (e.g., speed). Data were then sorted into 3-hour bins (for preparation for comparison with acoustic location data) and filtered using a custom R script to initially: 1) eliminate duplicate times or duplicate consecutive locations and (2) retain only "Successful" and "Resolved QFD" GPS data (i.e., the most accurate and most reliable data). Location data calculated from the ARGOS satellite system were not used because the GPS locations were more accurate. The final part of the R script was based in part on previous speed-filters (Austin et al. 2003; Flamm et al. 2001; Freitas et al. 2008; McConnell et al. 1992) and used to (3) remove spurious consecutive data points that resulted in calculated speeds either >20 km/h for maximum burst swimming speed or >10 km/h for maximum cruising speed (Marsh et al. 1981; Marsh et al. 2011). Outlier data plotted on land were deleted.

2.10 Data analysis for comparison

Data from GPS and acoustic transmitters were standardised by binning into three-hour periods to allow direct comparisons of the data from the two technologies and to minimize autocorrelation. Comparisons were made through activity space calculations resulting in visual and area (km²) comparisons. GPS data used to analyse movements outside the

acoustic array (e.g., between Moreton and Hervey Bays) were filtered as above but not binned to make use of all valid locations. Complete GPS datasets were used to calculate the duration of satellite tag deployment for each tag. All GPS data from the Moreton Bay region (Fig. 2.1) were used to analyse the duration of satellite tag deployment; the duration of acoustic tag deployment was estimated from the data recorded by the array.

Chapter 2 Summary

- The Moreton Bay study site and the methods common to Chapters 3 6 are described.
- The description of Moreton Bay includes the local marine mammal species and details about seagrass beds, water depth, and the species protections in place within the Moreton Bay Marine Park.
- The tracking hardware is described including how acoustic receivers were deployed in an array, and how data were collected.
- Technical specifications and capabilities of the acoustic and satellite-GPS receivers and transmitters and corresponding data analyses are provided.

Chapter 3

Automated acoustic tracking versus ARGOS/GPS tracking

In this chapter, I use data from satellite and acoustic technologies to determine the efficacy of satellite and acoustic telemetry to define dugong movement patterns; compare the benefits and limitations of each approach; examine the costs of each approach in relation to the amount and type of data provided; and relate telemetry data to the boundaries of a Go Slow Zone designed to protect dugongs and turtles from vessel strike within an urbanised coastal embayment. I conclude that the relative merits of the two technologies depend on the research question in the context of the species of interest, the location of the study and whether the study site has an established acoustic array.



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3.1 Introduction

The growth of coastal ports and urban areas has increased pressure on marine animals through expanded shipping and recreational activities. For example, the speed of recreational boats has been shown to put dugongs, turtles, and other marine species at higher risk of collision or disturbance (Grant and Lewis 2010; Hazel et al. 2007; Hodgson and Marsh 2007; Maitland et al. 2006; Ponnampalamet al. 2020). Data showing the presence and movement patterns of animals in relation to factors such as critical habitat and human use of coastal waters fill a key knowledge gap for managing coastal developments and provide important insights for the effective conservation of exploited or endangered species (Bograd et al. 2010; Cooke 2008). For managers responsible for protecting these species, defining movement and behavioural variables is challenging due to the dynamic nature of these coastal environments and the difficulty in determining what an individual is doing (e.g., feeding, moving) at a given time. Researchers have used various forms of telemetry to understand these aspects of marine animal behaviour. Telemetry data have been employed to elucidate a wide array of biological factors including migration, home range, habitat use, mortality, site fidelity, diel and seasonal patterns, and habitat preference (see reviews by Hart and Hyrenbach 2009; Hazen et al. 2012; Heupel and Webber 2012). Telemetry analyses have also been used to address management and conservation challenges (Bograd et al. 2010).

As explained in Chapter 1, two main approaches that are widely used are satellite and acoustic telemetry (e.g., Cooke 2008; Deutsch et al. 2022a; Deutsch et al. 2022b; Heupel and Webber 2012). For example, data from acoustic telemetry have been used to calculate the mortality rates of juvenile sharks to improve stock assessment models for fisheries management (Heupel and Simpfendorfer 2002; Knip et al. 2012b; Pillans et al. 2014), to evaluate the efficacy of marine protected areas (Heupel and Simpfendorfer 2005; Knip et al. 2012a), and to provide data on the locations and dive movements of humpback (Baumgartner et al. 2008) and right whales (Winn et al. 1995). Similarly, data from satellite tagging have been used to analyse home range and habitat use for management and conservation (Armstrong et al. 2020; Jaine et al. 2014; James et al. 2005; Lipscombe et al. 2020; Shillinger et al. 2008; Slone et al. 2013), and for understanding animal movements including migrations in relation to coastal development (Costa et al. 2012; Pendoley et al. 2014; Sheppard et al. 2006).

Passive acoustic telemetry arrays offer considerable benefit for studying behaviours of marine species because the associated small transmitters are light, less expensive, and

have longer battery life than satellite transmitters. Indeed, acoustic receiver arrays have been used to track over 80 species of marine animals to study migration, home range, and habitat use (Ellis et al. 2019; Heupel et al. 2006; Heupel and Webber 2012). This approach has been facilitated to some extent by the installation of passive acoustic arrays through national networks such as the Integrated Ocean Observing System (IOOS, the United States, Luczkovich et al. 2012; Malone 2003; Raynor 2010), the Australian Animal Tagging and Monitoring System (Heupel and Simpfendorfer 2014) of the Integrated Marine Observing System (IMOS, Australia), and the Pacific Ocean Shelf Tracking (POST, Canada; Welch et al. 2009) Array. Large arrays are being considered on all the United States and Canadian coasts with plans to be integrated through the Ocean Shelf Tracking and Physics Array (Grothues 2009). Large arrays that are installed and maintained collectively rather than by individual researchers offer considerable benefits to marine wildlife tracking because many species can be tracked using the same acoustic array (due to the pseudorandom repeat rate of each individual transmitter, designed to avoid signal collision) offering solutions to understanding the behaviour of animals in and around ports and industrial development. The main limitation of acoustic arrays is that movements and activity are not recorded while the animals are outside the array.

When continuous spatial and temporal information is required across long distances, most marine mammal and reptile studies have used satellite telemetry (Block et al. 2011; Cooke 2008; Costa et al. 2012). A major limitation of satellite tracking is that tags are externally attached to the animal (e.g., by attachment to the dorsal fin, Gales et al. 2012; Pennisi 2005) or attached via a tether with a weak link (Deutsch et al. 1998; Marsh and Rathbun 1990; Reid et al. 2001) which makes them susceptible to bio-fouling and early loss (acoustic transmitters were also external but were attached inside the harness tube, making them less susceptible to bio-fouling). In addition, deployment times are limited by battery life; thus, animals are typically tracked only for relatively short periods (often weeks to months; Hart and Hyrenbach 2009) depending on programming of transmission rates as well as battery life (more transmissions equal shorter battery life). Typically, satellite tags will be larger than acoustic tags, which constrains the size of animals that can be equipped. Understanding the relative costs and performance metrics of both acoustic and satellite technologies is important because both approaches offer the potential to obtain important insights into behaviour of animals, especially around coastal developments. Despite the broad application of both acoustic and satellite technologies to track animal movements, few studies have fitted animals with both technologies to test and compare the efficacy of each.

While application of both technologies is not appropriate for many small species, larger marine animals provide an opportunity to examine the benefits and limitations of each approach. The dugong, which is listed as Vulnerable to extinction by the IUCN (Marsh 2008) and is one of the Great Barrier Reef Region's World Heritage Values (GBRMPA 1981), provides an excellent research opportunity. Individuals are large enough to carry both satellite and acoustic transmitters and they are not likely to be disturbed by the acoustic transmitter frequency of 69 kHz since it is probable that their hearing range is similar to the 400 Hz to 46 kHz range of manatees, *Trichechus spp.* (Marsh et al. 2011; D. Ketten, pers. comm.).

Human activities that affect populations of dugongs and other threatened marine wildlife must be managed more intensively in high human-use areas to reduce the potential for reproductive isolation of populations that remain in the dwindling number of coastal wild places. Although many dugong habitats in eastern Queensland have been protected from incidental fishing by spatial closures (Dobbs et al. 2008; Fernandes et al. 2010), several critical habitats are adjacent to current major or proposed port developments. Managers face significant challenges in protecting dugongs from anthropogenic impacts in these areas. High density human activities occurring within and adjacent to dugong habitats at several of Queensland's major ports such as Brisbane, Gladstone and Townsville greatly increase the risk of exposure to a host of threats that may not exist in less developed areas (Chilvers et al. 2005).

I collected data from acoustic and satellite technologies to describe the presence and movement patterns of dugongs in an urbanised area (Moreton Bay, Queensland) adjacent to the Port of Brisbane, Australia's third busiest port. The study focused on an area of shallow seagrass and an associated Go Slow Zone to define the use of this region by dugongs and the efficacy of the current management arrangements to protect dugongs from boat strikes. Go Slow Zones are reduced speed zones designed to reduce the likelihood of risk of vessel collision (Calleson and Frohlich 2007; Laist and Shaw 2006; Marsh et al. 2011). Study site selection was based on persistent dugong presence in this area as representative of conditions in coastal port environs to provide proof of concept for using acoustic telemetry on dugongs. For details of the capture method, refer to Chapter 2.

Data analyses from satellite and acoustic technologies were used to: 1) determine the efficacy of satellite and acoustic telemetry to define dugong movement patterns; 2) compare the benefits and limitations of each approach; 3) examine costs of each approach in relation to the amount and type of data provided and; 4) relate telemetry data to the boundaries of a

Go Slow Zone designed to protect dugongs and turtles from recreational vessel strike in an area of considerable recreational and commercial boat traffic. I also evaluated the relative merits of the two technologies for other species of air-breathing marine animals.

3.2 Materials and Methods

The general methods and catching specifics are explained in Chapter 2, Methods, including specifics on satellite and acoustic equipment and data processing relevant to this chapter.



Figure 3.1: Map of Moreton Bay study site location. The study site is located the mid-eastern Australian coast (A). Research was conducted within B) the Moreton Bay Region and C) the acoustic array. The acoustic array encompassed a variety of habitats as indicated in the figure legend. The acoustic receiver locations were mostly deployed in areas dominated by seagrass as indicated by the symbols.

3.2.1. Duration of tracking

All GPS data from the Moreton Bay Region (Fig. 3.1B) were used to analyse the duration of satellite tag deployment; the duration of acoustic tag deployment was estimated from the data recorded by the array (see Fig. 3.1C). A subset of 21 consecutive days of tracking for

13 individuals was used for detailed comparative analysis for indices derived from GPS and acoustic data within the acoustic array and the Moreton Bay Region (see Appendix Table 3.1 for dates). The range of 21 consecutive days was the maximum number of days that data were simultaneously available from both technologies for the greatest number of dugongs. Further, using the same time range for all individuals enabled the calculation of composite estimates of activity space of all individuals within the array. GPS data only were used to calculate Array Presence, Seagrass Presence and Go Slow Zone Presence because those analyses are a percentage of the movement in the Moreton Bay Region (not only within the acoustic array itself).

3.2.2. Comparison of acoustic and GPS data outputs

Eight dugongs were omitted from the analyses because their GPS transmitters detached after a few days or because they remained within the array for only a few days (see Appendix 3.1). Minimum convex polygons (MCP) were calculated to define the extent of movement of individuals. Space use was further refined by calculating 50% and 95% kernel utilisation distributions (KUDs). The 50% KUD represents the core use area of an individual while the 95% KUD represents the extent of movement, similar in scale to MCP estimates. Acoustic telemetry data were restricted to the confines of the acoustic array, but the GPS data extended to the Moreton Bay Region. Composite activity space estimates were produced by combining the 13 individual data files into a single file each for GPS and acoustic tracking datasets, respectively.

MCPs were calculated using the using the Convex Hull tool in ArcGIS 10.1 (ESRI 2013). KUDs were calculated using the kde and isopleth tools in the Geospatial Modelling Environment (Beyer 2012). KUDs are sensitive to sample size and smoothing parameter (Millspaugh et al. 2006; Pillans et al. 2014). After exploratory data analysis, likelihood cross validation (CVh) was chosen as the most biologically relevant smoothing parameter to compare the acoustic and GPS KUDs given the small sample sizes present (Horne and Garton 2006; Seaman and Powell 1996); e.g., sample sizes for 21-day acoustic activity centres were less than 44. This approach is consistent with the work of Gredzens et al. (2014) on dugong home ranges. Land masses were excluded from all KUDs and MCPs using the XTools Pro 9.2 extension for ArcGIS (Data East 2013). Table 3.1: Analyses applied to the 21 day subset of GPS and acoustic data from 13 dugongs within the Moreton Bay Region (MBR) (i.e., including areas beyond the acoustic array; Anderson and Barclay 1995; Austin et al. 2003; Bartol and Ketten 2006; Baumgartner et al. 2008; Beyer 2012) and comparison of acoustic and GPS data within the array (Block et al. 2011; Bograd et al. 2010) where MCP = minimum convex polygon, KUD = kernel utilisation distribution.

Reference	Term	Description	Use
Anderson and Barclay (1995)	Array Presence	Percentage of GPS positions inside the acoustic array relative to the MBR	Calculate proportion of locations within the acoustic array
Austin et al. (2003)	Seagrass Presence	Percentage of GPS positions inside seagrass beds relative to the MBR	Calculate proportion of locations within the seagrass
Bartol and Ketten (2006)	Go Slow Zone Presence	Percentage of GPS positions inside the Go Slow Zone relative to the MBR	Calculate proportion of locations within the Go Slow Zone
Baumgartner et al. (2008)	Array use	GPS MCP within the acoustic array relative to GPS MCP of movement the entire MBR	Measure the overlap in area between MBR
Beyer (2012)	Spatial overlap: MCP	Measure of overlap between acoustic and GPS MCP areas within array	Determine how similar MCP area estimates were between methods
Block et al. (2011)	Spatial overlap: 50%	Measure of overlap between acoustic KUD and GPS 50% KUD areas within array	Determine how similar 50% KUD estimates were between methods
Bograd et al. (2010)	Spatial overlap: 95%	Measure of overlap between acoustic KUD and GPS 95% KUD areas within array	Determine how similar 95% KUD estimates were between methods

3.2.3. Size and overlap of activity spaces (21-day data for 13 dugongs)

Activity space estimates were used to define the amount of space used and identify whether different metrics (MCP, KUD) produced overlapping spatial outputs. Intersections of activity space estimates were calculated between (GPS and acoustic) MCPs, 50% KUDs and 95% KUDs for individuals using the Intersection tool in ArcGIS. Areas of intersection were calculated and the ratio of intersected area to GPS area was calculated as a percentage for each individual. The percentage of intersection provided an indication of the level of agreement between activity space estimates.

3.2.4. Day-night comparisons

Data from the composite 21-day GPS and acoustic tracking dataset were divided into day (0600 to 1800 h) and night (1800 to 0600 h) time periods. Activity space estimates were used to define the amount of space used during day and night periods. Intersections of activity space estimates were calculated between (GPS and acoustic) MCPs, 50% KUDs and 95% KUDs for the composite dataset using the Intersection tool in ArcGIS. Areas of intersection were calculated and the ratio of intersected area to GPS area was calculated as a percentage of the composite dataset. The percentage of intersection provided an indication of whether different areas were used during the day or night.

3.2.5. Stability of activity space

Patterns of residency and habitat usage within Moreton Bay, the acoustic array, the seagrass area, and Go Slow Zone (Fig. 3.1C) for each dugong were estimated using indices of time, distance, and area (Table 3.1). To determine whether the full extent of activity space had been identified based on GPS and acoustic telemetry, activity space stability was calculated using cumulative area analysis. Cumulative analysis consisted of weekly MCP areas summed across weeks (e.g., week 1 + week 2, week 1 + week 2 + week 3) to determine whether activity space plateaued over time.

3.2.6. Cost comparisons

To determine the cost effectiveness of acoustic versus satellite telemetry, the cost of tracking dugongs fitted with GPS and acoustic transmitters was compared for nine scenarios. Scenarios included the two tracking methods (GPS and acoustic) times three levels of logistical difficulty: 1) easy catching and accessible location (e.g., Moreton Bay); 2) difficult catching and accessible location (e.g., Townsville); and 3) difficult catching and remote location (e.g., Boigu, Torres Strait). In addition, scenarios with and without an established acoustic array were considered. Costs were based on dugong catching trips conducted by James Cook University in 2012 and 2013 (e.g., Gredzens et al. 2014). Logistical assumptions are presented as Appendix 3.2. Total cost estimates were based on the cost of different parameters, including equipment, travel, salary, and operating costs. Only direct costs were considered.

3.3 Results

3.3.1 Overall results

The tailstock harness that contained the acoustic tag tended to remain on the dugong longer than the tether to which the GPS transmitter was attached. Thus, the mean tracking period for acoustic transmitters was 107 days (SD = 95 days, median = 60 days), significantly greater than the mean tracking period of 39 days for GPS (SD=26 days, median = 35 days, Welch Two Sample t-test, p < 0.01). Four dugongs were still being acoustically tracked at the last download in early April 2014, 256–266 days after deployment. The longest GPS track period was 108 days which reflected the battery life of the GPS transmitter.

Habitat use was calculated from GPS data and compared for 13 dugongs. Array Presence values, Seagrass Presence values and Go Slow Zone Presence values all showed high presence of dugongs in these areas (Table 3.3). Despite this, only five individuals had Go Slow Zone Presence values greater than 80% and one animal spent less than 18% of its time within the Go Slow Zone. Habitat use from composite data also indicated that most of the dugongs' time was spent within the three Go Slow Zones. Array Presence for 13 dugongs over the 21 day period had a mean value of 78% (median = 90%; SD = 23%; range = 32 - 96%) providing further evidence that the activity spaces of tagged dugongs were mostly within the acoustic array.

	Spatia	al Overlap N	MCP	Spatial Overlap 50% KUD			Spatial Overlap 95% KUD		
Tag ID	GPS	Acoustic	(%)	GPS	Acoustic	(%)	GPS	Acoustic	(%)
QA30696	93.4	12.1	12.3	6.8	5.4	24.4	46.5	34.4	50.3
QA30723	94.5	54.5	52.7	10.2	15.7	2.1	68.3	92.4	72.4
QA30677	39.1	61.2	69.3	5.6	26.6	100.0	24.5	169.5	100.0
QA30541	45.0	15.4	33.6	3.3	3.5	42.8	22.1	24.2	60.3
QA30710	104.4	181.1	99.7	10.2	48.3	100.0	81.5	247.1	95.3
QA30676	31.5	14.7	46.6	5.8	1.1	7.3	22.5	7.1	20.9
QA30712	101.0	42.5	41.8	5.9	0.5	0.9	39.1	4.5	8.3
QA30694	41.4	52.8	88.4	2.9	1.3	3.4	16.7	9.2	15.8
QA30709	34.2	21.9	44.9	3.7	10.2	88.9	19.3	56.8	88.6
QA18399	122.1	84.9	68.9	7.4	4.9	19.3	61.9	38.6	33.3
K88240	67.5	50.0	72.2	3.1	7.6	44.4	33.2	47.3	59.8
T71561	113.9	104.8	85.1	85.0	17.0	55.6	55.5	95.5	74.5
QA33315	93.3	37.2	38.6	2.5	8.2	0.0	46.5	54.2	45.0
Composite	167.1	196.0	92.2	6.2	1.2	4.5	64.0	16.3	11.4
Mean	75.5	56.4	58.0	5.8	11.6	37.6	41.4	67.8	55.7
SD	33.2	46.5	25.0	2.7	13.3	38.1	20.8	70.5	30.2

Table 3.2: Activity spaces of the 13 dugongs within the array over the 21-day periods using both GPS and acoustic data.

Table 3.3. Comparison of the presence of 13 dugongs and composite data in the acoustic array, seagrass, and Go Slow Zone over the 21 day periods in which each animal was tracked.

	Go Slow Zolle						
	GPS points	Array Brossnas (%)	Seagrass	Zone			
		Flesence (%)	Flesence (%)	Flesence (%)			
QA30696	157	87.9	77.1	79.0			
QA30723	170	88.8	68.8	69.4			
QA30677	171	94.7	89.5	91.8			
QA30541	65	92.3	83.1	84.6			
QA30710	141	83.0	85.8	79.4			
QA30676	172	98.3	95.3	97.7			
QA30712	162	77.8	73.5	73.5			
QA30694	160	84.4	60.6	17.5			
QA30709	169	91.7	89.9	89.3			
QA18399	121	76.0	63.6	60.3			
K88240	162	93.8	84.6	87.7			
T71561	141	88.7	80.1	76.6			
QA33315	173	97.1	42.2	63.6			
Composite	1964	89.1	76.3	74.6			



Figure 3.2. Maps illustrating the variation in MCP, 50% KUD and 95% KUD estimates for the 21-day data using GPS (left hand column) and acoustic (right hand column) technologies. A) An individual with good agreement between the methods where MCP, 50% KUD and 95% KUD estimates were very similar for GPS and acoustic tracking data. B) An individual with low agreement between methods where 50% KUD estimates had similar locations but MCP and 95% KUD estimates were different in area although locations were consistent. C) Comparison of daytime composite data from the 13 animals.

3.3.2. Size and overlap of activity spaces (21 day data for 13 dugongs)

The estimates of MCPs, 50% KUDs, and 95% KUDs varied between dugongs for the two technologies (Table 3.2), which is to be expected as the data generated by the two techniques are not directly comparable. The results were very close for some dugongs, but varied for others (Fig. 3.2), suggesting that individual dugong movements played a role in resulting activity space estimates. However, these metrics also reflect the acoustic array geometry, the number of acoustic receivers recording individual animal signals and the analytical methods used. The intersection of (GPS and acoustic) MCPs as a percentage of the GPS MCP ranged from 12% to almost 100% (Table 3.2). The corresponding figures for 50% KUDs ranged from 0–100%, and 8–100% for 95% KUDs. The composite GPS and acoustic MCPs overlapped by 92%, composite 50% KUDs by 4.5%, and composite 95% KUDs by 11%. These data indicate that a reliable picture of the activity space use of dugongs in the confines of an acoustic array can be obtained by acoustically tracking several animals. (See Fig. 3.2.)

3.3.3. Day-Night comparisons (21 day data for 13 dugongs)

The resulting MCP, 50% KUD, and 95% KUD estimates calculated for day and night periods were nearly identical indicating that for the 13 animal composite data there was little difference in behaviour between day and night periods. The intersections of the acoustic and GPS day and night MCPs were 87% (day) and 84% (night) as percentages of the corresponding GPS MCPs, indicating a high level of agreement. The overlap of KUD areas was much smaller with only 4.2% (day) and 20.3% (night) overlap of the 50% KUDs and 33.8% (day) and 25.0% (night) overlap of the 95% KUDs. Although these 50% and 95% KUD ratios were small, the mapped KUDs (See Fig. 3.2.)show that the locations of the respective GPS and acoustic 50% and 95% KUDs were spatially close. Thus, comparisons using both technologies indicated little difference between day and night use of the array area by the tagged dugongs.



Figure 3.3. Cumulative space use of dugongs based on MCP analysis. The horizontal bar shows the median value of days tracked, boxes indicate 75th and 25th percentiles and whiskers show the maximum and minimum values of y (activity space area).

3.3.4. Stability of activity space

Analysis of cumulative MCP home ranges indicated that space use of dugongs in the Moreton Bay Region continued to increase over five weeks for the 13 dugongs for which the requisite acoustic tracking data were available (Fig. 3.3). However, MCP estimates stabilised after two weeks for the nine dugongs tracked using GPS technology (Fig. 3.3). These data suggest that during this short term study, GPS tracking captured the extent of movement more quickly than acoustic tracking although there was a high degree of overlap and agreement in activity space size using both methods (Fig. 3.2). However, it is not possible to separate the confounding influences of technology and the analytical methods used and so these conclusions are tentative.

3.3.5. Cost comparisons

Regardless of the method used, tracking is least costly in easily accessible areas where dugongs are easy to catch, such as in Moreton Bay. In areas where acoustic arrays are established, acoustic tracking is more economical than GPS tracking regardless of the scenario (Fig. 3.4). However, if an array is not in place, it is likely to be more cost effective to use GPS tracking unless tracking longevity is a priority or an array can also be used for other species to spread costs across projects or among collaborators. Difficulty of capture also

increased costs because catching dugongs in areas of high turbidity will take a greater amount of time and necessitates the use of spotter aircraft compared with catching in clear water where dugongs are more easily spotted. A high proportion of the costs associated with GPS tracking are from equipment costs (>35%), whereas most (>50%) of the expenses with acoustic tracking are associated with operating costs. The proportion of operational costs increases by approximately 20% when acoustic arrays need to be deployed (see Appendix 3.3).

3.4 Discussion

My study showed that acoustic and satellite telemetry data provided reliable location results for comparable periods of time with some differences in benefits and limitations. The duration of acoustic tracking was greater than that of satellite tracking although the range of tracking days was highly variable for both technologies largely due to the attachment mechanism (see Appendix 3.1). The factors contributing to these differences in longevity between technologies include: 1) operational difficulties with the tether attachment in 2013, which caused several satellite-GPS units to detach in a few days; 2) the tether arrangement which is designed to break if the tether becomes entangled; 3) the duty cycle of the GPS transmitters which limited the battery life; 4) the corrodible link in the tailstock belt which in 2012 detached after a maximum of 69 days; and 5) acoustically tracked animals leaving the array area.



Figure 3.4. Costs for each tracking method for each scenario. Scenario 1 — easy catching and accessible location (e.g., Moreton Bay, where the water is clear); Scenario 2 — difficult catching and accessible location (e.g., Townsville, where the water has high levels of suspended sediment); and Scenario 3 — difficult catching and remote location (e.g., Boigu, Torres Strait, where the water can be clear, but mangroves and corals make for difficult access).



Figure 3.5. Comparison of marine animals' hearing ranges with the frequency of the acoustic transmitter. Thin lines represent animal hearing ranges and thick lines represent vocalisation ranges. (¹Stirling et al. (1987), *Odobenus rosmarus rosmarus*; ²Hanggi and Schusterman (1994), *Phoca vitulina*; ³Anderson and Barclay (1995), *Dugong dugon*; ⁴Gerstein et al. (1999), *Trichechus manatus*; ⁵Wartzok and Ketten (1999), *Zalophus californianus*; ⁶Kastelein et al. (2002), *Odobenus rosmarus divergens*; ⁷Kastelein et al. (2003), *Stenella coeruleoalba*; ⁸Southall et al. (2003), *Mirounga angustirostris*; ⁹Bartol and Ketten (2006), *Chelonia mydas*; ¹⁰Popov et al. (2007), *Tursiops truncatus*; ¹¹Sayigh et al. (2007), *Tursiops truncatus*; ¹²Nachtigall et al. (2008), *Lagenorhynchus albirostris*; ¹³Dow Piniak et al. (2012), *Dermochelys coriacea*; ¹⁴Gaspard III et al. (2012), *Trichechus manatus latirostris*; ¹⁵Martin et al. (2012), *Caretta caretta*, ¹⁶Reichmuth et al. (2013), *Zalophus californianus*; ¹⁷Ferrara et al. (2014), *Dermochelys coriacea*; ¹⁸Gridley et al. (2014), *Tursiops aduncus*). The frequency of the acoustic transmitter is 69 kHz (shown by a dashed line).

The requirement to maintain the satellite-GPS tag at the surface via a tether mechanism produces a significant limitation to tag life because of the need to incorporate a weak link in the attachment mechanism for animal welfare reasons (Deutsch et al. 1998; Reid et al. 2001). Longevity in tracking can vary by species. For example, West Indian manatees (*Trichechus manatus*) in Florida, USA, have been satellite tracked for longer periods (29 manatees out of 78 were tracked for over 1 year) by the use of re-tagging without recatching in most cases (Deutsch et al. 2003). In a study of migrating green turtles (*Chelonia mydas*) several turtles were satellite tracked for over 15 months (Hays et al. 2014).

In contrast, acoustic tags are much smaller, producing less drag and enabling a more durable attachment (in this case a tailstock belt) with the capacity to provide data for longer periods. If the acoustic tags had been surgically implanted in the dugongs, the differences in the longevity of the two techniques should have been much greater. The acoustic tags have longevity of 894 days; the battery life of the GPS tags would have lasted no more than a year even with a duty-cycle designed to maximise battery-life.

Cumulative home range analyses indicated that home ranges did not increase by large amounts over the tracking period which also suggests residence within defined spaces for the dugongs that did not leave the area during the tracking period. Spatial residency in various locations was high for many individuals, a result consistent with Sheppard et al. (2006). Although most of these data only span periods of several weeks, they suggest high use of specific areas over the short to medium term, a result confirmed by my 21-day analyses. Most data collected during the 21 day periods (>75% of satellite locations) were within the acoustic array. Similarly, 70% of individuals spent over 85% of their time within the array when considering the entire GPS tracking period with limited movement into deeper regions outside the barrier islands. This pattern indicates high fidelity to this region and highlights the importance of the seagrass meadows around the Moreton Banks for dugongs as has been established by other studies (e.g., Lanyon 2003) and is part of the rationale for the Go Slow Zone on the Eastern Banks.

My studies indicated that in the area of the array, there was very little evidence of diurnal differences in dugongs' activity space. Initial information suggests that sirenians do not have well defined periods of circadian activity (see Marsh et al. 2011, for review) but new information indicates that this conclusion may be incorrect (Deutsch et al. 2022a) and that many sirenian populations forage more at night.

The boundaries of the Go Slow Zone overlap much of the mapped seagrass areas. All tracked individuals spent large amounts of time over seagrass areas, so it was not surprising that the spatial residence of most individuals examined in the 21 day analyses overlapped extensively with Go Slow Zones (>60% of space used was in Go Slow Zones). However, location data indicated that individuals regularly moved in and out of the Go Slow Zone. This result suggests that the spatial extent of the Go Slow Zone is providing some protection for dugongs from boat strikes but that it is unlikely to be 100% effective. There was a high degree of individual variability in the number of recorded locations within the Go Slow Zone indicating that some dugongs will receive more protection than others from that regulatory initiative. Thus, my data indicate that the current Go Slow Zone does not provide full

protection for all dugongs within this region but will mitigate some of the potential interactions with boaters.

Cost is a big factor in decision making for both scientists and funding agencies. Which methodology is more appropriate should be considered in light of the scientific question asked as well as resource availability. Cost–benefit analysis indicated that each method (GPS vs acoustic) can be justifiably costed depending on questions and resources. The use of telemetry can lead to understanding complex animal movements in the context of an animal's use of its environment (Cagnacci et al. 2010; Rutz and Hays 2009). For example, an investigation of habitat use may include depth data as an indication of feeding activity in dugongs and manatees (Chilvers et al. 2004; Hagihara et al. 2011). Satellite telemetry costs are largely related to equipment or capital type expenses while acoustic telemetry costs are dominated by the installation and maintenance of the network resulting in higher personnel costs. Array costs would of course have been much higher if I had installed a denser array with overlap between the ranges of individual receivers.

A large, national network of acoustic receivers (the Australian Animal Tagging and Monitoring System facility of the Integrated Marine Observing System) provides a platform for the detection of acoustically tagged animals at a broad scale (Heupel and Simpfendorfer 2014). This network includes receivers in an array of habitats around Australia although there is no guarantee that equipment will be located in areas useful to specific study species. Satellite tracking of dugongs had one distinct advantage over acoustic tracking; it could record locations for individuals beyond the boundaries of the acoustic array. This is an important consideration for dugongs as animals are known to make large- and meso-scale movements (Sheppard et al. 2006). For example, my GPS tracking data showed all animals moved beyond the boundaries of the acoustic array and two animals moved over 250 km to Hervey Bay.

This raises the question about which is easier or cheaper to cost and support: equipment or people. The answers to this question will vary based on location, agency, and funding body. Disregarding costs that are common across approaches at the same location (e.g., animal capture costs), it is more cost-effective to use acoustic telemetry if an array already exists within the focal area and if the research questions are directly related to a local study site. If broader-scale movement questions are being asked, a larger acoustic network would be required, and satellite telemetry would be a more cost effective option. Costs of both approaches also differ depending on the study site. Working in remote locations is better

suited to satellite telemetry than acoustic telemetry, a direct result of the differences in costs within approaches.

The suitability of using acoustic and satellite tracking technologies with dugongs was dependent upon animal size and hearing range of the species. When considering acoustic tracking for other coastal marine mammals, the use of acoustic transmitters makes size less critical so that smaller species could be tracked. The hearing range of the species is important: 69 kHz is within the hearing range of many marine mammals, especially dolphins (D. Ketten, pers.comm. 2014; Ketten 2000; Wartzok and Ketten 1999) and could interfere with their intraspecies communications or searching for prey. Hearing ranges of most pinnipeds and sea turtles have maxima well less than 69 kHz, the frequency of the acoustic transmitter, and thus might be considered suitable candidates for acoustic tracking (D. Ketten, pers. comm. 2014; Ketten 2000; Wartzok and Ketten 1999). Tubelli et al. (2012) predicted that the hearing range of the minke whale is below 10 kHz making it another possible candidate. Dolphins, however, appear to have hearing ranges clearly including the 69 kHz transmitter frequency. Therefore, acoustic tracking using currently available technologies is unlikely to be suitable for all marine mammal species.

3.5 Conclusion

Data indicated that both satellite and acoustic technologies provided reliable location data for individuals for comparable periods of time demonstrating that acoustic tracking is a potentially valuable and cost-effective tool for monitoring local dugong habitat use in environments equipped with acoustic receiver arrays, although failure of the attachment device used in this study led to early loss of satellite transmitters in many cases. The two technologies each have benefits and limitations in the data that they provide. Cost-benefit analysis indicated that each method (GPS vs acoustic) can be appropriate depending on questions and resources. The cost-effectiveness of using acoustic rather than GPS technology for tracking dugongs clearly depends on the research question and the location. When the dugongs are within the range of an acoustic array, this research has shown overall good correspondence between the MCPs and KUDs of the GPS and acoustic transmitters.

Ultimately, the cost effectiveness of the method applied must be driven by the species and the research question. Researchers should then consider what resources are on hand. Is an existing array present or can a collaborative array be established? Is the study site remote? Is staff time limited? Does the animal exhibit stable residency? Careful consideration of available resources in conjunction with the question being addressed should lead to a clear

conclusion about which of these two technologies is most cost effective in gaining a research outcome.

I conclude that acoustic tracking is a potentially valuable and cost effective tool for monitoring dugong habitat use in environments equipped with acoustic receiver arrays. As dugongs are not wilderness animals (Marsh et al. 2011) and ports in developed countries are increasingly fitted with acoustic arrays, I conclude that acoustic transmitters should become the preferred methods of tracking dugong habitat use in the vicinity of ports because they enable more animals to be tracked for longer and with fewer animal welfare problems than GPS transmitters. I expect that similar methods will work as well for some other marine species but advise that each species' hearing and sound production ranges will need to be considered.

Chapter 3 Summary

- Marine animals face increased pressure through expanded shipping and recreational activities.
- Effective conservation and management of large species like marine mammals or sea turtles depend on knowledge of movement and habitat use.
- Previous studies have used data collected from either satellite or acoustic telemetry but rarely both.
- In this study, data from satellite and acoustic technologies were used to: determine the efficacy of satellite and acoustic telemetry to define dugong movement patterns; compare the benefits and limitations of each approach; examine the costs of each approach in relation to the amount and type of data provided; and relate telemetry data to the boundaries of a Go Slow Zone designed to protect dugongs and turtles from vessel strike within an urbanised coastal embayment (Moreton Bay, Queensland, Australia).
- Twenty-one dugongs were captured in seagrass habitats on the Eastern Banks of Moreton Bay in July–September 2012 and July 2013 and fitted with GPS and acoustic transmitters.
- Both satellite and acoustic telemetry produced reliable presence and movement data for individual dugongs.
- When the dugongs were within the range of the acoustic array, there was relatively good correspondence between the overall space use measures derived from GPS and acoustic transmitters, demonstrating that acoustic tracking is a potentially valuable and cost-effective tool for monitoring local dugong habitat use in environments equipped with acoustic receiver arrays.
- Acoustic technology may be particularly useful for species that establish home ranges with stable residency especially near large urban or port environs.
- However, the relative merits of the two technologies depend on the research question in the context of the species of interest, the location of the study and whether the study site has an established acoustic array.

Chapter 4

Quick Fix GPS technology highlights risk to dugongs moving between protected areas.

In this chapter, I discuss the threat of incidental capture in fishing gear and how protected areas of fisheries closures tend to protect areas of high marine mammal density but generally offer much less protection to movement corridors because they are often unknown and difficult to detect. This chapter describes the movements of four dugongs (tagged with GPS satellite transmitters) between Moreton Bay and Hervey Bay along a path where dugongs are occasionally caught in inshore shark nets set for the protection of bathers. The results suggest that dugongs would benefit from netting closures that extend beyond seagrass meadows.



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4.1 Introduction

Incidental capture in fishing gear is the most serious threat to the survival of many species of marine mammals (Grech et al. 2008; Lascelles et al. 2014; Read 2008; Read et al. 2005; Reeves et al. 2005). Fisheries closures to protect marine mammals have tended to concentrate on areas of high marine mammal density (Dobbs et al. 2008; Fernandes et al. 2005; Rayment et al. 2010; Rojas-Bracho et al. 2006; Slooten and Dawson 2010). The conservation of habitats encompassing the extent of a species' movement is an essential component of ecological management (Hooker et al. 2011; Lascelles et al. 2014); yet movement corridors may be less adequately protected than high density areas (Corrigan et al. 2014) because they are often unknown (Hyrenback et al. 2000) or variable (Grüss et al. 2011; Lascelles et al. 2014; Marsh et al. 2011). The necessary spatial information about distribution and movements of species of concern is typically difficult and costly to obtain (Grech et al. 2011).

In south-eastern Queensland Australia, Moreton Bay (Grech et al. 2011; Lanyon 2003; Marsh et al. 1999; Preen 1992; Preen 1995a) and Hervey Bay (Grech et al. 2011; Marsh et al. 1999; Preen and Marsh 1995) support nationally significant populations of dugongs. Large multiple use marine parks have been established in both bays. The Moreton Bay Marine Park (area 3,400 km²) encompasses the entire bay and adjacent waters and includes no-take, limited activity and Go Slow Zones in areas recognised as critical habitats for dugongs (see Fig. 4.1). The Great Sandy Marine Park (area 5,800 km²), which includes Hervey Bay, Great Sandy Strait, Tin Can Bay Inlet, and the waters off the east coast of Fraser Island seaward to three nautical miles includes similar no-take, limited activity, and Go Slow Zones. In addition, Hervey Bay includes a Dugong Protection Area of 1703 km² (Marsh et al. 2000) which was established in January 1998 via a *Fisheries Amendment Regulation* (no. 11, 1977) under the *Fisheries Act*, 1994. Gill and mesh netting practices have been modified in this area to reduce the risk of dugong bycatch.

Moreton and Hervey Bay marine parks are separated by more than 200 km with extensive open surf coast including the Sunshine Coast and Rainbow Beach, which are very different environs from the typical dugong seagrass habitats in the bays. Cope et al. (2015) confirmed substantial dugong movements between Moreton and Hervey bays using pedigree analysis based on genetic and ancillary biological data. Approximately 30% of assigned parents had at least one offspring found in a different location, implying recent movement of the parent or offspring (Cope et al. 2015). Dugongs are occasionally caught in the shark nets set for protection of bathers along the Sunshine Coast and Rainbow Beach (Marsh et al. 2005; Marsh et al. 1999; Meager et al. 2013), suggesting that the area close to the coast may act as a dugong movement corridor. For reference, 39 dugongs were recorded drowned in shark nets from 1989 to 2011 (catch data obtained from the Queensland Shark Control Program, Queensland Department of Agriculture and Fisheries).

Dugongs do not undertake seasonal migrations. Their movements are individualistic (Marsh et al. 2011; Sheppard et al. 2006) and include long-distance movements up to 560 km (Sheppard et al. 2006). Twenty percent of the 70 dugongs satellite-tracked by Sheppard et al. (2006) moved 100-560 km but none were detected moving between Moreton and Hervey bays despite more than 10 dugongs being satellite-tagged in each of those locations. Thus Cope et al.'s (2015) pedigree analysis suggested more movement between locations than detected through repeated direct sampling of individuals (Seddon et al. 2014), genetic analysis of population structure (Sneddon et al. 2014) or telemetry (Sheppard et al. 2006).

Despite nearly 30 years of satellite tracking, dugong movement corridors have proven difficult to map, presumably because the tethered satellite transmitter is dragged under the water while the animal is swimming (Marsh and Rathbun 1990; Sheppard et al. 2006). Standard high-accuracy GPS-based locations can only be obtained when the transmitter's antenna surfaces for at least 20 sec (Tomkiewicz et al. 2010). Systems with Quick Fix Pseudoranging (QFP) have been designed to reduce the time required to obtain a GPS fix when tracking marine mammals and sea turtles (Tomkiewicz et al. 2010). Within 5 sec of surfacing, QFP systems can collect and transmit all the information necessary to fix the GPS position via post-processing at a later time using Telonics Data Converter software (Telonics Inc. USA 2007) on a standard personal computer. I used this technology to provide information on dugong movement corridors for the first time and discuss the implications of the results for dugong conservation.

4.2 Materials and Methods

The general methods are explained in Chapter 2, Methods, including specifics on satellite and acoustic equipment and data processing methods.





4.2.1. Tracking Duration.

Complete GPS datasets were used to calculate the duration of satellite tag deployment for each tag. Successive data points signifying movement between the two bays were identified

by the relatively large distances (mean = 42 km; SD = 38, median = 23) between the GPS data points. Travel start dates were determined from the data location immediately preceding bay to bay movement. Similarly, travel end dates were determined by choosing the data location immediately following the bay to bay movement. The number of days between tagging, the travel start date, the number of travel locations, the average speed (km/hour) and the distance travelled (km) were calculated using the GPS locations. The average distance to the coastline (km) from each GPS travel location was derived using the Near tool in the ArcGIS 10.2 Proximity Toolbox (ESRI 2014). GPS data for each dugong were used to calculate the percentage of time: (1) locations were within the marine park boundaries for travelling and non-travelling dugongs and (2) travel locations were within 5 km of the coastline. The duration of acoustic tag deployment was calculated from the data recorded by the individual acoustic receivers summarised by transmitter ID.

Minimum convex polygons (MCP) were calculated to estimate the maximum extent of movements for individuals. Space use was refined by calculating 50% and 95% kernel utilisation distributions (KUDs). The 50% KUD represented the core use area of an individual while the 95% KUD represented the extent of home range movement, comparable in scale to MCP estimates.

4.3 Results

Thirty dugongs were tagged in Moreton Bay in July - September 2012, July 2013, and April – May 2014; one dugong was tagged in both 2013 and 2014. The 29 individuals were of mixed ages based on body lengths as defined by Lanyon et al. (2010): Adults (7 females, 10 males, body length > 260 cm), sub-adults (5 females, 4 males, body length 241 to 260 cm) and small sub-adults (3 males, body length \leq 240cm). Four dugongs (1 adult male, 1 sub-adult male and 2 adult females) were tracked from Moreton Bay to Hervey Bay. One of these adult females was GPS tracked travelling to Hervey Bay in July 2013 and returning to Moreton Bay in August 2013. It was also detected by acoustic receivers in Moreton Bay in May – June 2014. (See Fig. 4.1 for acoustic array.)

For three dugongs, 52% of the between-bay locations (32 locations) were within 5 km of the coast and 46% (28 locations) were within the boundaries of either the Moreton Bay or Great Sandy Marine Parks. Only two GPS location points were available for one dugong (PTT ID 112595): a location in Moreton Bay Marine Park immediately after it was released and a location in the Great Sandy Marine Park (suggesting possible speedy movements between the two locations with the transmitter underwater). The only available satellite points were

eleven unfiltered ARGOS satellite locations, one of location class A and 10 of location class B, which confirmed PTT ID 112595's trip north but suggested sea travel away from the coast. Location classes A and B have no accuracy estimation (ARGOS User's Manual ©2011) so that these positions must be considered approximate. A further 579 GPS data locations were obtained from PTT ID 112595's transmitter in Hervey Bay over 10 weeks. The spatial pattern of these locations indicated that the transmitter was still on the dugong.

All of the dugongs began their movements north shortly after tagging (1, 2, 5, 12 days) and took nearly a week (5, 6, 7, 9 days north and 5 days south) to travel between the bays (Table 4.1). The number of GPS travel locations logged varied from 2 to 38 (mean = 12.2, SD = 14.6). The duration of GPS tracking ranged from 35 to 145 days (mean = 86.5, SD = 46.2). The number of GPS locations per day ranged from 8.3 to 13.8 (mean = 11.1, SD = 3.6). The overall average for the combined total of 346 GPS tracking days was 9.7 detections per day (Table 4.1). The total number of tracking days as detected by the acoustic array in Moreton Bay varied from 1 to 53 (mean = 17.5, SD = 24.1) and the number of locations per day ranged from 2.4 to 21 (mean = 9.6, SD = 9.0) (Table 4.1).
Table 4.1: Tracking metrics for dugongs that moved between Moreton and Hervey (HB) Bays, separated into groups (A) all days tracked and (B) travel days only. For each dugong except PTT ID 112597, the number of travel points was low, an indication of relatively fast travel speed dragging the transmitter underwater. Thirty-eight GPS travel points were recorded from PTT ID 112597 which had the longest trip duration. N: northward; S: southward; –: not applicable.

A All days tracked						Average			
						Filtered	locations		
PTT ID	Sex/	Class	Tagged date	Days t	racked	locations	per day		
43619	Female/	Adult	12-Jul-13	3	35	393	11.2	_	
43718	Male/Ad	ult	30-Apr-14	8	36	1187	13.8		
112595	Male Su	b-adult	8-Jul-13	7	70	582	8.3		
				7	91	10961	13.91		
112597	Female/	Adult	29-Apr-14	1	47	1205	8.2		
B. Travel	days only	Days			Travel			Distance	
		after		Travel	data	Av. speed	Av. dist. to	travelled	Days in
PTT ID	Direction	tagging	Start date	days	points	(km/hr)	coast (km)	(km)	HB
43619	Ν	1	13-Jul-13	6	8	1.5	2.45	278	23
	S	-	9-Aug-13	5	7	1.66	3.78	230	-
43718	Ν	12	12-May-14	5	6	2.21	2.62	338	70
112595	Ν	2	10-Jul-13	7	2	-	-	293	72
				11 ^a	11 ^a	-	-	-	min 68ª
112597	Ν	5	4-May-14	9	38	1.76	5.12	311	134
2									

^aARGOS GPS data

Individual dugongs' activity spaces were variable. Minimum convex polygons ranged from 2.3 km² to 242.6 km² in Moreton Bay Marine Park (n = 4) and 87.2 km² to 2143.6 km² in the Great Sandy Marine Park (n = 4). In the Moreton Bay Marine Park, 95% kernel utilisation distributions (KUDs) ranged from 101.7 to 260.0 km² (n = 2) and 50% KUDs ranged from 4.9 to 60.9 km² (n = 2). In the Great Sandy Marine Park, 95% KUDs ranged from 16.8 to 1116.9 km² (n = 4) and 50% KUDs ranged from 2.3 to 182.1 km² (n = 4) (see Table 4.2).

Table 4.2: Minimum convex polygons (MCPs) and kernel utilization distributions (KUDs) in Moreton Bay (MB) and Hervey Bay (HB) for each of the tagged dugongs that moved between the two bays.

		Data	MCP	95% KUD	50% KUD	95% KUD
PTT ID	Location	points	(km²)	(km²)	(km²)	/MCP (%)
43619	MB Start	11	83.2	_	_	-
	HB	330	674	531.3	49.2	78.8
	MB End	37	19.2	18.5	4.7	96.4
43718	MB Start	392	242.6	101.7	4.9	41.9
	HB	789	87.2	15.8	2.3	18.1
112595	MB Start	3	2.3	-	-	-
	HB	579	440.2	67.1	8.8	15.2
112597	MB Start	70	174.2	260	60.9	149.3
	HB	1097	2143.6	1116.9	182.1	52.1

4.4 Discussion

GPS technology enabled us to determine the routes of three dugongs that travelled 278 – 338 km from Moreton Bay to Hervey Bay and the return journey of one of these animals. All individuals stayed within 5 km of the coast during their journeys. GPS locations received from a fourth dugong in both Moreton and Hervey bays revealed movement between these bays, but no GPS locations were recorded enroute. Unreliable ARGOS locations suggested that this dugong may have taken an ocean route. These four dugongs represented 14% of the 30 datasets initiated in Moreton Bay and satellite tracked. The movement data recorded when the dugongs moved between Moreton Bay and Harvey Bay demonstrate the importance of applying satellite/GPS tracking to dugong movements. With just a few locations, the paths of the dugongs became visible where they were previously uncertain.

The four dugongs that moved between bays left Moreton Bay within 1, 2, 5 and 12 days of capture suggesting possible flight responses for at least two of the animals. Gredzens et al. (2014) reported an animal undertaking a 90 km movement two days after it was captured and tagged. Sheppard et al. (2006) recorded 14 of 70 radio-tracked dugongs made macroscale movements (>100 km) 18.1 to 513 days (mean= 89.9 days) after they were tagged. The mean time between tagging and initial large-scale movement for the 70 animals tracked varied (mean = 33.4 ± 10.3 days, min = 0 days, max = 271.6 days) clearly indicating that not all macro-scale movements documented through satellite tracking can be explained by flight responses.

All the macro-scale movements of satellite-tracked dugongs reported to date have been rapid and directed and my results are consistent with these observations (e.g., Gredzens et al. 2014; Sheppard et al. 2006). These movements involved adult and sub-adult animals of

both sexes. In contrast, the pedigree data based on a much larger sample size suggest that male dugongs move between populations more than females (Cope et al. 2015). Our sample size is too small to further investigate sex differences in the likelihood of making macro-scale movements.



Figure 4.2: Maps displaying movements of two dugongs between Moreton Bay Marine Park and Great Sandy Marine Park. The paths were created from GPS locations of two dugongs that moved between Moreton Bay Marine Park and Great Sandy Marine Park. Frames A-B map the movements of dugong Q44111, and frames C-D map the movements of dugong Q18400. All the coastal movement data points are within 5 km of the coast (within the 5 km buffer) which contains the Sunshine Coast and Rainbow Beach shark nets. The data for dugong Q18400 included few GPS locations (8) and the ARGOS locations are also shown. The precision of reliable ARGOS locations (location classes 1, 2 or 3) is < 1km; the error of unreliable ARGOS location (classes 0, A or B error) is unknown. The track for dugong Q44111 was created from 38 GPS points.

Location	KUD range (km ²)	Ν	Source
Lease Islands, Indonesia	127.9	4	De longh et al. (1998)
Shoal water Bay, Qld	1444.5	5	Gredzens et al. (2014)
Torres Strait	264.3 to 1269.2	6	Gredzens et al. (2014)
10 locations, Qld	33.0	50	Sheppard et al. (2006)
Moreton Bay, Qld	68.3	13	Chapter 3
Moreton Bay, Qld	531.3	2	This chapter
Hervey Bay, Qld	1116.9	4	This chapter

Table 4.3: The reported calculated 95% KUD activity spaces of dugongs vary widely by location. See Appendix Table 5.4 for more detail.

The activity spaces of the tracked dugongs varied by individual (Table 4.2), a result consistent with the literature (Table 4.3). Gredzens et al. (2014) suggested that the size of an individual's activity space may be dependent upon the area of available seagrass habitat, but this hypothesis does not explain the differences I observed. The seagrass areas in Hervey Bay are larger than those in Moreton Bay (Hervey Bay seagrass 2480 km² vs. Moreton Bay seagrass 384 km², McKenzie 2014) but the datasets of location points for Moreton Bay were smaller than those in Hervey Bay (see Table 4.1) so no attempt was made to formally test this hypothesis in this paper.

The home ranges for each animal I tracked confirmed that the Eastern Banks in the Moreton Bay Marine Park and Hervey Bay in the Great Sandy Marine Park were the centres of the dugongs' activity spaces. As explained above, these two marine parks are established dugong hotspots with significant numbers of dugongs and some areas have been zoned to protect them (Grech et al. 2011; Lanyon 2003; Marsh et al. 1999; Marsh et al. 2011; Preen 1992; Preen 1995a; Preen and Marsh 1995; Sobtzick et al. 2012). However, there is no such protection along the ~200 km of open coast between the northern boundary of Moreton Bay Marine Park and Rainbow Beach in the southern portion of Great Sandy Marine Park. Shark nets for protection of bathers are located immediately offshore from several Sunshine Coast beaches and Rainbow Beach and 39 dugongs were recorded drowned in shark nets from 1989 to 2011 (catch data obtained from the Queensland Shark Control Program, Queensland Department of Agriculture and Fisheries). Shark nets are located typically with 5 km of the coast depending on the shape of the bay and are deployed in 3, 4 or 6 m depths as appropriate per water depth (QDAF 2016). (Alternatives, like SharkSafe Barriers, are

discussed in Box 7.2 in Chapter 7.)The directed movement of three tracked dugongs through this region (Fig. 4.2) confirms longshore movements within the shark protection net areas and demonstrates that some individuals successfully avoid entanglement. Three of the four dugongs we tracked stayed within 5 km of the open coast. Dugongs tracked by Sheppard et al. (2006) stayed mostly within 7 km of the coast but were often found up to 20 km away from the coast. How much these differences reflect the lack of precision of the earlier technologies used by Sheppard et al. (2006) is not known.

The Great Barrier Reef World Heritage Area spans some 14° latitude from just north of Hervey Bay to Cape York. An extensive series of Dugong Protection Areas and marine park zoning has been established to protect relatively high density dugong areas in this World Heritage Area (Dobbs et al. 2008; Grech and Marsh 2008; Marsh 2000). Mesh netting has been banned from areas close to major headlands to protect dugongs travelling between bays (GBRMPA 1983). The results presented here suggest that this protection may be insufficient for dugongs moving along stretches of coast between seagrass beds. However, more dugong tracking studies are needed to confirm this hypothesis. One way this could be accomplished would be to conduct new acoustic tracking along the movement path (see Box 7.5 in Chapter 7).

Marine protected areas (MPAs) are typically designed to protect areas of high biodiversity or species of significant conservation concern. The areas used by megafauna such as marine mammals are typically larger than that afforded by individual MPAs although MPAs can reduce the risk of human-induced harm (Marsh et al. 2011). The frequency of travel between patches of suitable habitat varies greatly among individuals and species (Hilty et al. 2006). Conserving suitable and adequate habitat to maintain connectivity is an essential component of ecological management (Hooker et al. 2011; Lascelles et al. 2014), yet movement corridors are often unknown (Hyrenback et al. 2000) or vary for natural reasons (Grüss et al. 2011; Lascelles et al. 2014; Marsh et al. 2011) making conservation in these areas difficult. Protection for important habitats within movement corridors can be less adequate than high density foraging areas (Corrigan et al. 2014) due to the difficulty and costliness of defining necessary spatial information (Grech et al. 2011).

This study is an example of how modern technology can reveal previously unknown movement corridors. Some 87 species of marine mammals are listed under the Convention for Migratory Species (CMS 2015). The application of GPS/satellite technology to discover and record the movement corridors of such species promises to be a powerful tool to inform their conservation.

Chapter 4 Summary

- Seagrass meadows in Moreton and Hervey bays in south-eastern Queensland support significant populations of dugongs.
- Pedigree analysis based on genetic and ancillary biological data indicates that there
 is substantial movement of dugongs between these bays which are separated by
 open surf coasts where dugongs are occasionally caught in inshore shark nets set for
 the protection of bathers.
- This bycatch suggests that the dugong movement corridor between Moreton and Hervey bays is close to the coast, a hypothesis that nearly 30 years of dugong satellite tracking using PTT technology has failed to confirm because of the few data points collected during dugong movements by previous technologies.
- Movement corridors have generally been less protected because they are often unknown and difficult to detect than areas of high density marine mammal populations.
- Twenty-nine dugongs were captured in seagrass habitats on the Eastern Banks of Moreton Bay in 2012-2014.
- Four dugongs were tracked moving from Moreton Bay to Hervey Bay covering distances of 278 – 338 km over 5 – 9 days; one dugong made the return journey.
- Three of the four animals travelled along and very close to the coast; the exact track of the fourth animal is uncertain.
- These results suggest that dugong would benefit from netting closures that extend beyond seagrass meadows.

Chapter 5

Using passive acoustic telemetry to study two and threedimensional space use by dugongs: a proof of concept²

In this chapter, I explore the potential of passive acoustic telemetry to provide insights into the local scale 2D and 3D activity space use of dugongs in the Eastern Banks-South Passage area of Moreton Bay.



² I plan to submit a revised version of this chapter to Marine Mammal Science as: Zeh DR, Lédée EJI, Hamann M, Limpus CJ, Marsh H, Simpfendorfer, CA, Udyawer V, Heupel, MR. Using passive acoustic telemetry to study two and three-dimensional space use by dugongs: a proof of concept.

5.1 Introduction

As explained in previous chapters, scientists have analysed the movements of many marine species using two-dimensional (2D) planar coordinate geometry to describe their habitat use and movements. These results can support conservation and management efforts by revealing previously unknown or undocumented details of space use. The difficulty of implementing the results into policy changes lies in whether the results can be explained in terms that fit the existing conservation issues or whether the results come at a time when policy-makers are focusing on those particular issues (Hays et al. 2019). An example of research that may fit into management objectives is the work done by Baird et al. (2012), who used satellite tracking to calculate the 2D habitat use and population density of three social clusters of Hawaiian insular false killer whales (Pseudorca crassidens) to identify areas for critical habitat designation. Sheppard et al. (2006) used satellite tracking to construct 2D home ranges based on satellite tracking data for dugongs moving along the east coast of Queensland and showed that their movement patterns were diverse. Some animals moved hundreds of kilometres between seagrass meadows in a few days while others made mostly tidally-mediated local movements. These results have informed the spatial management of dugongs, especially in the Great Barrier Reef region (Marsh et al. 2011).

Marine mammals live and forage in a moving three-dimensional (3D) environment (Simpkins et al. 2001). Thus, quantifying movements in three dimensions should greatly improve the understanding of space use (Belant et al. 2012) with the potential for consequential improvement in conservation and management policies (Braun et al. 2015; Harcourt et al. 2000; Lee et al. 2017; Levin 1992). To that end, researchers began integrating depth and location data (Cooke et al. 2004) to extend movement analysis to 3D. Time-depth studies have often been limited to quantifying the vertical component of foraging behaviour (Belant et al. 2012; Simpkins et al. 2001). Bestley et al. (2015) documented the vertical feeding strategy of four seal species in the Australian East Antarctica territory, noting behaviour variations in vertical movements corresponded to the foraging component of horizontal movements.

Researchers developed more informative 3D analyses by developing new methodologies or by applying statistical methods to combined 2D tracking data and dive data from time-depth recorders (TDRs). Tracey et al. (2014) calculated movement-based kernel utilization distributions KUDs (MKUDs) from GPS/satellite location data and combined them with timedepth/height data. The resultant 3D activity spaces greatly improved the visualization of the activity spaces of three completely different species: dugongs, giant pandas (*Ailuropoda melanoleuca*), and California condors (*Gymnogyps californianus*). Hagihara (2015) categorised dugong dive profiles using time-depth data combined with local environmental data (identifying presence/absence of seagrass) and calculated the probability of the dugongs feeding in certain sections of the dives by applying a logistic regression approach. Udyawer et al. (2019) combined satellite tracking data with time-depth data to calculate activity spaces for 10 dugongs in the Gulf of Carpentaria, Northern Territory, demonstrating that the dugongs generally kept closely to seagrass areas with minor diel differences.

As explained in earlier chapters, an alternative approach to collecting satellite-GPS data for the collection of location data has been the use of acoustic tracking technology. This approach was first used to track animals in three dimensions by combining data collected from a three-point acoustic receiver array with time-depth data. Harcourt et al. (2000), for example, constructed 3D dive paths for individual Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. In the Bahamas, Laplanche et al. (2015) used acoustic data to verify the 3D track of a Blainville's beaked whale (*Mesoplodon densirostris*). They reconstructed the track using the 3D orientation, depth and speed recorded by a digital tag (DTAG – see Box 7.4, Chapter 7, for information about DTAGs).

As 3D tracking technology improved, researchers were able to better calculate 3D activity spaces. Simpfendorfer et al. (2012) calculated 3D kernel utilization distributions (KUDs) from acoustic data collected on European eels (*Anguilla anguilla*) in Norwegian waters. Using custom R scripts, Simpfendorfer et al. described the 3D activity spaces for each eel and estimated the volumetric overlap between pairs of eels. Williams-Grove and SzedImayer (2017) also applied the 3D KUD method (described in Simpfendorfer et al. 2012) to evaluate diel changes in the activity spaces of red snapper (*Lutjanus campechanus*), highlighting this fish's use of the entire water column.

Understanding species interactions and overlap in space use is important for defining population and ecosystem dynamics due to resource limitations and competition. Home range overlap calculations can be used to define interactions between animals to show how space use relates to other individuals in the population, and to define changes in the area used by an individual over time, allowing for an assessment of site fidelity for a particular individual (Fieberg and Kochanny 2005). For example, Udyawer et al. (2015) used the methods developed by Simpfendorfer et al. (2012) to create 3D diel activity spaces used by two sea snake species (*Hydrophis* (*Lapemis*) *curtus* and *Hydrophis elegans*) and compared the spatial overlap of sea snake activity spaces to the impact zones of trawling and dredging

operations. This approach demonstrated a significant improvement over 2D methods since it brought out the relationships between the sea snakes' 3D activity spaces, their 3D environment, and the possible 3D impacts from threats, in this case, trawlers.

A pioneer of the home range concept, Burt (1943) noted that individual home ranges often overlap but that the calculated overlap can be exaggerated depending on how the home range was calculated. This observation appears to hold for 2D and 3D calculations. Cooper et al. (2014) and Lee et al. (2017) concluded that areas of overlapping 2D home ranges can be over-estimated compared to 3D calculations. Simpfendorfer et al. (2012) suggested the over-estimate error could be as high as 20%, concluding that 3D data are integral to a full understanding of space use and overlap in marine species. Other advantages of using 3D calculations are that some activity space differences may only be seen in 3D. For example, in the construction and calculated overlap of home ranges of the eastern blue groper (*Achoerodus viridis*), differences in home ranges not detected by the 2D analyses were evident in 3D analyses (Lee et al. 2017). In contrast, Simpfendorfer et al. (2012) found that individual home ranges that appeared to overlap in horizontal 2D space sometimes showed spatial separation between individuals in 3D.

As explained in Chapters 1 and 3, passive acoustic telemetry has been used much less for marine mammals than for bony fish and shark species, at least partially because of the overlap of the typical acoustic transmitter frequency of 69 kHz (Vemco 2012) with the hearing frequencies of some species (see Fig. 3.5). The dugong is an ideal marine mammal to test the potential of this technology to study 3D space use. The acoustic transmitter frequency is outside their likely sensitive hearing range (Anderson and Barclay 1995), and even though most dugong dives are relatively shallow (Chilvers et al. 2004; Marsh et al. 2011), they are capable of deeper dives than manatees (Keith-Diagne et al. 2022), suggesting that understanding their 3D space use is more important. Using time-depth recorders, Hagihara (2015) recorded a maximum dive depth of 31.5 m and (Sheppard et al. 2006) recorded a dugong diving to 35.5 m. Earlier, Lee Long et al. (1996) recorded dugong feeding trails to 33 m.

In Chapter 3, I demonstrated good agreement between the 2D patterns of space use obtained using GPS satellite transmitters and passive acoustic telemetry. In this chapter, I used the analytical methods developed by Simpfendorfer et al. (2012) to demonstrate the potential of acoustic tracking to describe dugongs' 2D and 3D space use in the area of the array established on the Eastern Banks and adjacent areas in Moreton Bay (see Fig. 5.1).

5.2 Materials and Methods

5.2.1. Field methods

Acoustic tracking was used to study dugong space use in Moreton Bay within the Eastern Banks–South Passage area adjacent to Moreton and North Stradbroke Islands (see Fig. 5.1), an area containing a variety of benthic habitat types including sand and seagrass (Roelfsema et al. 2009). South Passage links the major dugong habitat in Moreton Bay, the Eastern Banks, which is dominated by seagrass to the adjacent oceanic environment where seagrass has not been detected (Lanyon 2003; Marsh and Sinclair 1989; Preen 1992).

As explained in Chapter 2, an array of 28 acoustic receivers was deployed in the Eastern Banks and included five receivers placed in oceanic waters. The location of the receivers, the process of placing them, and how the recorded data were retrieved are described in detail in Chapter 2 – Methods. Dugongs were captured opportunistically in this area during blocks of dedicated fieldwork in 2012, 2013 and 2014, and fitted with acoustic transmitters that recorded temperature (°C), and depth (m) data at regular intervals as described in Chapter 2. When the dugongs were within range, the receivers recorded the signals, which indicated the presence of individual dugongs, and movements were noted by the successive signal recordings received at receivers within the array. Raw datasets, which included a time stamp, temperature (°C), and depth (m) for every detection, were downloaded from the receivers at regular intervals. Seasons were defined as: Summer (December to February), Autumn (March to May), Winter (June to August) and Spring (September to November). Only adult and sub-adult individuals (length >230 cm) provided sufficient data to be used in this analysis.

5.2.2. Data analysis

Residency and Attendance Indices

Residency and Attendance Indices were computed for each dugong. The Residency Index (sometimes called a detection index) is the ratio of the number of days a dugong's unique transmitter was recorded within the monitored area (the acoustic array) to the total number of days tracked (as defined by Lusseau 2005):

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Residency Index (RI) % = <u>No. of days detected</u>
No. of days between first and last detection.
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The Attendance Index is similar but measures the largest number of consecutive days the dugong was detected divided by the total number of days tracked. (as defined by Vianna et al. 2013):

Attendance Index (AI) % =The longest time series of consecutive days detectedNo. of days between first and last detection.

5.2.3. Depth use

I tallied the number of depth records > 10 m for each dugong and calculated the percentage of the total number of records for that individual. Detection data for all individuals were imported into the R Statistical Environment (R Development Core Team 2018) for analysis. The data were organised by months per year (hereafter called year-months) per individual. Individuals with >10 detections per year-months were further analysed in R. Depth use was estimated for each month of each year that an individual was detected, and depth profiles including the mean and maximum depths reached were plotted for each dugong.



The sea bottom depth was calculated by adding the receiver height from the sea bottom to the receiver depth from the sea surface (at deployment). Each dugong was assumed to be on the bottom when its depth data were between the sea bottom to 2 m above the sea bottom. The 2 m correction allowed for the acoustic transmitter's position on the dugong tail stock and the likely angled position of the dugong at the bottom. (Hagihara et al. 2011). Similarly, each dugong was assumed to be at the surface when the recorded depth data were between the sea surface (0 m) and 0.75 m below the sea surface (known as dive threshold; Hagihara et al. 2011). Illustration by D. Zeh.

I calculated the percentage of depth data at the sea surface (see Box 5.1 above) by dividing the number of data records at the sea surface by the total number of depth data records for each dugong. Similarly, I calculated the percentage of depth data at the sea bottom by dividing the number of data records at the sea bottom (see Box 5.1) by the total number of depth data records for each dugong.



Figure 5.1: Map of the study area in Moreton Bay showing the location and density of seagrasses and the acoustic array. Each circle represents an acoustic receiver location inside an 800 m buffer. Inset: Location of the study area within the Moreton Bay Marine Park in Queensland, Australia.

5.2.4. Space use

Individual horizontal (2D) and three-dimensional (3D) kernel utilisation distributions (KUD-50% and 95% areas and volumes) were estimated for each year-month that the individual was detected. Individual depths and locations were first averaged over 1h intervals using the Centre of Activity (COA) approach of Simpfendorfer et al. (2002). Only individuals with >10 COAs and with >2 spatially different year-month COAs were used for further analyses. Using the "kde" function in R ('ks' package; Duong 2019), individual year-month core use (50%) and extent (95%) areas and volumes were calculated. Area sizes were calculated based on COA locations and a 2x2 fixed bandwidth matrix and volume sizes were calculated using COA depths and locations and a 3x3 fixed bandwidth matrix.

Fixed bandwidth matrices were calculated using a method adapted from Heupel and Simpfendorfer (2014) and used to facilitate comparisons between individuals. Monthly KUD core size areas and volumes were estimated using an automated bandwidth matrix (or H) from the ks function. The median (the mean was too large) was calculated from all the automated H values generated and used in a ks function to be able to compare individual and month. This approach resulted in many individuals having zero values for their 50% area and 50% volume KUDs. To overcome this problem, a logarithmic regression was used to determine the adequate H that could be used to estimate the kernel density estimates (kdes) with fewer resulting zero values. To do this, monthly kde areas and volumes were calculated for each individual and month using different H values starting with the median H up to 100 times the median H (to reach maximum automated H calculated). The intercepts (areas or volumes) from the regression equations for each month were determined and assigned to the corresponding H (i.e., median, 5 times or 10 times the median). The resulting mean H was used for further analysis. Core use and extent areas were calculated using a fixed bandwidth matrix based on the 20x median-fixed bandwidth matrix array (c(6025321.868, 1562799.684, 1562799.684, 7542556.076),c(2,2)). Core use and extent volumes were calculated using a fixed bandwidth matrix based on 16x median-fixed bandwidth matrix array (c(3910122.311, 1110949.083,75.8156001,1110949.083,4472435.508, -187.5378065, 75.8156001, -187.5378065, 5.840276164),c(3,3)).

Percent overlaps in space use in consecutive months were estimated for each dugong to quantify whether individuals were consistent in their space use over time. First, year-month overlap sizes were calculated using COA locations and depths (for volumes), fixed bandwidth matrices (same as above) and grid size determined by minimum and maximum longitude, latitude, and depth (for volumes) using the "kde" function in R ('ks' package; Duong 2019). Available year-month percentage overlaps were calculated for each year-month pairing (2 consecutive months) by dividing the overlap value (size – for each month pairing) by the first month (of same month pairing) area value (size).

5.2.5. General additive mixed models

Mixed-effect models

Following the Fisher et al. (2018) method (i.e., evaluating a set of candidate models based on multiple predictors), general additive mixed models (GAMMs) with full-subsets analyses were implemented using the 'gam' function from the 'mgcv' package (Wood 2017). Response variables were tested, and transformed to normality when required using the square root function (i.e. year-month mean depth, year-month core volumes, year-month extent areas and volumes, and extent areas percent individual year-month overlap), log transform (i.e. year-month minimum depth, year-month core use areas, core use areas and volumes percent year-month overlaps and core areas percent individual year-month overlap), and arcsine transform (i.e. year-month extent areas and volumes percent overlaps). A smoothing factor was included in the GAMMs for continuous predictors. Individual body length and water temperature were centred to simplify interpretation. ID was included as a random effect to enable population-level prediction, account for the repeatedmeasures nature of the data, and year or combined year (for year-month percent overlap models) was used in a weight function to account for unequal sample size across years (Bolker et al. 2009). Full subsets analyses, with k limited at 5 to enforce strictly monotonic relationships, were run using the 'generate.model.set' function in the FSSgam package (Fisher 2020). Collinearity between factors was assessed and no model with included correlated factors was included in the final subsets. Diagnostics plots (i.e., model fits and auto-correlation function plots) were used to evaluate goodness of fit (Burnham and Anderson 2002; Zuur et al. 2010). To account for temporal autocorrelation when required, models could be fitted with different correlation functions. Autocorrelation was not present in models; therefore, no models were fitted with autocorrelation functions. The relative importance values of fixed factors were estimated from subsets of models and only important variables with values >0.5 were plotted for each model.

5.26. Depth analysis using GAMMs

General additive mixed models (GAMMs) with full-subsets analyses (i.e., evaluation of sets of candidate models based on multiple predictors) were used to examine the influence of biological factors (individual length, sex) and environmental factors (water temperature, month of the year and season) on year-month minimum, mean and maximum depths. Individual length and water temperature were centred to simplify interpretation. Individual ID was included as a random effect to enable population-level predictions and account for the repeated-measures nature of the data. Year was included in a weight function to account for

unequal numbers of detections and individuals across years (Bolker et al. 2009; see Mixed Effects Models section for more details).

GAMMs with full subsets analyses were used to examine the influence of biological and mean year-season environmental factors on core use and extent area and volume yearmonth sizes and percent year-month overlaps within individuals. Individual length, sex, water temperature, month of the year and seasons were used as factors for the core use and extent area and volume year-month size models. Individual length, sex, water temperature, combined consecutive months and combined seasons were used for year-month core use and extent area and volume percent overlaps. Combined months and combined seasons variables were used to determine if individuals were using the same areas in certain consecutive months or consecutive seasons more than others. See the Mixed effect models section below for more details.

5.2.7. Relative importance of independent variables

The relative importance of the response variables to the corresponding environmental and biological factors tested in the GAMMS models were analysed using AICc. The weight for each individual variable was calculated separately based on all the models using the wi.AICc (weighted) value and the number of models in which the variable appeared. The weight for variables (combined) in each model was filtered, selecting only those with Δ AICc < 3.

5.3 Results

5.3.1. Dugongs tracked.

Twenty-nine dugongs were tagged in the three field seasons, 2012 – 2014; one individual was tagged in both 2013 and 2014 resulting in a total of 30 datasets. The size of each dataset depended upon how long the dugong stayed within the acoustic array. Hence, some datasets were too small to be useful for these analyses. I obtained sufficient data for meaningful analysis of the diving behaviour and 2D and 3D activity spaces of 11 dugongs (five females and six males) caught over the three field seasons. All these animals were adults or sub-adults. The body lengths of the females ranged from 250-285 cm (mean = 261.4 cm); the body lengths of the males ranged from 239-297 cm (mean = 281.2 cm). The females were tracked for three to 10 months (mean = 5.6 months); the males from three to six months (mean = 4.3 months) (see Appendix Table 5.1 for details). Given the small samples sizes, narrow range of body lengths and relatively short sampling periods per individual, the results must be interpreted with caution and used as a proof of concept only.

5.3.2 Residency and Attendance Indices

The Residency Indices for the 11 dugongs ranged from 0.53 to 0.80 with a median of 0.68 (see Appendix Table 5.3 and Fig. 5.2 below). The Attendance Indices ranged from 0.11 to 0.30 with a median value of 0.16. The greatest number of consecutive days that an animal was detected in the array area was 77 days of 226 days tracked (male, ID 14242 in years 2013-2014). These two indices collectively demonstrate that the tracked dugongs consistently used the space within the array but that all animals also spent time outside the array or within the array in areas not covered by receivers.





5.3.3. Depth Records > 10 m

Females dived deeper more often than males and their dives were more variable. The results show considerable individuality; most of the data > 10 m were recorded from two females (Fig. 5.3 and Fig. 5.4). All the data for summer were recorded by two females and there were no data > 10 m for the six males in summer. In winter, three females reached depths > 10 m, but one female accounted for 166 of the 171 relevant data records. The total depth records for the five females and six males were nearly equal (females: 53%, males: 47%) but nearly 15 times as many data records > 10 m were from females (see Appendix Table 5.2). The total number of records was 842. Given the small sample sizes, it is not

possible to be certain whether these results reflect individual rather than sex differences. The fact that there were considerable individual differences within the females suggest that most of the heterogeneity is between individuals.



Figure 5.3: Seasonal percentages of depth records > 10 m for female and male dugongs. This graph illustrates the large numbers recorded by females versus the relatively few records >10 m recorded by males. The largest share of the records were from one female dugong with acoustic ID 14244_1314 as shown above. Part of the explanation for this lies in the fact that these records cover two years, 2013 and 2014; nevertheless, the percentage of records for this one dugong is so large in comparison to others, it indicates individuality in depth use. The number of records > 10 m for each season is shown at the top of each column.



Figure 5.4: Monthly totals of dive records > 10 m recorded for females and males. Deep dives were less common in the late autumn and the early winter months. As with Fig. 5.3 above, the largest share of the records were from female dugongs with the acoustic IDs 14244_1314 and 14248_1314. The number of records > 10 m for each month is shown at the top of each column.

Table 5.1: Comparison of bottom and surface records between 11 individuals. Since dugongs spend much time foraging on benthic seagrass, many of the percentages are greater than 25%. There are likely to be many unquantified factors contributing to the estimated time spent on the bottom, presumably including the relative density of the seagrass and the water depth when feeding. The water depth in the study region changes constantly due to the tidal influences.

		Data Records				
ID	Sex	Total	Bottom	Bottom %	Surface	Surface %
13004_14	Μ	1008	294	29.2%	15	1.5%
13006_14	F	822	153	18.6%	544	66.2%
13010_14	F	181	109	60.2%	4	2.2%
14236_12	Μ	479	56	11.7%	97	20.3%
14240_12	F	433	63	14.5%	48	11.1%
14242_12	Μ	2837	2372	83.6%	30	1.1%
14242_13	Μ	197	49	24.9%	14	7.1%
14244_13	F	1555	616	39.6%	0	0.0%
14244_14	F	1884	897	47.6%	1	0.1%
14248_13	F	1059	292	27.6%	59	5.6%
14248_14	F	1413	284	20.1%	97	6.9%
14258_13	Μ	272	63	23.2%	35	12.9%
14260_13	Μ	692	122	17.6%	30	4.3%
14270_13	Μ	1439	213	14.8%	9	0.6%
	Total	14271	5583	39.1%	983	6.9%

5.3.4. Mean depth and maximum depth per month per individual (m)

The mean depth per year-month to which females dived was -4.31 m (range -2.09 m to -7.31m); the corresponding figure for males was -2.76 m (range -1.70 to -3.30 m) (see Appendix Table 5.1: A). The maximum depth per year-month and its range was also greater for females than males. Females dived to a mean of -14.3 m (range -9.7 m to -19.93 m); the corresponding figure for male was -11.9 m (range -8.94 m to -15.26 m) (see Appendix Table 5.1).

5.3.5. Bottom and surface percentages

Percentages for time spent at the bottom and at the surface were calculated based on the number of data records available for dugongs recorded in both areas. Since dugongs are bottom feeders, it is unsurprising that the percentage of records at the bottom was 39% of the total data records compared to about 7% at the surface (see Table 5.1).

5.3.6 Relative importance of independent variables

The relative importance of the response variables to the corresponding environmental and biological factors tested in the GAMMS are shown below. Individual body length and Season had the most impact upon Maximum Depth (relative importance values 0.8 - 0.9). Sex and Season had the most impact upon the Extent Volume (95% 3D KUD). As can be seen in Fig. 5.5, most of the response variables appeared be of low importance to the environmental and biological factors.

	Individual length	Water temp.	Month	Sex	Season	
Mean depth	0.1 - 0.2	0.2 - 0.3	0.0 - 0.1	0.4 - 0.5	0.0 - 0.1	
Maximum depth	0.8 - 0.9	0.0 - 0.1	0.0 - 0.1	0.1 - 0.2	0.8 - 0.9	
Core area (50% 2D KUD)	0.4 - 0.5	0.4 - 0.5	0.0 - 0.1	0.2 - 0.3	0.0 - 0.1	
Extent area (95% 2D KUD)	0.0 - 0.1	0.0 - 0.1	0.6 - 0.7	0.1 - 0.2	0.2 - 0.3	
Core volume (50% 3D KUD)	0.4 - 0.5	0.1 - 0.2	0.0 - 0.1	0.3 - 0.4	0.6 - 0.7	
Extent volume (95% 3D KUD)	0.1 - 0.2	0.0 - 0.1	0.0 - 0.1	0.8 - 0.9	0.9 - 1.0	Cold
Core area (50% 2D KUD) Percent overlap	0.0 - 0.1	0.2 - 0.3	0.0 - 0.1	0.2 - 0.3	0.1 - 0.2	0.9 -
Extent area (95% 2D KUD) Percent overlap	0.1 - 0.2	0.3 - 0.4	0.0 - 0.1	0.1 - 0.2	0.0 - 0.1	0.7 - 0.6 - 0.5 -
Core volume (50% 3D KUD) Percent overlap	0.1 - 0.2	0.3 - 0.4	0.0 - 0.1	0.3 - 0.4	0.0 - 0.1	0.4 -
Extent volume (95% 3D KUD) Percent overlap	0.2 - 0.3	0.2 - 0.3	0.0 - 0.1	0.1 - 0.2	0.0 - 0.1	0.2 - 0.1 - 0.0 -

Figure 5.5: Relative importance of the GAMMs response variables (rows) and factors and the corresponding environmental and biological factors tested in the GAMMS models (columns). Higher values indicate greater importance for that variable. Individual length and Season had the most impact upon Maximum Depth (relative importance values 0.8 - 0.9). Sex and Season had the most impact upon the Extent Volume (95% 3D KUD). All percentage overlaps refer to overlaps in space use in consecutive months within individuals

5.3.7. Dive depths – GAMMs

The top GAMMs for mean year-month depths included three factors: sex, sex + water temperature, and individual length (Table 5.2 A). However, none was significant with no R^2 values > 0.5 importance for Mean depth. For Maximum depth, however, Season + Individual length * Season was significant, with R^2 = 0.548 (Table 5.2 A). Season and individual length were significant factors with > 0.5 relative importance (Fig. 5.5).

Tables 5.2 A, B, C: Top GAMMs (Δ AICc <3) were used to explore the relationship between the variables measured using the passive acoustic telemetry and the various environmental and individual dugong factors. Differences were reported between lowest reported corrected Akaike Information Criterion (Δ AICc), weighted AIC (ω AICs), variance explained (R²) and effective degrees of freedom (EDF) for model comparison.

A. Year-month Depth

	Best Models	<u>∆AICc</u>	ωΑΙϹϲ	\underline{R}^2	EDF
Mean depth	Sex	0.000	0.426	0.165	3.00
	Sex + Water temperature	1.228	0.230	0.176	4.00
	Individual length	2.697	0.110	0.194	5.86
Maximum depth	Season + Individual length * Season	0.000	0.863	0.548	13.42
B. Year-month ar	ea and volume sizes				
	Best Models	<u>∆AICc</u>	ωAICc	\underline{R}^2	<u>EDF</u>
Core use area	Individual length + Water temperature	0.000	0.426	0.237	4.51
(50% 2D KUD)	Sex + Water temperature	0.885	0.274	0.211	4.00
	Water temperature	2.345	0.132	0.162	3.00
Extent area	Month	0.000	0.543	0.367	13.00
(95% 2D KUD)	Season	2.385	0.165	0.234	5.00
	Month + Sex	2.823	0.132	0.367	14.00
Core volume	Season + Individual length	0.000	0.337	0.205	6.00
(50% 3D KUD)	Season + Sex	0.221	0.302	0.203	6.00
	Sex + Water temperature	2.883	0.080	0.139	4.00
Extent volume (95% 3D KUD)	Season + Sex	0.000	0.832	0.351	6.00

C. Within individual percent overlap in successive months

	Best Models	<u>∆AICc</u>	ωAICc	\underline{R}^2	<u>EDF</u>
Core use area	Sex + Water temperature * Sex	0.000	0.210	0.125	7.50
(50% 2D KUD)	Water temperature	0.122	0.197	0.052	3.93
	Season	0.344	0.177	0.091	9.00
	Null	1.996	0.077	0.000	2.00
	Individual length + Water temperature	2.027	0.076	0.103	6.38
	Sex + Water temperature	2.301	0.066	0.053	4.92
	Individual length	2.501	0.060	0.084	4.90
	Season + Sex	2.566	0.058	0.089	10.00
	Month	2.879	0.050	0.177	13.00
Extent area	Water temperature	0.000	0.357	0.059	4.01
(95% 2D KUD)	Individual length + Water temperature	1.486	0.170	0.064	5.08
	Sex + Water temperature	1.916	0.137	0.060	5.02
	Individual length	2.239	0.116	0.002	3.00
	Null	2.392	0.108	0.000	2.00
Core volume	Sex + Water temperature * Sex	0.000	0.361	0.206	9.84
(50% 3D KUD)	Water temperature	0.804	0.241	0.111	4.17
	Individual length + Water temperature	2.118	0.125	0.131	5.65
	Sex + Water temperature	2.552	0.101	0.115	5.21
	Null	2.961	0.082	0.043	2.00
Extent volume	Individual length + Water temperature	0.000	0.210	0.076	5.31
(95% 3D KUD)	Null	0.186	0.192	0.000	2.00
	Individual length	0.262	0.185	0.048	3.93
	Water temperature	0.627	0.154	0.047	3.75
	Sex + Water temperature	1.256	0.112	0.037	4.21
	Sex	1.380	0.106	0.005	3.00

Individuals reached deeper areas and individual variation was greater in summer compared to the other seasons (Fig. 5.6). The maximum depths reached for individuals with body lengths between 260 and 280 cm were less than for smaller (≤250 cm) or larger individuals (>290 cm) but both the range of body lengths and sample sizes are small, so the results should be interpreted with caution and are not considered further here.



Figure 5.6: Relationship between maximum depth per month and season per individual (±95% Confidence Interval) and season obtained from the relevant GAMM. The depth below 30m reflects the uncertainty in the model. The model cannot be constrained to the depths of the study site.

5.3.8. Mean space use per individual

Core area-A50% KUD (km²)

The mean 2D core area (A50 (km²)) per individual was about 25% greater for females than males but the range of values was about 50% greater for males than females. Females used an area with a median of 9.1 km² (range 2.9 km² – 10.0 km²) and males an area with median 7.1 km² (range 2.5 km² – 13.2 km²), (see Appendix Table 5.1 B and Appendix Table 5.2). The top GAMMs for mean space use per individual included individual length, sex, and water temperature. However, none of these factors was important (no R² values \geq 0.5 importance, Fig. 5.5) so I can't draw any firm conclusions.

Extent area-A95% KUD (km²)

The mean 2D extent area (A95 (km²)) per individual was about 6% greater for males than females although the range of values were similar. Females used an extent area with a median of 82.5 km² (range 62.9 km² – 125.5 km²); the corresponding values for males were median 75.3 km² (range 55.1 km² – 123.4 km²), (see Appendix Table 5.1 B and Appendix Table 5.2). The top GAMMs for mean space use per individual included month, sex, and season (Table 5.2 B). Month was significant with a relative importance value between 0.6 – 0.8 (see Fig. 5.5). The 2D 95% KUDs were greatest in the middle of the year (peaking in July, Fig. 5.7). See Appendix Table 5.4 for a comparison of 2D activity spaces across geographic areas and research projects.



Figure 5.7: 2D extent areas (KUD) by month. 2D extent KUD (95% KUD \pm 95% Confidence Interval) by month were obtained from the top GAMM (Table 5.2). 2D extent area increased in size during the summer months and decreased greatly during the initial winter months. The trends may reflect the amount of effort required for foraging.

Core volume-V50% KUD (km³)

The mean 3D space use (V50 (km³)) per individual and the range were much greater for females than males with a ratio of nearly 2:1. Females used a volume with median 0.034 km³ (range 0.015 km³ – 0.060 km³); males a volume with median 0.022 km³ (range 0.006 km³ – 0.029 km³), (see Appendix Table 5.1 B). The top GAMMs for mean space use per individual included individual length, sex, season, and water temperature (Table 5.2 B). Season was significant with an R² value between 0.6 – 0.8 importance (Fig. 5.5). The 3D 50% KUDs were greatest in autumn, least in summer and winter and intermediate in spring, Fig. 5.8).



Figure 5.8: Seasonal core volumes (3D 50% KUD). Seasonal values of 3D 50% KUD. The box plots show the means \pm 95% Confidence Interval of the 50% 3D (core) KUD for each season.

Extent volume-V95% KUD (km³)

The mean 3D space use (V95 (km³)) per individual was about 55% higher for females than males, although the ranges were similar for males and females. Females used a median volume of 0.76 km³ (range 0.38 km³ – 0.80 km³); males a median volume of 0.40 km³ (range 0.34 km³ – 0.75 km³), (see Appendix Table 5.1 B). The top GAMMs for mean space use per individual included sex, and season (Table 5.2 B). Both factors were significant with R² values \geq 0.5 importance (Fig. 5.5). The extent volume (95% KUD) was smaller in spring than in the other seasons and for males than females. (See Fig. 5.9 and Fig. 5.10.)



Figure 5.9: Seasonal extent volumes (3D 95% KUD). The box plots show the means \pm 95% Confidence Interval of the 95% 3D KUD for each season.



Figure 5.10: Relationship between sex and extent volume (3D 95% KUD). The box plots show the means \pm 95% Confidence Interval of the 95% 3D KUD for each sex.

5.3.10. Mean space use overlap by individuals in consecutive months.

Overlap in core area-A50% KUD (%)

Mean space use overlap per individual (A50 (%)) was about 15% higher for females (39.7%) than males (34.0%) and the range was nearly identical for the two sexes (females' range 1.0%-51.4% versus males' range 0.4 %–52.2%), (see Appendix Table 5.1 C). Top GAMMs for mean space use overlap per individual A50 (%) included individual length, sex, water temperature, month, and season (Table 5.2 C). However, no factor was significant with \geq 0.5 importance (Fig. 5.5).

Overlap in extent area-A95% KUD (%)

Mean space use overlap per individual (A95 (%)) was about 4 % greater for females (62.8%) than males (60.3%) and the range was about 40% greater for females (9.9%-88.6%) than males (19.9%-71.5%), (see Appendix Table 5.1 C). Top GAMMs for mean space use overlap per individual A95 (%) included individual length, sex, and water temperature (Table 5.2 C). However, no factor was significant with \geq 0.5 importance (Fig. 5.5).

Overlap in core volume-V50 (%) KUD

Mean space use overlap per individual (V50 (%)) was about 4% greater for males (35.4%) than females (35.0%); the range was about 36% greater for males (1.9%-60.5%) than females (1.0%-44.0%), (see Appendix Table 5.1 C). Top GAMMs for mean space use

overlap per individual V50 (%) included individual length, sex, and water temperature (Table 5.2 C). However, no factor was significant with \geq 0.5 importance (Fig. 5.5).

Overlap in extent volume V95 (%) KUD

Mean space use overlap per individual (V95 (%)) was nearly identical between females (60.2%) and males (60.4%) but the range was about 20% greater for females (20.7%-72.0%) than males (28.0%-70.8%), (see Appendix Table 5.1 C). Top GAMMs for mean space use overlap per individual A95 (%) The top GAMMs for mean space use overlap per individual A95 (%) The top GAMMs for mean space use overlap per individual length, sex, and water temperature (Table 5.2 C). However, no factor was significant with \geq 0.5 importance (Fig. 5.5).

5.3.11 Comparing 2D and 3D results in Moreton Bay

The importance of analysing space use in 3D is illustrated by comparing the 2D and 3D activity space results. This analysis supports the case for using acoustic tracking technology to study local scale movements within an acoustic array. For example, consider the comparison in Fig. 5.11 below of the 2D and 3D space use of a single female in two seasons.



Figure 5.11: Visual differences in 3D activity spaces for the same individual for two years. Core (50% 3D KUD) and extent (95% 3D KUD) volumes illustrated.

The activity spaces of the female identified as 14244, illustrated in Fig. 5.11 above, was active in both 2013 and 2014 and was responsible for the bulk of the data records > 10 m as is illustrated in Fig. 5.3 and Fig. 5.4 (see also Appendix Table 5.2). The 3D volumes shown above make an interesting comparison between years 2013 and 2014. In the top row (3D Output from R script) pink represents the 3D extent volumes (95% 3D KUDs) and green represents the 3D core volumes (50% 3D KUDs). In the second row (3D View), the 3D extent volumes (95% 3D KUDs) are shown in medium blue, and the 3D core volumes (50% 3D KUDs) are shown in medium blue, and the 3D core volumes (50% 3D KUDs) are shown in dark blue. These diagrams are overlaid on the Moreton Bay bathymetry and the local seagrass areas. In the third row (2D View), the 3D output from the R script has been rotated to a flat view and located accurately on a 2D map of Moreton Bay created in ArcGIS. The landforms of upper North Stradbroke Island and lower Moreton Island are shown in dark brown. Note that the 3D bathymetry has been exaggerated for

easier viewing. Note also that the 3D Output graphic as shown is the original R script output before it was rotated to create the 3D and 2D views.

5.4. Discussion

5.4.1. Proof of concept

The research presented in this chapter expands knowledge of the local scale space use of dugongs using the Eastern Banks in Moreton Bay and provides proof of concept that acoustic tracking technology can produce useful insights into the movements and habitat use of dugongs. The Eastern Banks of Moreton Bay provide year-round habitat for an estimated 1000 dugongs (Lanyon 2003; Lanyon et al. 2019b). Nonetheless, as all previous studies have shown (Gredzens et al. 2014; Marsh et al. 2011; Marsh and Rathbun 1990; Preen 1992; Sheppard et al. 2006; Zeh et al. 2016; Zeh et al. 2015), the movements of tracked dugongs are heterogeneous. Thus, my conclusions are tentative due to the small sample size and the fact that the data for sex are confounded by season.

This study provided new information on mean and maximum depth, core, and extent areas (2D KUDs) and volumes (3D KUDs), and the overlap of core and extent areas (2D KUDs) and volumes (3D KUDs) of individual dugongs over time. Overlapping areas and volumes provide insight into the consistency of individual space use over the tracking period. I also explored the relationships between these factors and biological variables (body length and sex), and environmental variables (water temperature, month, and season). None of these variables was associated with mean depth but maximum depth was strongly associated with individual length and sex. Extent area (2D 95% KUD) was significantly different between sexes and seasons. Sex and season were both strongly associated with extent volume (3D, 95% KUD) was significantly different between sexes and seasons. No biological or environmental value showed strong association with the overlapping core and extent areas or volumes. In the remainder of this discussion, I concentrate on the significant associations.

5.4.2 Residency and Attendance Indices

The residency indices for the 11 dugongs studied in this chapter indicated that all stayed in the vicinity of the array more than half the time they were tracked. The attendance index suggested that the dugongs spent long periods (up to 77 consecutive days) in the region of the array. Taken together, these indices also suggest that the tagged animals were undertaking local movements in and out of the array area. This result accords with the results reported in Chapter 6 (Zeh et al. 2018) in which I showed that all 30 dugongs made

return trips outside Moreton Bay, past the outer edges of the acoustic array. Preen (1992) noted that the six dugongs he tracked in 1988 made similar trips in the winter of 1988-1989 (see also Sheppard et al. 2006).

5.4.3 Depth use

Dugongs and manatees spend much of their time near the surface or in shallow water (Marsh et al. 2011), frequently diving to feed and rest. Typical manatee dives are < 5 m but they have been tracked to a depth of 16 m in Tampa Bay, Florida (Edwards et al. 2016). Dugongs undertake deeper dives than have been recorded for manatees (Keith-Diagne et al. 2022) and have been recorded diving as deep as 35.5 m (Sheppard et al. 2006). The actual depths reached by manatees and dugongs may be greater than records indicate (e.g., up to 2 m in dugongs) due to the animal's position in the water and the harness location on the tailstock (Hagihara 2015; Marsh et al. 2011).

Hagihara (2015) summarised dugong diving depths from four studies in Moreton Bay (including Zeh et al. 2015), noting that all dugongs exceeded 20 m depth with a recorded maximum of 31.5 m and that dugongs were frequently recorded at depths > 10 m. During my PhD research, 27 of 30 datasets recorded depths > 10m. A total of 14,970 data records were collected from the 11 dugongs that are the focus of this chapter. Of these, over 5% (846) were recorded at depths > 10 m but 67% of these records were from only one female. This deeper activity was focused in areas covered by only a few of the acoustic receivers. Of the 29 receivers, ~20 were placed at depths less than 10 m. The movements studied in detail in this chapter indicated that dugongs are heterogeneous in their pattern of 3D as well as 2D space use. In the sections below, I explore why some dugongs might use deep-water areas in Moreton Bay.

5.4.4. Feeding

The large number of deep-water data recorded for the acoustically tagged dugongs suggest that seagrass communities may have been present in the region of the array at depths greater than 5 m. Hagihara (2015) did not confirm the presence of seagrass at the time of her research but noted that all dives over known seagrass were < 7 m.

There is little definitive information about whether seagrass communities occur in Moreton Bay at depths > 10 m because most mapping studies have been restricted to shallow water (see Fig. 5.12). Preen (1992) recorded seagrass in water as deep as 8.1 m from samples at 512 random sites, which he identified from survey transects in aerial survey photos. Preen (1995a) noted seagrass growing at the maximum depth of 7 m during his surveys to examine the impact of dugongs on seagrasses within his pre-determined transects. Preen (1992) also noted that above-ground seagrass biomass was seasonal, which he interpreted as an effect of light and nutrient variation. Abal and Dennison (1996) surveyed the depth range of seagrasses at eight sites in southern Moreton Bay (where the water clarity is much less than on the Eastern Banks) but no seagrass was recorded below 3 m. Depth was determined along transect lines using a survey staff placed every 5 - 10 m. Roelfsema et al. (2014) completed the most recent seagrass mapping to depths < 5 m by combining seagrass photo transect field data with high spatial resolution satellite image data dating from 2004 to 2013.

In contrast, Rasheed et al. (2014) detected seagrass communities as deep as 14 m in northeastern Queensland. They described deep-water seagrasses as highly variable and seasonally ephemeral, possibly absent for months or years in areas with reduced water quality. York et al. (2015) also documented deep-water seagrasses (by definition, depths > 15 m) at four sites in the Great Barrier Reef from 2004 to 2012, noting that seagrass can return quickly when water quality improves. These sites near Hay Point, Queensland were chosen because of their proximity to a port expansion project so that the effects of dredging could be documented. York et al. (2015) concluded that the Halophila species present at these depths died more quickly than other seagrass species but recovered more quickly using sexual reproduction and seed dispersal and that deep-water seagrasses were ephemeral and seasonal. This research suggests that it is possible that deep-water seagrass communities were present on the Eastern Banks in the years I tracked dugongs but were absent or undetected at the times when the local seagrasses were mapped, which differed from the timing of my study. The Eastern Banks are a relatively pristine area compared to the rest of Moreton Bay (Dennison and Abal 1999). Strong tidal currents rush through South Passage resulting in a twice daily exchange of water between the eastern bay and the ocean, so that the impact of terrestrial runoff is much less than in the western bay (Abal and Dennison 1996; Pantus and Dennison 2005; Young and Kirkman 1975).



Figure 5.12: Seagrass cover of Eastern Banks, Moreton Bay (Lyons et al. 2013) showing incoming water exchange (tide influx) through South Passage. The authors were unable to display deep-water seagrass because of the inaccuracies created by the changing depths as a result of the tides. The image was developed from a true colour Landsat 5 TM image (23 September 2009; United States Geological Survey). Water exchange label added by D Zeh.

It is unknown how long dugongs must spend feeding each day. Chilvers et al. (2004) estimated 16 hours feeding per day (66%) based on the dive profiles developed for five dugongs. However, this figure is questionable because of the difficulty in predicting activity from TDR dive profiles in shallow water (Hagihara et al. 2011). On the basis of focal follows of individual dugongs in shallow water on the Eastern Banks at high tide, Hodgson (2004) estimated that dugongs spent 41% of their time feeding but her results were restricted to high tide when intertidal seagrass is accessible and thus may be overestimates. In comparison, Etheridge et al. (1985) and Bengtson (1983) reported that Florida manatees feed seasonally for about 4 to 7 hours per day (17-29%). Marsh et al. (2011) hypothesized that dugongs feed for longer than Florida manatees because tropical seagrass communities generally have lower biomass than the communities of aquatic plants on which Florida manatees typically feed but this hypothesis has never been tested.

Seagrass leaves and rhizomes are the staple constituents of the dugong's diet (Marsh et al. 2011). When feeding in excavating mode, dugongs may eat algae and benthic invertebrates incidentally, sometimes disturbing the invertebrate communities as observed by Nakaoka et al. (2002). In the Darwin region, (latitude ~ 12.46°S), dugongs sometimes target algae (as documented by Whiting 2002) and benthic invertebrates. Preen (1995b) noted the presence

of ascidians in dugong faecal samples and polychaetes in the stomach contents of a dugong accidently killed on Moreton Bay (latitude ~ 27.24°S). Other benthic fauna from the area, such as soft sea pens, large anemones, and small gastropods were not recorded in the stomach contents (Preen 1995b). In a north Queensland study based on the locations of dugong feeding trails, (Coooya Beach, Yule Point, Double Island, latitude ~ 16.57°S), Tol et al. (2016) observed that dugongs preferred high biomass seagrass meadows foremost, but that seagrass species and nitrogen content were important. In contrast in Hervey Bay in south-east Queensland (latitude ~ 25.29°S), Sheppard et al. (2010) found that dugongs' habitat use was focused on seagrass areas with high nitrogen content. However, when tides or other disturbances made those areas less accessible, dugong habitat use shifted to seagrass areas with high biomass. It follows that dugongs might make deep dives to augment their feeding resources if food resources were available. For example, a deepwater seagrass community (or perhaps even a community of algae or benthic invertebrates) would be a valuable resource for dugongs when much of the seagrass meadows on the Eastern Banks are unavailable for feeding at low tide.

5.4.5. Navigation

Sheppard et al. (2006) estimated that when dugongs made large-scale movements along the Queensland coast (LSMs, movements > 15 km), they were only at the surface (within 1.5 m of the surface) about 16% of the time, indicating that most of the travel was done within the water column at depths deeper than 1.5 m. Multiple deep dives to (27.0 - 36.5 m) were made during some LSMs, similar to the movements of Florida manatees swimming across Tampa Bay, Florida, where manatees sometimes made consecutive deep dives when crossing the shipping channel (Edwards et al. 2016). Although he could not be sure if the dugongs were actually diving to the bottom, Sheppard et al. (2006) hypothesised that the deep dives could be used as navigational guides. Hagihara (2015) suggested that navigation might be the reasons dugongs appeared to make several deep dives to the seafloor outside South Passage as they travelled between Moreton Bay and the outside marine waters, but her findings were not conclusive. All sirenians have a highly developed somatosensory capacity, especially on their heads (Marshall et al. 2022) which likely plays a role in orientation and navigation, making diving to the bottom a plausible navigation aid. Nonetheless, dugongs cannot always use the bottom as a navigation aid, as they sometimes travel across oceanic trenches (Hill-Lewenilovo et al. 2019; Hobbs et al. 2007). The geography of Moreton Bay makes the deep-water navigation described by Sheppard et al. (2006) implausible for the animals I tracked within the boundaries of the array (Fig. 5.1) since depths > 10 m occur in isolated patches and channels. The animals I studied were
consistently detected in the region of the array and presumably knew the area well, making the navigation hypothesis an unconvincing explanation for the behaviour I recorded, even though it is a plausible explanation for deep diving during long-distance movements.

5.4.6. Predation

Sheppard et al. (2006) also suggested that deep dives might be a tactic to avoid sharks. Evidence to support this hypothesis is limited. In Shark Bay, Western Australia, both tiger sharks (*Galeocerdo cuvier*) and dugongs use shallow seagrass habitats (Heithaus et al. 2002). Within these areas, the dugongs favour edge microhabitats that are close to deeper water, which makes for ease of escape (Wirsing et al. 2007). Thus, Wirsing et al. concluded that dugong's habitat use reflected a strategy of reducing the risk of predation rather than predator avoidance *per se*. Given that deep-water habitat use was largely restricted to two of the dugongs I tracked, I conclude that my data cannot be used to support or refute the predation hypothesis.

5.4.7. Resting

The data on the resting behaviour of dugongs are limited. While tracking 15 dugongs in northern Australia, Chilvers et al. (2004) estimated that dugongs spent 3% of their time in shallow resting dives but her data were based on dive profiles that are difficult to interpret in shallow diving animals (Hagihara et al. (2011). Hodgson (2004) observed dugong herds in Moreton Bay via a blimp-cam in shallow water and reported that dugongs rested for 7% of their day and rested on the bottom for about 22% of that time. However, Hodgson (2007) later reported that her observed depth was limited to 3-4 m. Observations on manatee resting behaviour may be instructive. Castelblanco-Martínez et al. (2015) tracked five Antillean manatees (*Trichechus manatus manatus*) in Chetumal Bay, Mexico in depths < 6 m. The manatees were found to be bottom resting 32.2% of the time tracked. In the Drowned Cayes, Belize, Bacchus et al. (2009) compared 12 manatee resting holes with 20 non-resting holes, used by Antillean manatees. The resting holes were deeper (mean 3.5 ± 0.30 m) compared to non-resting hole depth (mean 2.0 ± 0.12 m) and exhibited surface water velocity much slower than that of the non-resting holes (mean velocity 0.89 ± 0.51 cm/s vs. 4.26 ± 1.14 cm/s); both areas were mostly devoid of seagrass or other vegetation.

On a receding or incoming tide, the velocity of water moving through deep channels is slower close to the bottom because of reduced turbulence (pers. comm., Prof. Eric Wolanski, James Cook University, to H. Marsh, 2021). The sheltering effect created by the combined effects of seagrass, water depth, and the irregular shape of the channels interacting with the water moving through the channels (see Fig. 5.13) should benefit both bottom feeding or resting dugongs. This benefit would depend on the irregularity of the channel shape, the changing shape of the channel due to water movement, and the speed of the water, making predictive calculations impractical if not impossible (Southard 2021; Wang et al. 2019). The deep water in the channels would be an energetically efficient place for dugongs to rest, especially at low tides when resting in shallow areas is not possible. Dugongs could certainly detect the changes in the hydrodynamic environment close to the bottom through their sensory hairs, which mediate exquisitely sensitive hydrodynamic reception, analogous to the function of the lateral line system in fish and amphibians (Marshall et al. 2022). I conclude that dugongs may be using deep-water patches in the channels in the Eastern Banks for resting.



Figure 5.13: Illustration of turbulence in a channel with vegetation from (Wang et al. 2019) illustrating the turbulence created in the channel with vegetation, which slows the water, making feeding on seagrass or resting on the bottom less energetically demanding for dugongs.

5.4.8. Sex differences in depth use

The maximum depths per year-month and their ranges were greater for the females than the males I tracked. Individual females were recorded in deeper areas and individual variation was greater in summer compared with the other seasons. In autumn and spring, the patterns were similar with the female data totals much greater than the male data totals. The female with the most data records > 10 m in summer also had the most records in spring and autumn suggesting that individual differences in behaviour were largely responsible for this result. Thus, these apparent gender differences must be interpreted with caution, although, as ID was used as a random factor, individual differences have been accounted for in the

analysis. My data were compromised by small sample size and confounded by the seasonal differences in when males and females were tracked.

Nonetheless, female dugongs may need to spend more time than males in feeding or resting in deeper water. Females may need to be more energetically conservative than males as they must be in good condition to meet the nutritional demands of ovulation, the later stages of pregnancy (Marsh and Kwan 2008), and lactation. Although dugong births are loosely timed to correspond with high plant productivity (Marsh et al. 2011), their long gestation and nursing periods mean that the energetic demands of late pregnancy and lactation are prolonged. Burgess et al. (2012) observed pregnant dugongs throughout the year in Moreton Bay and dugongs with attendant calves are consistently seen during aerial surveys (Lanyon 2003).

Mating dugongs have been observed in Moreton Bay during spring (September; see Lanyon et al. 2021; and late October to mid-November; see ; Preen 1989). Females swim to deeper water to avoid 'rushing' behaviour from males during mating attempts (see Adulyanukosol et al. 2007; Anderson and Birtles 1978 for a discussion of 'rushing' behaviour). The fact that female deep-water use was not seasonally limited suggests that the females were not using deep water solely to avoid the advances of males.

5.4.9. Comparisons of 2D and 3D results between sexes and environmental factors There were no significant biological or environmental variables accounting for the differences between males and females in 2D core areas (50% KUD). Females used about 25% more core area than males (refer to Appendix Table 5.1: B). Month was a significant explanatory factor for the 2D extent areas (95% KUD) which had similar means between females and males. Both sex and season were significant factors for the mean 3D volumes. The mean 3D extent volume for females was nearly twice that of the males (Appendix Table 5.1: B). The extent volume was smaller in spring than in the other seasons and smaller for males than females. Since the 2D areas were similar for females and males, the 3D space use presumably resulted from the females diving deeper as discussed above.

Some other male and female marine mammals have home ranges of different sizes. Lidgard et al. (2020) observed that season and sex were the best predictors of 95% 2D home ranges of grey seals (*Halichoerus grypus*). In that study, females displayed smaller median home ranges than males in both summer and autumn seasons. Sprogis et al. (2016) noted sexspecific differences in home range size for bottlenose dolphins (*Tursiops aduncus*), and

suggested the difference was explained by male mating behaviour. Mating behaviours may be responsible for differences in dugong space use but there are no data to support or reject this hypothesis in regard to the individual results documented above. Anderson (1997) observed marked but unquantified sex differences between dugong home ranges in what he described as lek mating behaviour in Shark Bay. To date, this behaviour has not been observed anywhere else and differs from all other accounts of dugong mating behaviour.

5.4.10. Comparing regional differences in 2D habitat use

Noting that the acoustic results reported here are necessarily truncated by the array, I compared the 2D habitat use results with eight other studies including results from Chapter 3 (Zeh et al. 2015), resulting in 15 data sets after separating females and males and 19 data sets after separating the results into close groupings and outliers. Compared to my results (median 2D (95% KUD) range 22.5 to 82.5 km²), four sets of results were within my median range, three were below, and eight were above. Other regions exhibited their own physical constraints due to common factors like geography (or bathymetry) or seagrass availability. I concluded that the major finding across these studies is that the dugongs' use of 2D space is heterogeneous and individualistic. (See the summary table in Appendix 5.4). Deutsch et al. (2022a) reached a similar conclusion.

5.4.11. Comparing regional differences in 3D habitat use

Few studies are available to compare the 3D dugong activity spaces obtained in this study with other work. Tracey et al. (2014) created 3D activity spaces for a single dugong which they broke down into probabilities of when the dugong would be in which depth range and the relationship to the tides. The results suggested that the dugong would be easier to detect at high tides when it was closest to shore and much more difficult to detect at low tides because it was away from shore, in deeper water. Udyawer et al. (2019) tracked eight males and two female dugongs in an area in the Gulf of Carpentaria < 20 m deep and created 3D activity spaces by combining locations from PTT/GPS transmitters and depth data from TDRs. The median 3D space use (95% KUD) calculated for the eight males was 0.083 km³; median 3D space use for the females was very much larger than any of the males at 2.94 km³. The values for the Gulf of Carpentaria males were much smaller than either the Moreton Bay females (0.76 km³) or the Moreton Bay males (0.40 km³), despite the constraints on the Moreton Bay values provided by the array. Udyawer et al. (2019) point out that most of the animals they tracked stayed close to the (map identified) seagrass areas of the coastal fringes of West Island and < 1% of all location data were from areas > 5 m deep. The results suggest that the differences between the dugongs' 3D activity spaces in the Gulf

of Carpentaria and those in Moreton Bay may be attributed to different patterns of seagrass distribution in the two regions.

5.5 Conclusions

The results of this preliminary study indicate avenues for future work. It would be particularly informative if 3D tracking data were combined with a study of seagrass community distribution, species composition, biomass, and nutrient composition along the lines of the 2D study of Sheppard et al. (2010) in Hervey Bay. Such a study might lead to the confirmation of deep-water seagrass in that area, similar to the way manatees were tracked to seagrass areas previously unmapped (Slone et al. 2013). Hays et al. (2018) and Cullen-Unsworth et al. (2018) provide examples of large seagrass beds that were discovered by 'ground truthing' areas of high dugong activity (e.g., Torres Strait). Underwater camera monitoring systems or camera-trap type devices described by Bicknell et al. (2016) might be useful after overcoming the immediate issue of the strong tidal currents through and near South Passage. Dugongs tagged with cameras ("crittercam" type equipment) can provide photo evidence of the dugongs' behaviour during dives. A documentary filmed by National Geographic with researchers Heithaus and Wirsing followed a dugong in Shark Bay Western Australia fitted with a crittercam (National Geographic 2004). However, the project failed to produce much data; photo-tagging and applying DTAGs may be a more promising approach as described in Chapter 3 and Zeh et al. (2015). This study points out that using an acoustic array to study dugong movements would depend on the research question as is often the case in tracking studies. Acoustic tracking will be most appropriate in a situation where an array is established take advantage of being able to track dugongs for a longer time at a local scale in a defined area. The results of this study strengthen that conclusion.

Chapter 5 Summary

- 30 datasets were collected from dugongs tracked in 2012 2014; of those, 27 dugongs recorded depths > 10 m.
- For the 11 dugongs which are the focus of the chapter, 53% of all data records were from females, 47% from males.
- Females' depth data accounted for most of the data records > 10 m.
 - Of 14,970 total data records, 5.6% were at depths > 10 m and of those, nearly 94% were from females (67% from one female).
- The large number of depth records > 10 m suggests that some dugongs use deepwater patches in the channels on the Eastern Banks in Moreton Bay as energetically efficient place to feed or rest but that this behaviour is individualistic. However, the reasons for this behaviour remain speculative.
- None of the biological variables (body length and sex), and environmental variables (water temperature, month, and season) was associated with mean depth.
- Maximum depth was strongly associated with individual length and sex.
- Core volume (3D, 50% KUD) was associated with sex and season.
- Extent volume (3D, 95% KUD) was strongly associated with sex and season.
- No biological or environmental value showed strong association with the overlapping core and extent areas or volumes.
- The combined records and calculated activity space areas and volumes highlight the individuality of the dugongs, and the behaviours cannot be broadly applied to the larger population due to the small sample size and the effects of season.
- The results provide proof of concept that acoustic tracking technology can produce useful insights into the movements and habitat use of dugongs.

Chapter 6

Evidence of behavioural thermoregulation by dugongs at the high latitude limit to their range in eastern Australia

I tracked dugongs undertaking trips from Moreton Bay, where the seagrass beds supplied their food, to the marine waters outside the bay where seagrass was not available. Most return trips were completed over several hours and occurred in the winter season when the bay temperatures were generally cooler than the marine temperatures. Differences between water temperatures inside and outside the bay were recorded, suggesting the trips were taken to regulate body temperature. The analysis adds to the evidence that dugongs undertake behavioural thermoregulation at least at the high latitude limits of their range.



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6.1 Introduction

Marine mammals live in thermally challenging environments. The thermal conductivity of water is nearly 25 times greater than air at 25°C and water temperatures are almost always lower than the mammalian core body temperature of 35 - 38°C (Gallivan et al. 1983; Irvine 1983; Ponganis 2015). Marine mammals have evolved a range of morphological, physiological, and behavioural adaptations to minimize heat loss to the environment (Estes 1989; Pabst et al. 1999). Much of the research has focused on pinnipeds, which face increased temperature challenges when they haul out (see Castellini 2018 for references). Associations between sea surface temperatures (SST) and the movements and behaviours of some whales have also been quantified. For example, bowhead whales (Balaena *mysticetus*) move within a narrow temperature range of -0.5 to 2 °C in the Arctic (Chambault et al. 2018) as do North Atlantic right whales (Eubalaena glacialis) in their winter calving grounds off Florida (Keller et al. 2006). Nonetheless, as pointed out by Ropert-Coudert et al. (2009), separating the direct effects of the physical environment on the movements of marine megafauna from the indirect effects of temperature on their food sources can be a significant challenge although it can be shown that the change in water temperature has a direct effect on internal temperature (see Appendix 6.5). Species such as sirenians that feed on stationary prey like benthic marine plants offer an opportunity to isolate the effects of temperature.

The extant sirenians (manatees and dugongs) are medium-sized marine mammals with limited morphological and physiological capacity to deal with heat loss (Elsner 1999). Sirenians have generally been restricted to tropical and subtropical waters throughout their evolutionary history (Marsh et al. 2011). The extinct Steller's sea cow was an exception, most likely due to its gigantism and resultant low surface area/volume ratio.

The behavioural response of sirenians to water temperature has been extensively studied in the Florida manatee, *Trichecus manatus latirostris* (see review by Marsh et al. 2011). Dugongs have higher metabolic rates than Florida manatees (Lanyon et al. 2006, Lanyon pers. comm. 2018), possibly enabling them to tolerate water a few degrees colder than the Florida manatee's lower limit of about 20°C (Horgan et al. 2014; Marsh et al. 2011). Nonetheless, with morphological and physiological limitations to their thermoregulatory capacity mostly similar to those of manatees, dugongs are also likely to have developed behavioural adaptations to cope with winter water temperatures at the higher latitude limits to their range. Indeed, dugongs exhibit different summer and winter distributions in widespread higher latitude habitats including Saudi Arabia (Preen 2004), western Australia

(Holley et al. 2006), eastern Australia (Sheppard et al. 2006) and New Caledonia (Cleguer et al. 2015), (see review in Deutsch et al. 2022b).

As explained in Chapter 2, Moreton Bay (27°S) is a large (~1500 km²) shallow embayment at the high latitude limit of the dugong's winter range on the east coast of Australia (Allen et al. 2004; Marsh et al. 2002). Minimum winter water temperatures in Pumicestone Passage at the western edge of the bay average below 16° C (Lanyon et al. 2005). Nonetheless, as many as 15 dugongs may be sighted at the southern end of Pumicestone Passage even in winter (Lanyon et al. 2005) although it is not known how long each individual stays in this region. Opinions differ (see Horgan et al. 2014; Lanyon et al. 2015; Owen et al. 2015) on whether dugongs are susceptible to the cold stress syndrome that affects Florida manatees (Bossart et al. 2004; Deutsch et al. 2003) and the way dugongs respond to water temperatures lower than about 18°C is not clear.

South Passage links the dugong's major seagrass habitat on the Eastern Banks in Moreton Bay to the adjacent oceanic environment (Fig. 6.1). Dugongs have been documented using oceanic areas that do not support seagrass close to South Passage in winter (Lanyon 2003; Marsh and Sinclair 1989; Preen 1992). Preen (1992) suggested that the only obvious resource for dugongs in these oceanic waters would be as a refuge from the colder water temperatures inside Moreton Bay. I used animal-borne telemetry to study the movements of dugongs in and out of Moreton Bay in winter to explore whether these movements could be interpreted as behavioural thermoregulation.

I asked the following research questions:

- What factors are associated with the likelihood of a dugong making a local scale trip to the oceanic waters outside Moreton Bay on any monitored day?
- What factors are associated with the timing and duration of dugong movements outside the bay within any monitored day?
- How do individuals change their activity space inside the bay across the winter months?

6.2 Materials and Methods

General methods are explained in Chapter 2, Methods, including specifics on satellite and acoustic equipment and data processing methods.

6.2.1. Dugong movements (trips) outside the bay

Specific areas were designated as inside and outside Moreton Bay to define the outward and inward movements of individual dugongs. These areas were separated by an exclusion zone polygon averaging 1.5 km wide representing South Passage. The polygon was drawn in ArcGIS 10.1 (ESRI 2013) to include the part of South Passage lying directly between Moreton and North Stradbroke Islands (Fig. 6.1, Inset A). Dugong locations within the polygon were excluded from analysis. A trip was defined as a movement of known duration of an animal from one point in space to another (Matthiopoulos 2003). The starting point for an outgoing trip was defined as the last location point inside the bay prior to points being located outside the bay. The trip endpoint was defined as the first location point beyond the exclusion zone occurring outside the bay. This approach enabled the time outside the bay to be estimated. An inward (return) trip was similarly defined in the opposite direction with the starting point in the outside waters. Outside duration (the amount of time dugongs spent outside Moreton Bay prior to making the return/inward trip) was estimated from the elapsed time between the endpoint of the outgoing movement and the start point of the return movement.

6.2.2. Difference in the temperature in the study areas outside and inside the bay Acoustic transmitter temperature data were averaged over each hour to correspond with trip end points. Gaps were more numerous in the data collected outside the bay where there were fewer receivers (five receivers outside vs 24 inside; see Fig. 6.1) than in the data from the Eastern Banks. When acoustic data were available, the difference between the water temperature inside and outside the bay was calculated at the date and time of the starting point for each outgoing trip. When acoustic data were unavailable, remotely sensed sea surface temperature (SST) data were used as outlined below.



Figure 6.1: Map of Moreton Bay showing seagrass distribution and receiver locations. Map of the Moreton Bay study area showing the distribution of seagrass and the locations of the receivers (Rec locations) in the acoustic array in the area where the dugongs were captured and tracked. Inset A highlights the South Passage polygon (also referred to as the exclusion zone) used to separate data as occurring inside the Eastern Banks or occurring in the oceanic waters immediately outside. A typical trip is shown and labelled with start and end points. Inset B shows the location of the study area in Queensland, Australia.

Sea surface temperature (SST) data in Kelvin degrees were sourced from the Australian Integrated Marine Observing System (IMOS) in the form of a daily raster image covering

14,000 km² with 2 km x 2 km cells. Two local buffers were created in ArcGIS 10.1 for clipping each SST raster into an inside and an outside dataset, each roughly 160 km². The inside buffer was centred on the combined calculated home ranges inside the bay for the tracked dugongs (2012 – 2014) using results from Chapter 3 (Zeh et al. 2015). A corresponding outside buffer was centred on the tracking data located outside the bay. Raster SST images were used only if corresponding images were available for both inside and outside Moreton Bay and incomplete SST images were excluded from the dataset. Usable raster images were converted from Kelvin to Celsius and the temperature values within each clipped image were averaged to provide mean daily temperatures. The temperature difference (outside minus inside Moreton Bay) was calculated at the start time of each outgoing trip. If temperature data were unavailable from either acoustic or SST sources, I estimated the missing data empirically for each study year using linear regression equations to describe the relationship between the acoustic and SST data inside and outside the bay (see Appendix 6.1.1). The inside and outside bay linear regression equations were based on the days when both acoustic and SST data were available for inside and outside the bay, respectively. Separate model equations for temperatures inside and outside the bay were shown to be substantially superior to a combined single model equation (see Appendix 6.1). This approach allowed us to add 187 outside temperature records to the original 87 for better coverage.

6.2.3 Alignment with the tides.

The start and end times of each trip outside the bay by a single dugong were matched to the nearest hour in the hourly tide chart for that year. Each trip was identified as outgoing or incoming and direction of the tide noted. The tidal alignment of a trip was classified as inconclusive if the time between the start and end points spanned two or more tides.

6.2.4 Statistical analysis.

Analyses of behavioural responses used mixed-effects models with individual dugong as a random effect. The probability of travel outside the bay on a monitored day was examined using mixed-effects logistic regression including year, period of the year (quarter), and the temperature difference between inside and outside the bay as fixed effects (Appendix 6.2.1). Each year was divided into quarters (Q1 Summer Quarter: January through March; Q2 Autumn Quarter: April through June; Q3 Winter Quarter July through September; Q4 Spring Quarter: October through December). The analyses also considered the data for Q2 Winter only as this was the only quarter for which data were available for all three years and

examined whether dugong size or sex appeared to influenced probability of travel (Appendix 6.2.A.3).

Mixed-effects logistic regression was used to analyse the effect of time of day and the tidal cycle on the direction of travel (Appendix 6.2.B). Linear mixed-effects models were used to analyse the duration of trips outside the bay (Appendix 6.1.3). All mixed-effects models used the Ime4 package in R (Bates et al. 2015) together with the car package (Fox and Weisberg 2011) to provide probability values from analyses of deviance.

6.3 Results

6.3.1. Dugongs tracked

Twenty-nine individual dugongs were tagged in 2012, 2013 and 2014; one individual was tagged in both 2013 and 2014 thus making a total of 30 tracking datasets. The data from eight dugongs could not be used: four travelled out of the area and four provided insufficient data. The remaining 21 dugongs (22 tracking datasets) all made one or more return trips from the Eastern Banks inside the bay to the adjacent oceanic waters via South Passage between Moreton Island and North Stradbroke Island. These animals included 12 adults (57%), six sub-adults (29%) and three juveniles (14%) made up of 14 males (67%) and seven females (33%). Dugong size (straight-line body length) ranged from 200 cm to 312 cm (SD = 30.6 cm, median = 256 cm) (see Appendix 6.3 for details).

6.3.2. Duration of tracking

Almost 10,000 satellite telemetry records were retained after filtering (for details see Appendix 6.3,) The number of tracking days per dugong ranged from 4 to 137 (mean = 63, SD = 35, median = 62). The number of outgoing trips per dugong was variable (mean = 12, SD = 18, median = 3; range = 1 to 66). Adult female 14_112599 made 66 trips over 137 days in 2014. Of the 260 total outgoing trips analysed here, 200 took place in 2014, likely an artefact of field trip timing and improvements in the attachment harness over time.

6.3.3. Temperatures in the study areas inside and outside the bay.

The time windows for which data were available differed between years, ranging from 11 weeks in 2012 (24 Aug – 12 Nov), 11 weeks in 2013 (08 Jul – 26 Sep), and 19 weeks in 2014 (28 Apr – 11 Sep). Appendix 6.1.2 shows that the unadjusted linear regression describing the relationship between temperature measurements obtained from acoustic transmitters attached to tracked dugongs and sea surface temperature (SST) sourced from the Australian Integrated Marine Observing System was slightly different for the records

obtained from outside compared with inside the bay. Inside the bay, there was also a difference between years in the relationship (Appendix 6.1.2). This difference did not occur outside the bay.

Temperatures on the Eastern Banks inside the bay ranged from 15°C to 24°C over the monitored months, dropping rapidly (though not monotonically) in autumn and winter and then increasing rapidly from about August (Fig. 6.2). Oceanic temperatures outside the bay changed more slowly, ranging from 18.5°C to 24°C, with the switch from decreasing to increasing temperatures occurring several weeks later than inside the bay.

The maximum temperature difference (outside – inside) on any monitored day was 6.5°C (Fig. 6.2). The water temperature outside the bay was up to 6.5°C warmer than on the Eastern Banks during the Winter Quarter in 2012 and 2014. However, the situation reversed later in the year. The oceanic water was up to 3° C cooler than inside the bay by the end of the Winter Quarter (September) in 2013 and up to 3°C cooler in the Spring Quarter in 2012. Differences between years were confounded with inter-annual variation in the timing of the days over which dugongs were tracked.



Figure 6.2: Daily temperature difference between outside-inside Moreton the Bay 2012 – 2014. This scatter plot shows the daily temperature difference (°C) between outside and on the Eastern Banks inside Moreton the Bay for the years 2012 - 2014 and Q2 Autumn through Q4 Spring. The variation between years was largely due to variability of the inside bay temperatures. The outside bay temperatures were less variable.

6.3.4. Factors associated with the likelihood of a dugong making a local scale trip to the oceanic waters outside Moreton Bay on any day.

The proportion of dugongs undertaking at least one trip outside the bay per day differed by quarter within year (Fig. 6.3) and year (see Appendix Fig. 6.1). The probability of making an outgoing trip was highest in 2014 and lowest in 2013 when water temperature inside the bay was higher than the other two years. These differences persist even after the varying time windows were accounted for in the models. The proportion of dugongs making a trip was highest in Q2 Autumn (Fig. 6.3), the months when temperatures inside the bay were declining and the temperature difference between the Eastern Banks and the adjacent oceanic waters was increasing (Fig. 6.2). The slopes of the relationship between temperature difference and the probability of making a trip were not significantly different between Q2 Autumn and Q3 Winter. However, the probability of making a trip declined progressively through Q3 Winter and Q4 Spring.



Figure 6.3: Temperature difference versus likelihood of a trip out of Moreton Bay. Association of the temperature difference between oceanic and bay waters with the likelihood of a trip out of Moreton Bay, separated by seasons (quarters). The association is consistently positive in Q2 Autumn and Q3 Winter, but slightly negative in Q4 Spring when temperatures inside the bay are increasing. Boxes indicate 25th and 75th percentiles; the whiskers indicate the maximum and minimum values.

The lack of balance in the data meant that a comparison between years was only possible in Q3 Winter. When the data for this quarter were considered, the significant average

differences in trip probability between years remained, but there was no difference between years in the relationship between trip probability and temperature difference (see Appendix 6.2.2).

In Q2 Autumn the odds of a dugong making a trip outside the bay on any given day increased by about 40% for each 1°C increase in the temperature difference between the bay and the warmer adjacent oceanic waters. In Q3 Winter, the odds of making a trip were lower when the outside – inside bay temperature differences were small or negative but increased by a factor of up to 2.12 for each 1°C difference in outside – inside temperatures. In Q4 Spring, this positive relationship reversed (see Fig. 6.3) as the temperature in the bay slowly became higher than outside oceanic waters, the odds of making a trip became higher when it was cooler outside the bay and decreased by a factor of nearly 0.5 for each 1°C difference in outside – inside bay temperatures (see Fig. 6.3 above).

Body length P(|z|) = 0.372 and sex (P(|z|) = 0.598) had no effect on the likelihood of a dugong moving out of the bay. Conclusions about both variables are tentative because of the relatively small sample sizes (see Appendix 6.2.A.3).

6.3.5. Factors associated with the timing and duration of dugong movements outside the bay within any given day.

<u>Timing</u>

Individual dugongs coordinated their movements in and out of Moreton Bay with the tidal flow (see Appendix Table 6.2.C.2). Of the 595 unidirectional trips (incoming and outgoing combined), 529 (89%) were in synchrony with tidal flow over the three field seasons. The tidal conditions could not be determined for the remaining 66 unidirectional trips because the data covered two or more tide cycles, presumably because the tethered satellite transmitter was dragged under the water while the animal was swimming in/out of the bay (Marsh and Rathbun 1990; Sheppard et al. 2006) so that intermediate data points were not received. Eighty-five percent of outgoing trips occurred between midnight and noon and 80% of incoming trips occurred between noon and midnight (see Appendix Table 6.2.C.2).

Dugongs were most likely to travel from the Eastern Banks to the oceanic waters immediately outside the bay between midnight and noon (AM) on an outgoing tide (Out) or at slack high water (NHigh) and return to the bay on an incoming tide (In) or slack low water (NLow) between noon and midnight (PM) (see Appendix 6.2.3). There was no significant interaction between period and tide (Fig. 6.4). See Appendix 6.4 regarding the odds of making a trip from the Eastern Banks of Moreton Bay to the oceanic waters outside of South Passage.



Figure 6.4: A mosaic plot showing the effects of tides on the direction of travel. This is a mosaic plot showing the effects of tide (Incoming (In), Outgoing (Out), Slackwater High (NHigh), Slackwater Low (NLow) and period (midnight to noon (AM) and noon to midnight (PM)) on the direction of travel. The plot shows that dugongs are more likely to go outside the bay between midnight and noon on an outgoing tide or at slack high water and come back into the bay on an incoming tide or slack low water between noon and midnight. The height of each rectangle is proportional to the sample size of movements in the tide - period combination. The plot results from the analyses in Appendix 6.2.3).

Duration.

The amount of time a dugong spent outside the bay on each trip was relatively short (overall median 5.9 hours) being typically less than 9 hours in 2012 and 2014 but reaching more than 30 hours in 2013. The time spent outside the bay increased with the temperature difference between the oceanic and Eastern Bank waters and varied with time of year, being lower in the Q4 Spring as the temperature of within-bay waters increased (Appendix 6.2.4). Individuals also spent significantly more time per trip outside the bay in 2013 than in the other years (Fig. 6.5, Appendix 6.2.4).



Oceanic temperature minus Bay temperature (°C)

Figure 6.5: Boxplot comparing the effect of temperature difference on time spent outside Moreton Bay. These boxplots compare the effect of the temperature difference between the oceanic and bay waters on the distribution of log-transformed number of hours spent outside Moreton Bay, separated by quarter (A) and year (B). Boxes indicate 25th and 75th percentiles and whiskers maximum or minimum values or +/- 1.5 x the interquartile range beyond the box, whichever is less. Any point beyond +/- 1.5 IQR is plotted separately as a potential outlier. Analyses are provided in Appendix 6.2.4.

6.4 Discussion

6.4.1. Overview

Our study adds to the evidence that dugongs undertake behavioural thermoregulation at the high latitude limits of their range by quantifying the relationship between dugong movements and water temperature in Moreton Bay, the southerly limit of their winter range on the east coast of Australia (Marsh et al. 2011). Oceanic waters outside South Passage do not support seagrass meadows and were up to 6.5°C warmer in winter suggesting that dugongs move outside the protected inshore bay habitats to access warmer waters. Cleguer (2015) documented similar movements for dugongs at another high latitude limit to their range in New Caledonia. Here, dugongs rest in warmer water outside the reef lagoon at Cap Goulvain in the winter (known locally as the 'cool season').

The movements from the Eastern Banks to the outside oceanic waters do not fit neatly into the typology of Sheppard et al. (2006), who divided dugong movements into three categories: macro-scale regional movements > 100 km, meso-scale inter-patch local movements (15-100 km) and tidally-driven micro-scale commuting movements (<15 km) between and within seagrass beds. Even though movements in and out of the Moreton Bay were tidally mediated, they could not be described as commuting movements as they did not occur on every tide (Sheppard et al. 2006). Rather the movements described here are connecting movements between two non-substitutable and spatially separate components of dugong habitat, both of which are important at the high latitude limits of the dugong's range. Thus, such movements are a form of landscape complementation (Dunning et al. 1992).

The reduction in heat loss resulting from a dugong moving from the Eastern Banks to warmer waters outside South Passage could be considerable. For example, Pabst et al. (1999) simplistically defined the variables that influence the rate of conductive heat loss from a body H', measured in watts (W) as:

$H'=(SA)C(t_b-t_a)$

where *SA* is the surface area in m^2 across which the heat is transferred, *C* is the thermal conductance of the given body t_b is body temperature and t_a is ambient water temperature. Thus, assuming the core temperature of a dugong is close to the mammalian norm of 37°C, and that its surface area and thermal conductance remain the same, moving from water at 17°C to 22°C will reduce the rate of conductive heat loss of an individual dugong by some 25%.

Dugongs also saved energy by taking advantage of tidal flow. Eighty-nine percent of trips in and out of Moreton Bay were in the same direction as the tide. Dugongs have frequently been observed utilising local tidal flows to access foraging and other areas (Anderson and Birtles 1978; Lanyon 2003; Sheppard et al. 2009; Sprogis 2008) because some seagrass areas are not accessible at low tides. Many marine species move with tides. For example, In Florida USA, Rappucci et al. (2012) showed that the probability of seeing manatee mother/calf pairs at the Florida Power & Light (FPL) Port Everglades Power Plant was higher at high tide than at low or mid-tides. In the Bay of Fundy, Canada, Johnston and Read (2007) observed harbour porpoises and two species of whales regularly feeding on schools of fish and plankton aggregations in large eddies during flood tides. In other studies, leopard sharks were observed regularly moving with the tides in a large estuary to access foraging areas in Elkhorn Slough, California USA (Carlisle and Starr 2010) and similarly in Tomales Bay, California, Ackerman et al. (2000) observed leopard sharks swimming with the tides to get to areas accessible only at high tides. Thus, tidal transport is exploited by many species of marine megafauna both to access intertidal habitats and save energy.

In addition to their movements being tidally mediated, dugongs were more likely to travel out of Moreton Bay between midnight and noon and return to the bay between noon and midnight. Edwards et al. (2016) found that Florida manatees were more likely to leave the warm waters of the discharge canal of the Big Bend power plant in the afternoon and evening. In winter, the highest high tides in Florida occur from 1600-0500 hours and Edwards et al. speculated that leaving the power plant in the later afternoon would enable manatees to maximize their access to inshore seagrass beds. Leaving Moreton Bay between midnight and noon would also enable dugongs to maximize their access to intertidal seagrass meadows on the Eastern Banks. Moreton Bay has a diurnal tidal regime and the higher spring tides occur in the evening before midnight in winter, the period when my tagged dugongs were mostly studied. Sheppard et al. (2010) documented the importance of night-time feeding in intertidal areas in Hervey Bay, a practice that enabled dugongs to access low biomass seagrass high in starch.

We found no statistical effect of gender or body size on the likelihood of a dugong making a trip outside the bay. Although the sample of immature animals is small, this finding was surprising because immature animals have higher surface to volume ratios and thus should be more susceptible to cold water. Gallivan et al. (1983)_ENREF_16 noted that the early reports of manatee deaths during cold weather included only large animals and commented that the data were the reverse of what would be expected from their surface to volume

ratios. Bossart et al. (2004), in contrast, recorded 11 of 12 manatee deaths from cold stress syndrome as subadults but only one adult. O'Shea et al. (1985) recorded many cold weather manatee deaths as subadults (111 of 248) with additional juvenile (74) and adult (63) deaths. O'Shea et al. suggested that subadults may get caught away from cold weather refuges due to lack of experience.

The number of trips dugongs made outside the bay varied by individual and dugongs did not make a trip outside every day. Significant differences in trip likelihood between years could be explained by the inter-annual variation in water temperature inside the bay. The probability of a dugong making an outgoing trip was highest in 2014 and lowest in 2013 when water temperature inside the bay was higher than the other two years.

The proportion of tracked dugongs undertaking at least one trip per day outside the bay also differed by quarter within year. Early in Q2 Autumn, both the dugongs (Burgess et al. 2013) and the seagrass on which they depend (McMahon 2005; Preen 1992; Roelfsema et al. 2014) should be in good condition. By Q3 Winter, the condition of dugongs is likely deteriorating (Burgess et al. 2013) because of reduced seagrass biomass (McMahon 2005; Preen 1992; Roelfsema et al. 2014); hence, dugongs would need to spend more time feeding in the bay (Burgess et al. 2013; Preen 1992). During this period, the energetic advantages of going outside the bay to rest and warm up is likely lessened, an inference supported by my observation that throughout the Winter and Spring quarters, dugongs spent more time just inside South Passage where the temperature of the mix of oceanic and bay waters would be warmer than the bay temperature enabling dugongs to invest more time in feeding. This inference is consistent with McMahon (2005) who noted August was the month the maximum amount of seagrass was removed on the Eastern Banks by dugongs. When their main feeding areas become less accessible due to lower temperatures, dugongs may change their diet, by including invertebrates or algae (Updated, edited extract from Chapter 3, Marsh et al. 2018 used by permission). By late in Q3 Winter, it is likely that the biological reasons for dugongs to stay inside the bay begin to increase. Male reproductive hormone levels increase (Burgess et al. 2013), body condition is at its annual nadir and individuals could be at risk of Cold Stress Syndrome (Owen et al. 2013). Mortality records show that the greatest number of dugong deaths occur during this time (Meager et al. 2013). By Q4 Spring, the inside-outside temperature relationship typically reverses with the inside bay waters being warmer than the outside waters making it likely that a dugong would go outside the bay only to cool off. In this same period, there are strong reproductive reasons for adult dugongs to remain inside the bay to mate (Burgess et al. 2013; Preen 1992).

Movements outside the bay were typically relatively short (overall median 5.9 hours) but reaching more than 30 hours in 2013. The longer periods spent outside the bay in 2013 (Fig. 6.5) were a surprise as the likelihood of a dugong leaving the bay was lowest in that year with water temperature inside the bay higher than the other two years and the temperature gain from leaving the bay lowest (Fig. 6.2). This result suggests that the stimuli for dugongs leaving and returning to the bay may be different. Seagrass densities were available for only some areas of the Eastern Banks and in 2012 and 2013 only (see Roelfsema et al. (2014) making statistical comparisons inappropriate. Inter-annual differences in water temperature are associated with inter-annual differences in movements between the Eastern Banks and the oceanic waters immediately outside the bay. Inter-annual differences in seagrass biomass may also be important and should be a topic for further investigation.

6.4.2. Comparison with the Florida manatee.

Both dugongs and manatees move between warm water refuges and feeding grounds. Warm water refuges that have been documented for the dugong are mostly natural, oceanic waters close to important higher latitude seagrass habitats in several geographically dispersed locations including: Shark Bay in Western Australia (Anderson 1986); Cap Goulvain in New Caledonia (Cleguer 2015); Hervey Bay (Sheppard et al. 2006) and Moreton Bay in eastern Queensland (Marsh and Sinclair 1989; Preen 1992, this study). However, there are also anecdotal reports of dugongs occasionally using human-produced warm water such as the warm water effluent stream from the Gladstone power plant in eastern Queensland (23.8°S, 141.25°E) (Limpus, pers ob.). Florida manatees also use natural warm water refuges such as warm water springs (Haase et al. 2017; Marsh et al. 2011; Sattelberger et al. 2017); but have learned to take advantage of power plant outflows (Edwards et al. 2016; Laist and Reynolds 2005a, b), especially in Central Florida.

In addition, Florida manatees and dugongs appear to use thermal winter refuges somewhat differently. For example, manatees seeking thermal refuge in the discharge canal at the big Bend Power station spent 45% -66% (mean 51%) of their time in the warm water refuge going out to feed for an average of 20.7 hours, while my study suggests that dugongs spend most of their time (82.8%) in their foraging habitats and much less time (8.2%) in warm water refuges. Thus, dugongs seem to prioritize access to food over warmer waters, whereas Florida manatees do the reverse. As dugongs seem to have higher metabolic rates (Lanyon et al. 2006 and Lanyon pers comm 2018) and to be able to tolerate lower temperatures than Florida manatees, their imperative to move to warmer waters may be less (see Marsh et al. 2011).

6.4.3. Conservation implications

The large number of trips made by dugongs in and out of Moreton Bay over the three years of this study highlights the importance of South Passage to dugongs in Moreton Bay, as a corridor for connecting movements between two non-substitutable and spatially separate components of their habitat. Consideration should be given to extending the Go Slow Zone designed to reduce the risk of vessel strike in the Moreton Bay Marine Park to include South Passage and the oceanic water outside the bay used by dugongs. Although it is possible for dugongs to use routes other than South Passage to access oceanic waters, these routes are much longer and would necessitate a greater period of absence from the Eastern Banks.

Movement corridors that enable dugongs to move efficiently between foraging areas and thermal refuges are likely to be vital components of other habitats at the high latitude limits to their range. My study adds to the body of evidence that dugong habitat conservation should not be restricted to seagrass meadows but be extended to include thermal refuges and movement corridors (Cleguer 2015; Zeh et al. 2016). Haase et al. (2017) similarly found that the spatial configuration of thermal refuges and foraging areas was an essential component of the quality and carrying capacity of manatee habitats in Florida.

Chapter 6 Summary

- I tracked 21 dugongs using acoustic and satellite/GPS transmitters in 2012, 2013 and 2014 in Moreton Bay, Queensland at the high latitude limit of the species' winter range in eastern Australia to examine if there was a relationship between movements and environmental temperature that might suggest behavioural thermoregulation.
- Oceanic waters immediately outside the bay where the dugong's seagrass food is unavailable exhibited temperatures from 6.5°C warmer to 3°C cooler than the Eastern Banks, the major dugong habitat in the bay.
- All tracked dugongs made at least one (and up to 66) return trip(s) from the Eastern Banks to the adjacent oceanic waters.
- The probability of making an outgoing trip was highest in 2014 and lowest in 2013 when the water temperature inside the bay was higher than the other two years.
- The odds of making an outgoing trip were lower when temperature differences (inside-outside) were small or negative but increased by a factor of up to 2.12 for each 1°C positive difference.
- Individual dugongs were most likely to travel out of the bay between midnight and noon on an outgoing tide or at slack high water and return to the bay on an incoming tide or slack low water between noon and midnight.
- The amount of time a dugong spent outside the bay on each trip was relatively short with an overall median of 5.9 hours.
- Our analysis adds to the evidence that dugongs undertake behavioural thermoregulation at least at the high latitude limits of their range.

Chapter 7

General Discussion

In this chapter, I summarise the outcomes of this thesis including the biological insights and the implications of the results for dugong conservation and suggest some areas for future research.



7.1 Introduction

Acoustic telemetry has revolutionised the tracking of many aquatic species because it enables their movements beneath the water surface to be studied in three dimensions (Roberts et al. 2017; Simpfendorfer et al. 2012; Udyawer et al. 2015). Although acoustic tracking has become the method of choice for marine species that rarely or never come to the surface, such as such as sharks, rays, and teleosts (Couturier et al. 2018; Heupel and Simpfendorfer 2008; Heupel and Webber 2012), a major limitation of this approach is the need for receivers to be strategically placed in the study area and consequently some prior knowledge of the tagged individual's range of movement. As acoustic telemetry becomes more widely practiced, receiver arrays are being deployed in increasing numbers of locations to provide more complete data on the movements of individual organisms, especially coastal species (Couturier et al. 2018; Espinoza et al. 2015) but questions remained about whether these arrays could also be used to study the movements and habitat use of co-occurring marine mammals.

As explained in previous chapters, acoustic telemetry has not been widely applied to the study of coastal marine mammals for several reasons:

- (1) Satellite-GPS tracking, which relies on the tracked animal coming to the surface to transmit its location to a satellite, is available for marine mammals, which have to surface to breathe.
- (2) Marine mammals often range widely, making satellite-GPS tracking the method of choice, as it is not restricted by the spatial limits of a purpose-built in-water receiver array.
- (3) There is concern that the hearing frequencies of most marine mammals overlap the frequency of acoustic transmitters and that acoustic transmitters will thus interfere with their tagged animals' ability to communicate.

As explained in earlier chapters, sirenians should be better suited to acoustic technology than most other coastal marine mammals because their hearing frequency (~0.30 Hz to 46 kHz; Anderson and Barclay 1995; Gerstein et al. 1999) does not overlap the acoustic transmitter frequency (69 kHz, Vemco). Within the sirenia, the methods should be best suited to dugongs. Compared with manatees, dugongs make much more use of 3-dimensional space. Manatees generally do not dive deeper than 5 m (Keith-Diagne et al. 2022), whereas in some parts of their range, dugongs are associated with deep-water seagrass beds and dives have been recorded to more than 30 m (Hagihara 2015; Lee Long et al. 1996; Sheppard et al. 2006).

Although tethered, floating telemetry tags have worked well for sirenians, generating highquality data on their behavioural ecology, collecting long-term data from satellite-GPS tags is often much more problematic for dugongs than manatees (Deutsch et al. 2022a). The safety features (corrodible connectors and engineered breaking point of the nylon tethers) often result in the satellite tags breaking away before the batteries are expended, and even under ideal conditions, battery life is relatively short. These two problems, in association with the difficulty and impracticality of re-catching dugongs to change out satellite tags, impede longterm tracking success (Deutsch et al. 2022a).

Members of the public have also expressed animal welfare concerns about the tethered, floating satellite-GPS tags (H. Marsh, pers. comm. 2021). Acoustic tags are much smaller and lighter than the current sirenian satellite-GPS tags (see Box 2.1, Chapter 2) and can be incorporated into the current tail-stock harness design. The harness would be much lighter without the tether and satellite tag attached, as these parts of the assembly cause drag on a swimming dugong. Using acoustic tags should reduce animal welfare concerns.

Using acoustic transmitters, which are much less expensive than satellite-GPS transmitters, could also result in cost savings, especially if an array of acoustic receivers is already available or shared between projects. Additional cost savings might accrue through the shared costs of receiver deployment, maintenance and data collection arising from the use of hardware and personnel for multiple projects.

7.2 This thesis

In view of the considerations outlined above, this thesis investigated whether acoustic technology could have advantages over satellite-GPS tracking for studying dugong movements and habitat use in an urban coastal environment as an example of a location where a receiver array is likely to be built. I investigated whether the results of acoustic tracking could mirror the results of satellite-GPS tracking in terms of measuring movements and activity spaces in two dimensions, and whether the costs of using acoustic technology could compete with the current "standard" of tracking via satellite-GPS technology. If the results were comparable, acoustic tracking could offer considerable advantages over satellite-GPS tracking with respect to tracking duration, animal welfare and cost. I then extended this work to investigate whether the acoustic tags could provide further biological and conservation insights.

To explore these matters, twenty-nine dugongs were captured in seagrass habitats on the Eastern Banks of Moreton Bay over three years (2012-2014) as described in Chapter 2 and outfitted with satellite-GPS and acoustic transmitters. After three months, the data from the two technologies were used to compare the resultant information on the dugong's two dimensional space use. I then compared the benefits and limitations of each approach and examined the costs of each approach in relation to the amount and type of data provided (Chapter 3)

The results of this work provided a proof of concept that acoustic technology can be a tracking alternative to 2-D satellite-GPS technology depending on the research question, and that the costs can be demonstrably less than satellite-GPS tracking within the constraints of an acoustic array. This conclusion was supported by further work to address the sub-objectives of this thesis, which are listed below, along with its main objective (Box 7.1).

Box 7.1: Objectives and sub-objectives of this thesis *Main objective*: To investigate use of satellite and acoustic technologies to study dugong movements and habitat use in an urban coastal environment by:

- a. Comparing the relative advantages and disadvantages of using automated acoustic tracking and satellite-GPS tracking to quantify the movement and residency patterns of dugongs in the urban environment of Moreton Bay. (Chapter 3)
- b. Using satellite-GPS tracking to investigate the use of movement corridors in large-scale dugong movements between Moreton Bay and Hervey Bay. (Chapter 4)
- c. Using acoustic tracking to understand dugong 3D habitat use in a feeding ground and adjacent areas in Moreton Bay. (Chapter 5)
- d. Using satellite-GPS tracking and acoustic tracking to quantify the movements of dugongs between their feeding grounds in eastern Moreton Bay and adjacent oceanic waters to explore whether these movements could be interpreted as behavioural thermoregulation. (Chapter 6)

The ways in which my research fulfilled these objectives were discussed in each of Chapters 3-6, three of which have been published. In this chapter, I consider these results in the context of their contribution to dugong ecology and management and outline options for future research.

7.3 Potential of using acoustic technology to track dugongs

Assuming sufficient acoustic receivers are present in a research area and that the acoustic array has sufficient density, I showed that 2D space use calculated from acoustic data can

be expected to be similar to results gained from satellite-GPS tracking within the array (Chapter 3). Satellite-GPS and acoustic telemetries each provide the data required to generate well-defined 2D activity spaces for tagged dugongs. In many instances, the activity spaces I calculated from acoustic data closely mirrored the satellite-GPS-based activity spaces (Chapter 3). In other instances, the results from the two approaches were less similar, pointing to the inherent differences between the technologies. Characteristics like acoustic receiver spacing, the pattern of residency of dugongs inside the array, quality of satellite location data, and satellite availability influenced the comparisons.

Acoustic transmitters demonstrated clear advantages over satellite-GPS transmitters in the analysis of dugong 3D space use. To date, satellite-GPS transmitters have only been used for 3D analysis when coupled with time-depth recorders (TDRs) (Hagihara 2015; Tracey et al. 2014) because of the length of the tether in the dugong tag assembly (Fig. 2.2, Chapter 2). I combined the depth data collected from the array receivers with the locations generated from the acoustic receivers in a custom R program using triangulation (Simpfendorfer et al. 2012) to estimate both 2D areas and 3D volumes for tagged dugongs within the array (Chapter 5). The 3D volumes provided additional insights into the dugongs' use of their environment in a manner more detailed than that of satellite-GPS technology combined with TDRs. In particular, the 3D data demonstrated that dugong space use is individualistic in three as well as two dimensions as discussed further below.

Acoustic transmitters also have the potential to record information on the movements and habitat use of individual dugongs for longer than satellite-GPS tags. The two largest numbers of data-days recorded by the satellite-GPS transmitters I deployed were 141 and 136 data-days (from satellite-GPS IDs 112597_14 and 112599_14 respectively). In contrast, the two largest numbers of data-days from acoustic transmitters were 483 and 524 data-days (from IDs 14242_1314 and 14244_1314 respectively), more than three times as long. By comparison, Sheppard et al. (2006) tracked 26 dugongs using satellite technology for periods ranging from 20 to 199 days with 15 days as the median.

These examples illustrate that acoustic transmitters have the potential to record more datadays than satellite-GPS transmitters. The differences noted are not a result of battery life but rather the workings of the harness attachment system, as the tethers with satellite-GPS tags attached tended to separate from the rest of the harness as explained above. The satellite-GPS tags continued to transmit after detachment and were usually located and picked up once stationary (on a beach for example) with the batteries still working. The harnesses holding the acoustic transmitters, on the other hand, tended to remain on the dugongs longer and the acoustic transmitters continued to transmit usable data, although this was unknown until after the acoustic receivers were downloaded when it became clear the transmitters were still attached and working. It is possible that the machine screw holding the harness together (the corrodible link) dissolved more slowly than predicted, allowing the harness to stay intact longer or biofouling may have contributed to a slower corrode rate. Although in typical applications it could be anticipated that the transmitters and receivers would be subject to biofouling (see Heupel et al. 2008), the transmitter was placed within protective plastic tubing (refer back to Fig. 2.3) and the receivers were replaced frequently (see Chapter 2) to minimise the issue. While none of the results reflected maximum battery life, the ratio of satellite-GPS data-days to acoustic data-days roughly paralleled the manufacturer's maximum battery life of 365 days maximum (satellite-GPS) and 824 days maximum (acoustic). The large difference in data-days between the two technologies indicates that acoustic technology has the potential to provide reliable tracking data over longer periods than satellite-GPS.

As discussed in Chapter 3, besides length of tracking period, cost and animal welfare issues, the relative merits inherent in the two technologies depend on the research question in the context of the species of interest, the location of the study, and whether the study site has an established acoustic array (for cost savings). The size and location of the activity spaces resulting from this study suggest that adding more receivers (building a higher density acoustic array) could increase the likelihood of acoustic results matching more closely to satellite-GPS technology. Although the establishment costs might be higher, using acoustic technology could be a cheaper approach than satellite-GPS technology if a site already equipped with an acoustic array is available since the data collection period is longer, and researchers were sharing the array for tracking multiple species (see Chapter 3 for the cost analysis of acoustic versus satellite-GPS technologies). My results certainly indicate the merit of including dugongs in a multi-species study of animal movements based on acoustic tracking.

7.4 Biological insights

7.4.1 Movements

Cope et al. (2015) used sophisticated genetic techniques to show that dugong movements between Moreton and Hervey Bays must be more common than indicated by the limited tracking studies; 5% of Moreton Bay parents had offspring in Hervey Bay and16% of Hervey Bay parents had offspring in Moreton Bay. As described in Chapter 4, the movements of four satellite-GPS tagged dugongs over 5 – 9 days demonstrated that when dugongs travel

between Moreton Bay and Hervey Bay at least some animals stay relatively near the coast. During this time few locations were recorded, most likely because when the dugongs are swimming, the satellite tag dips into the saltwater and a safety switch turns off the unit, as observed by Sheppard et al. (2006). The proximity of the three tracks suggests the presence of a dugong movement corridor between Moreton Bay and Hervey Bay. As discussed in Deutsch et al. (2022b), at least some individuals in all three species of manatees regularly make seasonal migrations in coastal and river systems. Coastal migrations by Florida manatees are typically rapid and directed movements in migratory corridors along the coast. Deutsch and Barlas (2016) confirmed the longevity migratory corridors via satellite-GPS tracked manatees about ten years after they were first described by Deutsch et al. (2003).

The results for dugongs are more equivocal and there is considerable doubt as to whether their large-scale movements (defined by Sheppard et al. 2006 as trips > 15 km) qualify to be described as migrations rather than movement responses to episodic declines in forage (Deutsch et al. 2022b). Nonetheless, tracking studies indicate that many dugongs make large –scale movements. For example, Sheppard et al. (2006) recorded 44 dugongs out of 70 making large-scale movements in the coastal waters of northern Australia. In most cases, it was not possible to determine the route travelled because the tag was under the water during the dugong's directed, relatively rapid movement as explained above. From a conservation perspective, it would be good to know if these animals used defined movement corridors. A way in which acoustic tagging might be used to test this idea is described below.

Individual dugongs often make commuting movements to or from regular feeding areas, a form of landscape complementation (see Haase et al. 2017) and defined as meso-scale inter-patch local movements by Sheppard et al. (2006). Ninety-seven percent (29 of 30) of dugongs I tracked made at least one trip between Moreton Bay and the adjacent oceanic waters (Chapter 6). The odds of making an outgoing trip were lower when temperature differences (outside minus inside) were small or negative but increased by a factor of up to 2.12 for each 1 °C positive difference in temperature. Individual dugongs were most likely to travel out of the bay between midnight and noon on an outgoing tide or at slack high water and return to the bay on an incoming tide or slack low water between noon and midnight. The amount of time a dugong spent outside the bay on each trip was relatively short with an overall median of 5.9 h. I interpreted these movements as a form of behavioural thermoregulation (see Chapter 6). Florida manatees exhibit central place foraging behaviour when they are behaviourally thermoregulating, spending most of their time in warm water refuges and venturing out to feed (Deutsch et al. 2022a). In contrast, dugongs are 'central place thermoregulators', spending most of their time close to their feeding areas and

venturing out to warm up. This difference is likely the result of the interspecific or locational differences in the trade-offs between thermoregulation and feeding, which would be interesting to investigate further.

7.4.2 Individualistic use of deep-water

Numerous studies of dugong movements have illustrated that dugong 2D space use is individualistic (see reviews in Deutsch et al. 2022a; Deutsch et al. 2022b). My acoustic tracking work (Chapter 5) showed that this is also true of their 3D space use. Two of the 11 dugongs studied in Chapter 5, both females, spent a significant percentage of their time at depths of > 10 m. The reason for this behaviour is unknown. Based on the bathymetry profiles the dugongs must have been spending their time in the deeper channels between the Eastern Banks. Were they feeding on deep-water seagrasses? Resting? Sheltering from roving males? Is this behaviour sex specific? Further research is clearly required as discussed below. This study demonstrates that acoustic technology could be an appropriate tool to investigate these questions.

7.5 Conservation implications

Because dugongs are seagrass community specialists (Marsh et al. 2011), the spatial design of dugong conservation initiatives has tended to concentrate on seagrass communities. My work has shown that this approach may not be enough as illustrated by the examples below.

The large number of trips made by dugongs from inside Moreton Bay to the outside oceanic waters (Chapter 6) highlights the importance of South Passage to Moreton Bay dugongs. Since all 30 dugongs tracked made trips outside Moreton Bay, it is reasonable to suppose that many more dugongs from the population also made the trips. Because the Go Slow Zone is largely restricted to the seagrass areas in the Eastern Banks, one might conclude that these numbers suggest additional zoning may be needed to protect dugongs from vessel strikes in the South Passage area. However, the recorded number of dugongs struck by vessels each year in this area is very low (only four were recorded in years 2013-2015; Meager 2016) so the optimum way forward is not clear. Documented watercraft injuries to Florida manatees are much higher than those to dugongs. In contrast to dugong deaths (3 in years 2013-2015), over 4,000 manatee mortalities were attributed to watercraft collusions between 1974 and 2016 (summarised in Ponnampalam et al. 2022).

New data collected along the movement corridors suggested by this research (Chapter 4) might be used to inform management of areas where dugong movements could overlap shark control gear, particularly shark nets (a type of gill net). The Queensland Shark Control Program (QSCP), established in 1962, uses a combination of shark nets and drumlines to protect swimmers at Queensland beaches. Over time, drum lines have increasingly replaced nets in most locations outside south-east Queensland, especially the Great Barrier Reef Marine Park (GBR Marine Park Authority 2019; Marsh et al. 2019). The QSCP currently uses a combination of 27 shark nets and 383 drum lines (baited lines) covering 86 beaches (QLD Dept of Agriculture and Fisheries 2020). As standard practice, the QSCP releases live by-catch animals from the drum lines as a more environmentally friendly practice (Cliff and Dudley 2011) and Marsh et al. (2005) noted that at the time of their summary, no dugongs had been caught on drum lines. StrandNet records (Meager 2016; Meager and Limpus 2012) indicate dugongs have only been infrequently caught in shark nets in recent years. Different species are caught in varying ratios of net/drumline, so the choice of gear combination is often a consequence of the local shark community composition (Sumpton et al. 2011).

Some alternatives to shark nets and drumlines have been or are being considered. Shiffman (2014) noted that shark culls and electromagnetic barriers/fields had not been shown to be effective on target species. However, deterring sharks using permanent magnets attached to artificial kelp has shown promise and has been effectively tested against bull sharks (*Carcharhinus leucas*) and great white sharks (*Carcharodon carcharias*), (SharkSafe Barriers; see Box 7.2 and O'Connell et al. 2018). The Queensland Government is also trialling catch alert drumlines, coordinating with the New South Wales Department of Primary Industries Shark Program which has developed Smart drumlines. The Smart drumlines send a satellite signal to alert contractors when an animal is caught, to reduce the time until release (QLD Dept of Agriculture and Fisheries 2020). Analysis of dugong movement data in close proximity to current existing shark control measures might be useful in helping to determine where these alternate shark protection methods might be placed.



Box 7.2: About SharkSafe Barriers SharkSafe Barriers are basically artificial kelp forests holding permanent magnets. These deter sharks because: 1.) Sharks resist moving through high density kelp forests and 2.) barium ferrite magnets irritate electroreceptive pores in shark's snouts (O'Connell et al. 2018). The barriers do not affect the

Photo credits: SharkSafe Barriers, movements of elasmobranchs and https://www.sharksafesolution.com teleosts species, however.

Incidental drowning in gill nets is the major source of dugong mortality worldwide (Marsh and Sobztick 2015). The Queensland Sustainable Fisheries Strategy: 2017–2027 (QLD Dept of Agriculture and Fisheries 2017), which sets out the Queensland government's reform agenda over 10 years, is a very welcome initiative. The 2019 Great Barrier Reef Outlook Report (GBR Marine Park Authority 2019) considers this Strategy to be the most significant change in fisheries management in the Great Barrier Reef World Heritage Area since 2014. Nonetheless, there are concerns about the implementation timetable for the Strategy, which has become more definite since the Outlook Report was written. For example, the staged implementation of electronic monitoring of the bycatch of protected species in high risk fisheries such as the East Coast Inshore fishery is not scheduled to begin until 2024 (H Marsh, pers. comm. 2021). As a result, it is not known whether the bycatch of species of conservation concern such as the dugong is sustainable and there is concern that dugong numbers are declining in the Great Barrier Reef region south of Cooktown (Marsh et al. 2019). At present, regulations ban gill nets within 500 m of headlands in the Great Barrier Reef Marine Park (Australian Government 2021; GBR Marine Park Authority 2009). If dugongs use movement corridors along the coast this ban may need to be extended to reduce dugong bycatch if confirmed by further research (see below).

7.6 Future research

7.6.1. Extending the duration of data for individual animals

My work has demonstrated that one of the chief advantages of acoustic technology is its potential to track individual animals for longer than satellite-GPS tracking. Implanting an acoustic transmitter into the dugong body cavity as has been done with other species (e.g., grey reef sharks (*Carcharhinus amblyrhynchos*) (Heupel et al. 2006) and walleye (*Sander vitreus*) (Schoonyan et al. 2017)) has the potential to extend tracking duration to the life of the battery (up to 10 years (Vemco)). There are significant animal ethics challenges associated with this approach, which would need to be explored. Lanyon et al. (2010) have regularly lifted dugongs out of the water onto a ship for purposes of examining the dugongs as part of a regular program to assess the health of the individuals and the health of the population. The dugong's vital signs (temperature, heart rate, and respiration) are taken regularly during the time onboard which ranged from 27 to 55 min. In principle, it may be possible to implant an acoustic transmitter during this time while the dugong was under close observation. The costs would be balanced against the likely gain of information and would

be viable if a sufficient number of acoustic arrays were added or expanded, for example, as described in Boxes 7.3 and 7.5 below.

7.6.2. 3D insights

More arrays in suitable locations could produce new data about dugongs' use of 3D space particularly in key locations such as port developments (e.g., Gladstone) and linear habitats near headlands (to support fisheries closures) or beaches along the Queensland coast (to measure risk to dugongs from bather protection measures like shark netting or bait lines) to identify risks to movement and new areas for conservation (Fraser et al. 2018). As noted earlier, higher density arrays would allow for finer location details for 3D analysis in areas of interest (e.g., to confirm dugongs' use of Eastern Banks deep-water seagrass meadows) and could be combined with habitat studies (e.g., see Tracey et al. 2014). The same arrays could be used to collect transmitter data from species tracked in other studies (e.g., bull sharks acoustically tagged in Townsville were detected in Moreton Bay in the array in the Eastern Banks; Mario Espinoza, pers. comm. 2014), thereby potentially saving costs by sharing among additional projects and at the same time, expanding the capability of each project.

The potential existence of deep-water seagrass in the Eastern Banks area was suggested by the analysis of dugong 3D habitat use in Chapter 5. To confirm such existence and to observe more fully the dugongs' use of those seagrass beds, a deep-water seagrass survey could be conducted throughout the Eastern Banks region (see Box 7.3). Upon the completion of the survey, additional acoustic receivers could be appropriately placed to record dugong activity in greater detail than was possible from the acoustic array in use during the research for this thesis or research in Hervey Bay done previously by Sheppard et al. (2010).





Photo: AIMS website .

Box 7.3: Deep-water seagrass within the Eastern Banks This map illustrates the results of doubling the number of acoustic receivers in the array (total \sim 60 receivers). The receiver symbol is approximately 800m dia. and so the Eastern Banks give the appearance of being completely covered in receivers! In reality, while coverage would be much greater, the size of each receiver shown on the map is less than the period at the end of this sentence in scale.

A problem with simply increasing the number of acoustic receivers is that the presence of deep-water seagrass is likely to be ephemeral (Waycott et al. 2005; York et al. 2015). A better approach might be to combine acoustic telemetry with emerging technologies that provide finer detail on dugong movements such as DTAGS (see Box 7.4) to further pinpoint potential deepwater seagrass search areas. The search might be coordinated using Autonomous Underwater Vehicles or AUVs, which are unmanned and self-powered. The CoralAUV is being developed by the Australian Institute of Marine Science (AIMS) and can dive to depths of 30 m. Although developed to investigate and photograph coral, the photographic capabilities are fine enough that the CoralAUV could investigate the deep trenches within the Eastern Banks, timing the excursions to fit within the confines of tidal movements (pers. comm. Paul Rigby, AIMS, 2021)
7.6.3. Detailed behavioural insights

The coupling of acoustic technology with tags designed to provide detailed information over a few days (i.e., digital acoustic recording tags, or DTAGs, see Box 7.4) would provide the opportunity to place the short-term detailed information obtained from D-TAGS in the context of long-term information provided by acoustic telemetry. Rycyk et al. (2018) successfully deployed DTAGs and satellite-GPS tags on 18 manatees in southwest Florida to study the reactions and/or interactions of manatees with boat traffic. Rycyk et al. (2018) built their study on the work of Nowacek et al. (2001) who studied the response of two Antillean manatees (*Trichechus manatus manatus*) to boat traffic in Belize using DTAGs. A study which used DTAGs in a way similar to what might be useful in the understanding the dugongs deep-diving behaviour is that of Shorter et al. (2017) who used DTAGs to record movement data on bottlenose dolphins (*Tursiops truncatus*) that could be reconstructed into an accurate 3D track. Thus, the project suggested above could combine acoustic data with a DTAG to integrate with 3D movement data (Deutsch et al. 2022b), which could then be set into the local bathymetry.



DTAG3. Photo credit: Tom Hurst WHOI, via soundtags.org from the University of St Andrews.

Box 7.4: About DTAGs. The DTAG3 was designed in 2010-12 at the Woods Hole Oceanographic Institution (WHOI) and has been successfully in over 980 projects worldwide since 1999. It has rechargeable batteries and can record for up to 3 days, depending on the set recording schedule The DTAG3 carries an accelerometer, magnetometer, and pressure sensor, and can record sound via two hydrophones (shown at the front of the unit). The unit attached via suction cups. The unit at left is pictured just prior to receiving its encapsulating protective covering. A new unit is being built with an ARGOS transmitter and a lithium battery that can last a month.

7.6.4. Movement corridors

My work tracking long-term movements of dugongs in Chapter 4, illustrates the need to confirm whether dugongs use movement corridors over long periods. A series of acoustic receivers could be placed linearly at intervals along a coast extending perpendicularly from the coastline. A linear array could record the passage of many other tracked species, particularly sharks and fishes, but also the data could identify species that are remaining locally. See Box 7.5 below.

Box 7.5: The potential for a series of lines of acoustic receivers at locations perpendicular to the coast. Lines of acoustic receivers could be placed perpendicularly from the coastline as suggested in this illustration to record not only dugongs, but other species of concern which make large-scale movements along the Queensland coast such as bull sharks (Haig et al. 2018) and species of sea turtles (Shimada et al. 2016). The new arrays (which are not to scale) would record virtually any acoustically tracked marine species passing near the receivers and informative movement data would be available for analysis. (Note that the Queensland government and IMOS are currently funding a new array of acoustic receivers along the Queensland coast. M. Heupel, pers. comm.)



7.6.5. Effects of climate change

Marsh et al. (2022) have reviewed the likely effect of climate change on sirenians. Climate change is causing temperature increases, sea level rise, changes in water chemistry and quality, increases in the intensity and nature of extreme weather events, and changes in rainfall patterns (Albouy et al. 2020, MacLeod et al. 2021, Marsh et al. 2022, Orgeret et al. 2022). The cumulative impacts will be locally variable but changes in habitat extent and continuity are likely to be widespread with consequential changes in habitat use and movement behaviour, requiring better predictive and mitigation strategies (Babcock et al. 2019). Thus, tracking studies are likely to become even more important as the locations of essential resources and the cues triggering the timing of movements change. The capacity of dugongs to alter their behaviour in response to climate change will be essential to their survival.

Major storms bring heavy rains leading to greater runoff and fine sediment volumes which decrease water clarity, increase chemical pollution, cause loss of habitat, resulting in increased dugong mortality (Brierley and Kingsford 2009; Wooldridge 2017). Lanyon et al. (2019b) suggest that the main threat to dugongs in Moreton Bay remains the loss or degradation of seagrass habitat due to local runoff events causing loss of water quality, and the influx of chemical pollutants, noting a surge in antibiotics was recorded even a year after a large flood event. The uncertainty highlighted the extent that these conditions will disturb the seagrass meadows, and whether dugongs will stay in the area during a food crisis versus how many will move to another area in search of food (i.e., small movements like those of manatees described by Deutsch et al. 2022b). Tracking a larger number of dugongs for a longer period may help to understand this threat in greater detail. The longevity of acoustic tags means they have the potential to be an important tool in documenting the response of the dugong to extreme weather events.

Another question deriving from the uncertainty of climate change, particularly the impact of warmer sea temperatures, will be the question of whether the dugongs' reaction to increased water temperatures will result in fewer trips between Moreton Bay and the ocean waters. Can dugongs adjust to the increased water temperatures by adjusting their thermoregulation routines? Will those adjustments be sufficient? Tracking a larger set of dugongs in Moreton Bay and comparing the number and timing of trips with the results from Chapter 6 may provide insight into these questions as outlined in Box 7.6.

Box 7.6: How acoustic tracking could inform the inter-annual variation in their use of South Passage. With 265 round trips in and out of Moreton Bay completed by the 29 dugongs I studied, South Passage was confirmed as critical habitat for Moreton Bay dugongs. An addition of acoustic receivers throughout South Passage would enlarge the acoustic array and allow for more detailed analysis. Tidal surges move very quickly throughout the area and finer movement details are difficult to obtain during satellite-GPS tracking due to a tethered tag being pulled under the water.



Finer temperature determinations from (many more) localised water temperature readings could enhance understanding of the probabilities of dugong making trips in and out of Moreton Bay. As sea temperatures continue to rise due to global climate change, changes in the dugongs' use of the area could be documented.

This map shows some of the possible locations for additional acoustic receivers (shown in red) in South Passage to add to the knowledge base of dugongs moving between Moreton Bay and oceanic waters. Due to the scale of the map, the number and locations of new receivers are conceptual only.

7.7 Concluding remarks

This thesis explored the use of acoustic technology to track dugong movements within the Eastern Banks regions of Moreton Bay. The technology was successful in its application and results compared favourably with analyses derived from satellite-GPS data describing 2D activity centres within the acoustic array. I was able to go a step further with the acoustic data to create 3D activity centres, results that were not directly accessible from satellite-GPS data alone. The analysis of acoustic data also highlighted the possibility of deep-water seagrass in the Eastern Banks area by recording the many trips to deeper areas of the Banks. Using the satellite-GPS technology, on the other hand, I was able to track dugong movements well outside the acoustic array, as dugongs travelled between Moreton Bay and Hervey Bay, discovering a likely movement corridor. The use of satellite-GPS technology also made possible the documentation of multiple trips made by dugongs in and out of Moreton Bay to warm oceanic waters in an apparent demonstration of dugong thermoregulation. Thus, this thesis has brought much new information to light about the movements and habitat use of dugongs and added to the existing knowledge of dugong behavioural thermoregulation.

References

- Aarts G, MacKenzie M, McConnell B, Fedak M, Matthiopoulos J. 2008. Estimating spaceuse and habitat preference from wildlife telemetry data. Ecography **31**:140-160.
- Abal EG, Dennison WC. 1996. Seagrass depth range and water quality in southern Moreton Bay, Queensland, Australia. Marine and Freshwater Research **47**:763-771.
- Abecasis D, Steckenreuter A, Reubens J, Aarestrup K, Alós J, Badalamenti F, Bajona L, Boylan P, Deneudt K, Greenberg L, Brevé N, Hernández F, Humphries N, Meyer C, Sims D, Thorstad EB, Walker AM, Whoriskey F, Afonso P. 2018. A review of acoustic telemetry in Europe and the need for a regional aquatic telemetry network. Animal Biotelemetry 6:12.
- Ackerman JT, Kondratieff MC, Matern SA, Cech JJ. 2000. Tidal Influence on spatial dynamics of Leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. Environmental Biology of Fishes **58**:33-43.
- Adulyanukosol K, Thongsukdee S, Hara T, Arai N, Tsuchiya M. 2007. Observations of dugong reproductive behavior in Trang Province, Thailand: further evidence of intraspecific variation in dugong behavior. Marine Biology **151**:1887-1891.
- Albouy C, Delattre V, Donati G, Frölicher TL, Albouy-Boyer S, Rufino M, Pellissier L, Mouillot D, Leprieur F. 2020. Global vulnerability of marine mammals to global warming. Scientific Reports **10**:548.
- Allen S, Marsh H, Hodgson A. 2004. Occurrence and conservation of the dugong (Sirenia: Dugongidae) in New South Wales. Proceedings of the Linnean Society of New South Wales **125**, 211-216.
- Allen SJ, Pollock KH, Bouchet PJ, Kobryn HT, McElligott DB, Nicholson KE, Smith JN, Loneragan NR. 2017. Preliminary estimates of the abundance and fidelity of dolphins associating with a demersal trawl fishery. Scientific Reports (Nature Publisher Group) 7:1-11.
- Anderson PK. 1986. Dugongs of Shark Bay, Australia Seasonal migration, water temperature and forage. National Geographic Research **2.4**:473-490.
- Anderson PK. 1997. Shark Bay Dugongs in Summer. I: Lek Mating. Behaviour 134:433-462.
- Anderson PK. 2001. Marine mammals in the next one hundred years: Twilight for a Pleistocene megafauna? Journal of Mammalogy **8**:623-629.
- Anderson PK, Barclay RMR. 1995. Acoustic signals of solitary dugongs: Physical characteristics and behavioral correlates. Journal of Mammalogy **76**:1226-1237.
- Anderson P, Birtles A. 1978. Behaviour and ecology of the dugong, *Dugong Dugon* (Sirenia): observations in Shoalwater and Cleveland bays, Queensland. Australian Wildlife Research **5**:1-23.
- Armstrong, AJ, Armstrong, AO, McGregor, F, Richardson, AJ, Bennett, MB, Townsend, KA, Hays, GC, van Keulen, M, Smith, J, Dudgeon, CL. 2020. Satellite tagging and photographic identification reveal connectivity between two UNESCO World Heritage Areas for reef manta rays. Frontiers in Marine Science, 7.
- Austin D, McMillan JI, Bowen WD. 2003. A three-stage algorithm for filtering erroneous ARGOS satellite locations. Marine Mammal Science **19**:371-383.
- Australian Government. 2015. State of Australian Cities 2014-2015: Brisbane.
- Australian Government. 2021. Great Barrier Reef Marine Park Regulations 2019; Compilation No. 6. Australian Government.
- Avila IC, Kaschner K, Dormann CF. 2018. Current global risks to marine mammals: Taking stock of the threats. Biological Conservation **221**:44-58.

- Ayram CAC, Mendoza ME, Etter A, Pérez Salicrup DR. 2017. Anthropogenic impact on habitat connectivity: A multidimensional human footprint index evaluated in a highly biodiverse landscape of Mexico. Ecological Indicators **72**:895-909.
- Babcock RC, Bustamante RH, Fulton EA, Fulton DJ, Haywood MDE, Hobday AJ, Kenyon R, Matear RJ, Plagányi EE, Richardson AJ, Vanderklift MA. 2019. Severe continentalscale impacts of climate change are happening now: Extreme climate events impact marine habitat forming communities along 45% of Australia's coast. Frontiers in Marine Science **6**:411.
- Bacchus M-LC, Dunbar SG, Self-Sullivan C. 2009. Characterization of resting holes and their use by the Antillean manatee (*Trichechus manatus manatus*) in the Drowned Cayes, Belize. Aquatic Mammals **35**:62-71.
- Bailey H, Hammond PS, Thompson PM. 2014. Modelling harbour seal habitat by combining data from multiple tracking systems. Journal of Experimental Marine Biology and Ecology **450**:30-39.
- Bailey H, Rice A, Wingfield JE, Hodge KB, Estabrook BJ, Hawthorne D, Garrod A, Fandel A D, Fouda L, McDonald E, Grzyb E, Fletcher W, Hoover AL. 2019. Determining habitat use by marine mammals and ambient noise levels using passive acoustic monitoring offshore of Maryland.
- Baird RW, Hanson MB, Schorr GS, Webster DL, McSweeney DJ, Gorgone AM, Mahaffy SD, Holzer DM, Oleson EM, Andrews RD. 2012. Range and primary habitats of Hawaiian insular false killer whales: Informing determination of critical habitat. Endangered Species Research 18:47-61.
- Bárcenas de la Cruz D, DeRango E, Johnson SP, Simeone CA. 2018. Evidence of anthropogenic trauma in marine mammals stranded along the central California coast, 2003–2015. Marine Mammal Science **34**:330-346.
- Barrett-Lennard LG, Smith TG, Ellis GM. 1996. A cetacean biopsy system using lightweight pnematic darts and its effect on the behavior of killer whales. Marine Mammal Science **12**:14-27.
- Bartol S, Ketten DR. 2006. Turtle and tuna hearing in Swimmer Y, and Brill R, editors. Sea turtle and pelagic fish sensory biology: Developing techniques to reduce sea turtle bycatch in longline fisheries. Technical Memorandum NMFS-PIFSC-7, National Ocean and Atmospheric Administration (NOAA), US Department of Commerce, pp 98-105.
- Barton SL, Reynolds III JE. 2008. Photo-identification and synoptic studies of manatees in southwestern Florida. Mote Marine Laboratory Technical Technical Report MTR 1269, Mote Marine Laboratory, Sarasota Florida USA.
- Bassett BL, Hostetler JA, Leone E, Shea CP, Barbeau BD, Lonati GL, Panike AL, Honaker A, Ward-Geiger LI. 2020. Quantifying sublethal Florida manatee–watercraft interactions by examining scars on manatee carcasses. Endangered Species research **43**:395-408.
- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using Ime4. Pages 1-48. Journal of Statistical Software.
- Baumgartner MF, Freitag L, Partan J, Ball KR, Prada KE. 2008. Tracking large marine predators in three dimensions: The real-time acoustic tracking system. IEEE Journal of Oceanic Engineering **33**:146-157.
- Beck CA, Clark M. 2012. Individual Identification of Sirenians. Pages 133-138 in Hines EM, Reynolds JE, III, Aragones L, McKenzie R, and Blanche R, editors. CH. 15 in

Sirenian conservation : issues and strategies in developing countries. University Press of Florida, Gainesville, United States.

- Beck CA, Langtimm CA. 2002. Application of the manatee photo-identification database for population research. Manatee Population Ecology and Management Workshop: poster. U.S. Geological Survey, Florida Caribbean Science Center, Gainesville, FL.
- Belant JL, Millspaugh JJ, Martin JA, Gitzen RA. 2012. Multi-dimensional space use: The final frontier. Frontiers in Ecology and the Environment **10**:11-12.
- Bengtson JL. 1983. Estimating food consumption of free-ranging manatees in Florida. The Journal of Wildlife Management **47**:1186-1192.
- Bestley S, Jonsen ID, Hindell MA, Harcourt RG. 2015. Taking animal tracking to new depths: synthesizing horizontal–vertical movement relationships for four marine predators. Ecology (Durham) **96**:417-427.
- Beyer HL. 2012. Geospatial Modelling Environment (Version 0.7.2.1). (software). See spatialecology.com/gme.
- Bicknell AWJ, Godley BJ, Sheehan EV, Votier SC, Witt MJ. 2016. Camera technology for monitoring marine biodiversity and human impact. Frontiers in Ecology and the Environment **14**:424-432.
- Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed GA, Harrison AL, Ganong JE, Swithenbank A, Castleton M, Dewar H, Mate BR, Shillinger GL, Schaefer KM, Benson SR, Weise MJ, Henry RW, Costa DP. 2011. Tracking apex marine predator movements in a dynamic ocean. Nature 475:86-90.
- Bograd SJ, Block BA, Costa DP, Godley BJ. 2010. Biologging technologies: New tools for conservation. Introduction. Endangered Species Research **10**:1-7.
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MH, White JS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution **24**:127-135.
- Bossart GD, Meisner RA, Rommel SA, Lightsey JD, Varela RA, Defran RH. 2004. Pathologic findings in Florida manatees (*Trichechus manatus latirostris*). Aquatic Mammals 30:434-440.
- Botsford LW, Parma AM. 2005. Uncertainty in Marine Management, Chapter 22. Pages 375-392 in Norse EA, and Crowder LB, editors. Marine Conservation Biology: the science of maintaining the sea's biodiversity. Island Press, Washington DC USA.
- Bowles AE, Denes SL, Shane MA. 2010. Acoustic characteristics of ultrasonic coded transmitters for fishery applications: Could marine mammals hear them? The Journal of the Acoustical Society of America **128**:3223-3231.
- Braun CD, Skomal GB, Thorrold SR, Berumen ML. 2015. Movements of the reef manta ray (*Manta alfredi*) in the Red Sea using satellite and acoustic telemetry. Marine Biology **162**.
- Breitburg DL, Riedel GF. 2005. Multiple stressors in marine systems. Pages 167-182 in Norse EA, and Crowder LB, editors. Marine Conservation Biology: The science of maintaining the sea's biodiversity. Island Press, Washington DC USA.
- Brierley AS, Kingsford MJ. 2009. Impacts of climate change on marine organisms and ecosystems. Current Biology **19**:R602-R614.
- Briscoe DK, Fossette S, Scales KL, Hazen EL, Bograd SJ, Maxwell SM, McHuron EA, Robinson PW, Kuhn C, Costa DP, Crowder LB, Lewison RL. 2018. Characterizing habitat suitability for a central-place forager in a dynamic marine environment. Ecology and Evolution **8**:2788-2801.

- Brodie S, Lédée EJI, Heupel MR, Babcock RC, Campbell HA, Gledhill DC, Hoenner X, Huveneers C, Jaine FRA, Simpfendorfer CA, Taylor MD, Udyawer V, Harcourt RG. 2018. Continental-scale animal tracking reveals functional movement classes across marine taxa. Scientific Reports (Nature Publisher Group) 8:1-9.
- Bröker KC. 2019. An overview of potential impacts of hydrocarbon exploration and production on marine mammals and associated monitoring and mitigation measures. Aquatic Mammals **45**:576-611.
- Burgess EA, Lanyon JM, Brown JL, Blyde D, Keeley T. 2012. Diagnosing pregnancy in freeranging dugongs using fecal progesterone metabolite concentrations and body morphometrics: A population application. General and Comparative Endocrinology 177:82-92.
- Burgess EA, Brown JL, Lanyon JM. 2013. Sex, scarring, and stress: understanding seasonal costs in a cryptic marine mammal. Conservation Physiology **1**.
- Burnham KP, Anderson DR. 2002. Information and Likelihood Theory: A Basis for Model Selection and Inference. Pages 49-97 in Burnham K, and Anderson D, editors. Model Selection and Multimodel Inference. Springer New York, United States of America.
- Burnham RE, Duffus DA. 2019. The use of passive acoustic monitoring as a census tool of gray whale (*Eschrichtius robustus*) migration. Ocean & Coastal Management:105070.
- Burt WH. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy **24**:346-352.
- Cagnacci F, Boitani L, Powell RA, Boyce MS. 2010. Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society B **365**:2157-2162.
- Calleson CS, Frohlich RK. 2007. Slower boat speeds reduce risks to manatees. Endangered Species Research **3**:295-304.
- Carlisle AB, Starr RM. 2010. Tidal movements of female leopard sharks (*Triakis semifasciata*) in Elkhorn Slough, California. Environmental Biology of Fishes **89**:31-45.
- Castelblanco-Martínez DN, Morales-Vela B, Slone DH, Padilla-Saldívar JA, Reid JP, Hernández-Arana HA. 2015. Inferring spatial and temporal behavioral patterns of free-ranging manatees using saltwater sensors of telemetry tags. Mammalian Biology - Zeitschrift für Säugetierkunde **80**:21-30.
- Castellini M. 2018. Thermoregulation in Würsig B, Thewissen JGM, and Kovacs KM, editors. Encyclopedia of Marine Mammals (Third Edition). Academic Press, London, 990-994.
- Chambault P, Christoffer Moesgaard A, Patterson TA, Hansen RG, Tervo O, Laidre KL, Heide-Jørgensen MP. 2018. Sea surface temperature predicts the movements of an Arctic cetacean: the bowhead whale. Scientific Reports (Nature Publisher Group) 8:1-12.
- Chilvers BL, Delean S, Gales NJ, Holley DK, Lawler IR, Marsh H, Preen AR. 2004. Diving behaviour of dugongs, (*Dugong dugon*). Journal of Experimental Marine Biology and Ecology **304**:203-224.
- Chilvers BL, Lawler IR, Macknight F, Marsh H, Noad M, Paterson R. 2005. Moreton Bay, Queensland, Australia: an example of the co-existence of significant marine mammal populations and large-scale coastal development. Biological Conservation **122**:559-571.
- Chung H, Lee J, Lee WY. 2021. A Review: Marine Bio-logging of Animal Behaviour and Ocean Environments. Ocean Science Journal 56:117–131.

- Cleguer C. 2015. Informing dugong conservation at several spatial and temporal scales in New Caledonia. Ph.D. thesis, College of Marine and Environmental Sciences. James Cook University, Townsville, Queensland.
- Cleguer C, Grech A, Garrigue C, Marsh H. 2015. Spatial mismatch between marine protected areas and dugongs in New Caledonia. Biological Conservation **184**:154-162.
- Cleguer C, Preston S, Hagihara R, Shimada T, Udyawer V, Hamann M, Simpson S, Loban F, Bowie G, Fujii R, Marsh H. 2016. Working with the community to understand use of space by dugongs and green turtles in Torres Strait: A project in collaboration with the Mura Badulgal Registered Native Title Bodies Corporate. Report to the National Environmental Science Programme. Reef and Rainforest Research Centre Limited. Cairns.
- Cleguer C, Garrigue C, Marsh H. 2020. Dugong (*Dugong dugon*) movements and habitat use in a coral reef lagoonal ecosystem. Endangered Species Research **43**:167-181.
- Cliff G, Dudley SFJ. 2011. Reducing the environmental impact of shark-control programs: a case study from KwaZulu-Natal, South Africa. Marine and Freshwater Research **62**:700-709.
- CMS. 2015. Appendices I and II of the Convention on the Conservation of Migratory Species of Wild Animals (as amended by the Conference of the Parties in 1985, 1988, 1991, 1994, 1997, 1999, 2002, 2005, 2008, 2011 and 2014). Effective: 8 February 2015. Accessed http://www.cms.int/en/species 15 May 2015.
- CMS. 2021. Convention on the Conservation of Migratory Species of Wild Animals, downloaded June 08, 2021, Available from https://www.cms.int/en/parties-rangestates.
- Coles RG, McKenzie LJ, Rasheed MA, Mellors JE, Taylor H, Dew K, McKenna S, Sankey TL, Carter A, Grech A. 2007. Status and trends of seagrass habitats in the Great Barrier Reef World Heritage Area. Cairns.
- CoML. 2010. Electronic tagging of marine animals, Available from http://www.coml.org/comlfiles/scor/SCOR-tagging.pdf (accessed August 24, 2011 2011).
- Committee on Taxonomy. 2020. List of marine mammal species and subspecies, Available from https://marinemammalscience.org/species-information/list-marine-mammal-species-subspecies/ (accessed July 29 2020).
- Cooke SJ. 2008. Biotelemetry and biologging in endangered species research and animal conservation: Relevance to regional, national and IUCN Red List threat assessments. Endangered Species Research **4**:165-185.
- Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, Wolcott TG. 2004. Biotelemetry: a mechanistic approach to ecology. Trends In Ecology and Evolution **19**.
- Cooper NW, Sherry TW, Marra PP. 2014. Modeling three-dimensional space use and overlap in birds. Auk **131**.
- Cope RC, Pollett PK, Lanyon JM, Seddon JM. 2015. Indirect detection of genetic dispersal (movement and breeding events) through pedigree analysis of dugong populations in southern Queensland, Australia. Biological Conservation **181**:91-101.
- Cope S, Hines E, Bland R, Davis JD, Tougher B, Zetterlind V. 2020. Application of a new shore-based vessel traffic monitoring system within San Francisco Bay. Frontiers in Marine Science. **7**:86.
- Corrigan CM, Ardron JA, Comeros-Raynal MT, Hoyt E, Notarbartolo Di Sciara G, Carpenter KE. 2014. Developing important marine mammal area criteria: Learning from

ecologically or biologically significant areas and key biodiversity areas. Aquatic Conservation: Marine and Freshwater Ecosystems **24**:166-183.

- Costa DP, Breed GA, Robinson PW. 2012. New insights into pelagic migrations: Implications for ecology and conservation. Annual Review of Ecology, Evolution, and Systematics **43**:73-96.
- Couturier LIE, Newman P, Jaine FRA, Bennett MB, Venables WN, Cagua EF, Townsend KA, Weeks SJ, Richardson AJ. 2018. Variation in occupancy and habitat use of *Mobula alfredi* at a major aggregation site. Marine Ecology Progress Series **599**:125-145.
- Cronin M, Gerritsen H, Reid D, Jessopp M. 2016. Spatial overlap of grey seals and fisheries in Irish waters; some new insights using telemetry technology and VMS. PLoS One **11**.
- Cullen-Unsworth LC, Jones BL, Seary R, Newman R, Unsworth RKF. 2018. Reasons for seagrass optimism: Local ecological knowledge confirms presence of dugongs. Marine Pollution Bulletin **134**:118-122.
- Currie DJ. 2007. Disentangling the roles of environment and space in ecology. Journal of Biogeography **34**:2009-2011.
- Data East. 2013. XTools Pro 9.2 ArcView Extension. Data East Soft, LLC, Novosibirsk, Russia.
- Davidson AD, Boyer AG, Kim H, Pompa-Mansilla S, Hamilton MJ, Costa DP, Ceballos G, Brown JH. 2012. Drivers and hotspots of extinction risk in marine mammals. Proceedings of the National Academy of Sciences **109**:3395-3400.
- De longh HH, Langeveld P, van der Wal M. 1998. Movement and home ranges of dugongs around the Lease Islands, East Indonesia. Marine Ecology **19**:179-193.
- de Vere AJ, Lilley MK, Frick EE. 2018. Anthropogenic impacts on the welfare of wild marine mammals. Aquatic Mammals **44**:150-180.
- de Vos A, Christiansen F, Harcourt RG, Pattiaratchi CB. 2013. Surfacing characteristics and diving behaviour of blue whales in Sri Lankan waters. Journal of Experimental Marine Biology and Ecology **449**:149-153.
- Dennison WC, Abal EG 1999. Moreton Bay Study: a scientific basis for the Healthy Waterways Campaign. Southeast Queensland Regional Water Quality Management Strategy. Moreton Bay Waterways and Catchment Partnership, Brisbane City Council, Australia.
- Deutsch CJ, Barlas ME. 2016. Manatee response to the conversion of the FPL Cape Canaveral power plant: movements, warm-water habitat use, and thermal regime of satellite-tagged manatees during winters 2010-11 through 2014-15. Final Report to Florida Power & Light Company. Florida Fish and Wildlife Conservation Commission FWC/FWRI file F2864-10-15-F. 113 pp.
- Deutsch CJ, Bonde RK, Reid JP. 1998. Radio-tracking manatees from land and space: tag design, implementation, and lessons learned from long-term study. Marine Technology Society. Marine Technology Society Journal **32**:18-19.
- Deutsch CJ, Reid JP, Bonde RK, Easton DE, Kochman HI, O'Shea TJ. 2003. Seasonal movements, migratory behavior and site fidelity of West Indian manatees along the Atlantic coast of the United States. Wildlife Monographs **151**.
- Deutsch CJ, Castelblanco-Martínez DN, Groom R, Cleguer C. 2022a. Chapter 5: Movement behavior of manatees and dugongs: I. Environmental challenges dreive diversity in migratory patters and other large-scale movements in Marsh H, editor. Ethology and Behavioral Ecology of Sirenia. Springer.

- Deutsch CJ, Castelblanco-Martínez DN, Cleguer C, Groom R. 2022b. Chapter 6: Movement behavior of manatees and dugongs: II. Small-scale movements reflect adaptations to dynamic aquatic environments in Marsh H, editor. Ethology and Behavioral Ethology of Sirenia. Springer.
- Dewar H, Wilson SG, Hyde JR, Snodgrass OE, Leising A, Lam CH, Domokos R, Wraith JA, Bograd SJ, Van Sommeran SR, Kohin S. 2018. Basking shark (*Cetorhinus maximus*) movements in the eastern north Pacific determined using satellite telemetry. Frontiers in Marine Science.
- Di Iorio L, Clark CW. 2010. Exposure to seismic survey alters blue whale acoustic communication. Biology Letters **6**:51-54.
- Di Sciara GN, Hoyt E, Reeves R, Ardron J. 2016. Place-based approaches to marine mammal conservation. Aquatic Conservation **26**:85-100.
- Dobbs K, Fernandes L, Slegers S, Jago B, Thompson L, Hall J, Day J, Cameron D, Tanzer J, Macdonald F, Marsh H, Coles R. 2008. Incorporating dugong habitats into the marine protected area design for the Great Barrier Reef Marine Park, Queensland, Australia. Ocean and Coastal Management **51**:368-375.
- Double MC, Andrews-Goff V, Jenner KCS, Jenner M-N, Laverick SM, Branch TA, Gales NJ. 2014. Migratory movements of pygmy blue whales (Balaenoptera musculus brevicauda) between Australia and Indonesia as revealed by satellite telemetry. PLoS One **9**.
- Dow Piniak WE, Mann DA, Eckert SA, Harms CA. 2012. Amphibious Hearing in Sea Turtles. Pages 83-87 in Popper AN, and Hawkins A, editors. The Effects of Noise on Aquatic Life. Springer New York.
- Dunic JC, Brown CJ, Connolly RM, Turschwell MP, Côté IM. 2021. Long-term declines and recovery of meadow area across the world's seagrass bioregions. Global Change Biology **27**:4096-4109.
- Dunning JB, Danielson BJ, Pulliam HR. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**:169-175.
- Duong T. 2019. ks: Kernel density estimation and kernel discriminant analysis for multivariate data in R. Journal of Statistical Software. **21**: 1-16.
- Edwards HH, Martin J, Deutsch CJ, Muller RG, Koslovsky SM, Smith AJ, Barlas ME. 2016. Influence of manatees' diving on their risk of collision with watercraft. PLoS ONE **11**:e0151450.
- Ellis, RD, Flaherty-Walia, KE, Collins, AB, Bickford, JW, Boucek, R, Walters Burnsed, SL, Lowerre-Barbieri, SK. (2019). Acoustic telemetry array evolution: from species- and project-specific designs to large-scale, multispecies, cooperative networks. Fisheries Research, 209, 186-195.
- Elsner R. 1999. Living in water: solutions to physiological problems in Reynolds III JE, and Rommel SA, editors. Biology of marine mammals. Smithosonian Institute, Washington.
- Erbe C, Reichmuth C, Cunningham K, Lucke K, Dooling R. 2016. Communication masking in marine mammals: A review and research strategy. Marine Pollution Bulletin **103**:15-38.
- Erbe C, Marley SA, Schoeman RP, Smith JN, Trigg LE, Embling CB. 2019. The effects of ship noise on marine mammals—a review. Frontiers in Marine Science.
- Espinoza M, Lédée EJI, Simpfendorfer CA, Tobin AJ, Heupel MR. 2015. Contrasting movements and connectivity of reef-associated sharks using acoustic telemetry: implications for management. Ecological Applications **25**:2101-2118.

- ESRI. 2013. ArcGIS Desktop: Release 10.1. Environmental Systems Research Institute, Redlands, CA USA.
- ESRI. 2014. ArcGIS Desktop: Release 10.2. Environmental Systems Research Institute, Redlands, CA USA.
- Estes JA. 1989. Adaptations for aquatic living by carnivores. Pages 242-282 in Gittleman JL, editor. Carnivore Behavior, Ecology, and Evolution. Springer USA, Boston, MA.
- Etheridge K, Rathbun GB, Powell JA, Kochman HI. 1985. Consumption of aquatic plants by the West Indian manatee. Journal of Aquatic Plant Management **23**:21-25.
- Evans PGH, Pierce GJ, Panigada S. 2010. Climate change and marine mammals. Journal of the Marine Biological Association of the United Kingdom **90**:1483-1487.
- Evans K, Lea MA, Patterson TA. 2013. Recent advances in bio-logging science: Technologies and methods for understanding animal behaviour and physiology and their environments. Deep Sea Research Part II: Topical Studies in Oceanography 88-89:1-6.
- Fernandes L, Day J, Lewis A, Slegers, S, Kerrigan B, Breen D, Cameron D, Jago B, Hall J, Lowe D, Innes J, Tanzer J, Chadwick V, Thompson L, Gorman K, Simmons M, Barnett B, Sampson K, De'ath G, Mapstone B, Marsh H, Possingham H, Ball I, Ward T, Dobbs K, Aumend J, Slater D, Stapleton K. 2005. Establishing representative notake areas in the Great Barrier Reef: Large-scale implementation of theory on marine protected areas. Conservation Biology **19**:1733-1744.
- Fernandes L, Dobbs K, Day J, Slegers S. 2010. Identifying biologically and physically special or unique sites for inclusion in the protected area design for the Great Barrier Reef Marine Park. Ocean & Coastal Management **53**:80-88.
- Ferrara CR, Vogt RC, Harfush MR, Sousa-Lima RS, Albavera E, Tavera A. 2014. First evidence of leatherback turtle (*Dermochelys coriacea*) embryos and hatchlings emitting sounds. Chelonian Conservation and Biology **13**:110-114.
- Fieberg J, Kochanny CO. 2005. Quantifying home range overlap: The importance of the utilization distribution. The Journal of Wildlife Management **69**:1346-1359.
- Fisher R. 2020. FSSgam: Full subsets multiple regression in R using gam(m4). Ecology and Evolution **8**:6104-6113.
- Fisher R, Wilson SK, Sin TM, Lee AC, Langlois TJ. 2018. A simple function for full-subsets multiple regression in ecology with R. Ecology and Evolution **8**:6104-6113.
- Flamm RO, Ward LI, Weigle BL. 2001. Applying a variable-shape spatial filter to map relative abundance of manatees (*Trichechus manatus latirostris*). Landscape Ecology **16**:279-288.
- Fox J, Weisberg S 2011. An R companion to applied regression. Sage, Thousand Oaks CA.
- Fraser KC, Davies KTA, Davy CM, Ford AT, Flockhart DTT, Martins EG. 2018. Tracking the conservation promise of movement ecology. Frontiers in Ecology and Evolution.
- Freitas C, Lydersen C, Fedak MA, Kovacs KM. 2008. A simple new algorithm to filter marine mammal Argos locations. Marine Mammal Science **24**:315-325.
- Gales R, Alderman R, Thalmann S, Carlyon K. 2012. Satellite tracking of long-finned pilot whales (*Globicephala melas*) following stranding and release in Tasmania, Australia. Wildlife Research **39**:520-531.
- Gallivan GJ, Best RC, Kanwisher JW. 1983. Temperature regulation in the Amazonian manatee *Trichechus inunguis*. Physiological Zoology **56**:255-262.
- Gaspard III JC, Bauer GB, Reep RL, Dziuk K, Cardwell A, Read L, Mann DA. 2012. Audiogram and auditory critical ratios of two Florida manatees (*Trichechus manatus latirostris*). The Journal of Experimental Biology **215**:1442-1447.

- GBR Marine Park Authority. 2009. For Commercial Net Fishermen about minor netting changes in DPA Bs (Dugong Protection Areas). Information Sheet. Australian Government.
- GBR Marine Park Authority. 2019. *Great Barrier Reef Outlook Report 2019*. GBRMPA, Townsville.
- GBRMPA. 1981. Nomination of the Great Barrier Reef by the Commonwealth of Australia for inclusion in the World Heritage List.
- GBRMPA. 1983. Great Barrier Reef Marine Park Regulations 1983. Federal Register of Legislative Instruments F2014C01241. Statutory Rules No. 262, 1983 as amended. Includes amendments up to: SLI No. 153, 2014. The Office of Parliamentary Counsel, Canberra.
- Gerstein ER, Gerstein L, Forsythe SE, Blue JE. 1999. The underwater audiogram of the West Indian manatee (*Trichechus manatus*). The Journal of the Acoustical Society of America **105**:3575-3583.
- Grant PBC, Lewis TR. 2010. High speed boat traffic: A risk to crocodilian populations. Herpetological Conservation and Biology **5**:456-460.
- Grech A, Marsh H. 2008. Rapid assessment of risks to a mobile marine mammal in an ecosystem-scale marine protected area. Conservation Biology **22**:711-720.
- Grech A, Marsh H, Coles R. 2008. A spatial assessment of the risk to a mobile marine mammal from bycatch. Aquatic Conservation: Marine and Freshwater Ecosystems **18**:1127-1139.
- Grech A, Sheppard J, Marsh H. 2011. Informing species conservation at multiple scales using data collected for marine mammal stock assessments. PLoS ONE **6**.
- Gredzens C, Marsh H, Fuentes MMPB, Limpus C, Shimada T, Hamann M. 2014. Satellite tracking of sympatric marine megafauna can inform the biological basis for species co-management. PLoS ONE **9**:e98944.
- Gridley T, Cockcroft VG, Hawkins ER, Blewitt ML, Morisaka T, Janik VM. 2014. Signature whistles in free-ranging populations of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*. Marine Mammal Science **30**:512-527.
- Groom RA, Lawler IR, Marsh H. 2004. The risk to dugongs of vessel strike in the Southern Bay Islands area of Moreton Bay. Townsville, Queensland.
- Grothues TM. 2009. A review of acoustic telemetry technology and a perspective on its diversification relative to coastal tracking arrays. Pages 77-90 in Nielsen JL, Arrizabalaga H, Fragoso N, Hobday A, Lutcavage M, and Sibert J, editors. Tagging and tracking of marine animals with electronic devices. Springer.
- Grüss A, Kaplan DM, Guénette S, Roberts CM, Botsford LW. 2011. Consequences of adult and juvenile movement for marine protected areas. Biological Conservation **144**:692-702.
- Haase CG, Fletcher Jr RJ, Slone DH, Reid JP, Butler SM. 2017. Landscape complementation revealed through bipartite networks: an example with the Florida manatee. Landscape Ecology **32**:1999–2014.
- Hagihara R. 2015. Linking wildlife tracking data with environmental features to improve understanding of dugong diving ecology and population size estimates. Ph.D. thesis, College of Marine and Environmental Sciences. James Cook University Townsville QLD, Townsville, QLD Australia.
- Hagihara R, Jones RE, Sheppard JK, Hodgson AJ, Marsh H. 2011. Minimizing errors in the analysis of dive recordings from shallow-diving animals. Journal of Experimental Marine Biology and Ecology **399**:173-181.

- Haig JA, Lambert GI, Sumpton WD, Mayer DG, Werry JM. 2018. Habitat features influence catch rates of near-shore bull shark (*Carcharhinus leucas*) in the Queensland Shark Control Program, Australia 1996–2012. Estuarine, Coastal and Shelf Science 200:289-300.
- Hammond PS. 2009. Mark–Recapture. Pages 705-709 in Perrin WF, Würsig B, and Thewissen JGM, editors. Encyclopedia of Marine Mammals (Second Edition). Academic Press, London.
- Hammond PS, Mizroch SA, Donovan GP. 1990. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Cambridge, UK.
- Hanggi EB, Schusterman RJ. 1994. Underwater acoustic displays and individual variation in male harbour seals, *Phoca vitulina*. Animal Behaviour **48**:1275-1283.
- Harcourt RG, Hindell MA, Bell DG, Waas JR. 2000. Three-dimensional dive profiles of freeranging Weddell seals. Polar Biology **23**:479-487.
- Harcourt R, Boomer A, Field I, Bainbridge S, Doherty P, Meedkan M, Cocklin C, Heupel M, Simpfendorfer C, Wallner B, Wachenfelt D, Semmens J, Buston, C, Williams R, Hindell M, Sainsbury K, Timms G, Rintoul S, Bruce B, Hopday A, Babcock R, Richardson A, Suther I, Taylor M, Goldsworthy S, Huveneers C, Arnould J,Pederson H, Gray C, Peddemors V, Robbins W, Otway N, Kennelly S. 2009. Australian Acoustic Tagging and Monitoring System: 2009-2013 IMOS EIF Facility Project Plan.
- Hart KM, Hyrenbach KD. 2009. Satellite telemetry of marine megavertebrates: the coming of age of an experimental science. Endangered Species Research **10**:9-20.
- Hastie G, Merchant ND, Götz T, Russell DJF. 2019. Effects of impulsive noise on marine mammals: investigating range-dependent risk. Ecological Applications **29**.
- Hays GC, Mortimer JA, Ierodiaconou D, Esteban N. 2014. Use of long-distance migration patterns of an endangered species to inform conservation planning for the world's largest marine protected area. Conservation Biology DOI:10.1111/cobi.12325 DOI: 10.1111/cobi.12325.
- Hays GC, Ferreira LC, Sequeira AMM, Meekan MG, Duarte CM, Bailey H, Bailleul F, Bowen WD, Caley MJ, Costa DP, Eguíluz VM, Fossette S, Friedlaender AS, Gales N, Gleiss AC, Gunn J, Harcourt R, Hazen EL, Heithaus MR, Heupel M, Holland K, Horning M, Jonsen I, Kooyman GL, Lowe CG, Madsen PT, Marsh H, Phillips RA, Righton, D, Ropert-Coudert Y, Sato K, Shaffer SA,Simpfendorfer CA, Sims DW, Skomal G, Takahashi A, Trathan PN, Wikelski M, Womble JN, Thums M. 2016. Key questions in marine megafauna movement ecology. Trends in Ecology & Evolution 31:463-475.
- Hays GC, Alcoverro, T, Christianen, MJA, Duarte, CM, Hamann, M, Macreadie, PI, Marsh, HD, Rasheed, MA, Thums, M, Unsworth, RKF, York, PH, Esteban, N. 2018. New tools to identify the location of seagrass meadows: marine grazers as habitat indicators. Frontiers in Marine Science.
- Hays GC, Bailey H, Bograd SJ, Bowen WD, Campagna C, Carmichael RH, Casale P, Chiaradia A, Costa DP, Cuevas E, Nico de Bruyn PJ, Dias MP, Duarte CM, Dunn DC, Dutton PH, Esteban N, Friedlaender A, Goetz KT, Godley BJ, Halpin PN, Hamann M, Hammerschlag N, Harcourt R, Harrison A-L, Hazen EL, Heupel MR, Hoyt E, Humphries NE, Kot CY, Lea JSE, Marsh H, Maxwell SM, McMahon CR, Notarbartolo Di Sciara G, Palacios DM, Phillips RA, Righton D, Schofield G, Seminoff JA,Simpfendorfer CA, Sims DW, Takahashi A, Tetley MJ, Thums M, Trathan PN, Villegas-Amtmann S, Wells RS, Whiting SD, Wilderman NE, Sequeira AMM. 2019.

Translating marine animal tracking data into conservation policy and management. Trends in Ecology & Evolution **34**:459-473.

- Hazel J, Gyuris E. 2006. Vessel-related mortality of sea turtles in Queensland, Australia. Wildlife Research **33**:149-154.
- Hazel J, Lawler IR, Marsh H, Robson S. 2007. Vessel speed increases collision risk for the green turtle *Chelonia mydas*. Endangered Species Research **3**:105-113.
- Hazen EL, Maxwell SM, Bailey H, Bograd SJ, Hamann M, Gaspar P, Godley BJ, Shillinger GL. 2012. Ontogeny in marine tagging and tracking science: technologies and data gaps. Marine Ecology Progress Series **457**:221-240.
- Heinsohn GE. 1981. Aerial survey techniques for dugongs. Pages 125–129 in Marsh H, editor. The dugong. James Cook University of North Queensland Press, Townsville., James Cook University 8–13 May 1979.
- Heinsohn GE, Spain AV. 1974. Effects of a tropical cyclone on littoral and sub-littoral biotic communities and on a population of Dugongs (Dugong dugon (Müller)). Biological Conservation **6**:143-152.
- Heinsohn GE, Wake J, Marsh H, Spain AV. 1977. The dugong (*Dugong dugon*, Müller) in the seagrass system. Aquaculture **12**:235-248.
- Heinsohn GE, Lear RJ, Bryden MM, Marsh H, Gardner BR. 1978. Discovery of a large population of dugongs off Brisbane, Australia. Environmental Conservation **5**:91-92.
- Heithaus MR, Dill LM, Marshall GJ, Buhleier B. 2002. Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. Marine Biology **140**:237-248.
- Heupel MR, Simpfendorfer CA. 2002. Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. Canadian Journal of Fisheries and Aquatic Sciences **59**:624-632.
- Heupel MR, Simpfendorfer CA. 2005. Using acoustic monitoring to evaluate MPAs for shark nursery areas: The importance of long-term data. Marine Technology Society Journal **39**:10-18.
- Heupel MR, Simpfendorfer CA. 2008. Movement and distribution of young bull sharks Carcharhinus leucas in a variable estuarine environment. Aquatic Biology **1**:277-289.
- Heupel MR, Simpfendorfer CA. 2014. Importance of environmental and biological drivers in the presence and space use of a reef-associated shark. Marine Ecology Progress Series **496**:47-57.
- Heupel MR, Webber DM. 2012. Trends in acoustic tracking: Where are the fish going and how will we follow them? Advances in fish tagging and marketing technology. Pages 219-231. American Fisheries Society Symposium 76.
- Heupel MR, Semmens JM, Hobday AJ. 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Marine and Freshwater Research **57**:1-13.
- Heupel MR, Reiss KL, Yeiser BG, Simpfendorfer CA. 2008. Effects of biofouling on performance of moored data logging acoustic receivers. Limnology and Oceanography: Methods **6**:327–335.
- Heupel MR, Simpfendorfer CA, Olsen EM, Moland E. 2012. Consistent movement traits indicative of innate behavior in neonate sharks. Journal of Experimental Marine Biology and Ecology **432-433**:131-137.
- Hill-Lewenilovo R, Vuiyasawa R, Piovano S. 2019. First record of a dugong (*Dugong dugon*, Müller, 1776) in Fiji. Pacific Conservation Biology **25**:324.

- Hilty JA, Dobson AP, Lidicker Jr WZ, Merenlender AM. 2006. Part III Corridor Design, Planning and Implementation. Corridor Ecology : the science and practice of linking landscapes for biodiversity conservation. Island Press, Washington, DC.
- Hobbs J-PA, Frisch AJ, Hender J, Gilligan JJ. 2007. Long-distance oceanic movement of a solitary dugong (*Dugong dugon*) to the Cocos (Keeling) Islands. Aquatic Mammals 33:175-178.
- Hodgson AJ. 2004. Dugong behaviour and responses to human influences. School of Tropical Environment Studies and Geography. James Cook University, Townsville.
- Hodgson A. 2007. "BLIMP-CAM": Aerial video observations of marine animals. Marine Technology Society Journal **41**:39-43.
- Hodgson AJ, Marsh H. 2007. Response of dugongs to boat traffic: the risk of disturbance and displacement. Journal of Experimental Marine Biology and Ecology **340**:50-61.
- Hoenner X, Huveneers C, Steckenreuter A, Simpfendorfer C, Tattersall K, Jaine F, Atkins N, Babcock R, Brodie S, Burgess J, Campbell H, Heupel M, Pasquer B, Proctor R, Taylor MD, Udyawer V, Harcourt R. 2018. Australia's continental-scale acoustic tracking database and its automated quality control process. Scientific Data 5:10 p.
- Holley DK, Lawler IR, Gales NJ. 2006. Summer survey of dugong distribution and abundance in Shark Bay reveals additional key habitat area. Wildlife Research 33:243-250.
- Hooker SK, Cañadas A, Hyrenback KD, Corrigan C, Polovina JJ, Reeves RR. 2011. Making protected area networks effective for marine top predators. Endangered Species Research **13**:203-218.
- Horgan P, Booth D, Nichols C, Lanyon JM. 2014. Insulative capacity of the integument of the dugong (*Dugong dugon*): Thermal conductivity, conductance and resistance measured by in vitro heat flux. Marine Biology **161**:1395-1407.
- Horne JS, Garton EO. 2006. Likelihood cross-validation versus least squares crossvalidation for choosing the smoothing parameter in kernel home-range analysis. The Journal of Wildlife Management **70**:641-648.
- Hoyt E. 2018. Tourism. Pages 1010-1014. Encyclopedia of Marine Mammals (Third Edition). Elsevier Inc.
- Hyrenback KD, Forney KA, Dayton PK. 2000. Marine protected areas and ocean basin management. Aquatic Conservation: Marine and Freshwater Ecosystems **10**:437-458.
- Ichikawa K, Tsutsumi C, Akamatsu T. 2004. Acoustic detection of dugong using automatic underwater sound monitoring systems : AUSOMS-D. Pages 64-68. The International Symposium on SEASTAR2000 and Bio-logging Science (The 5th SEASTAR2000 Workshop), Kyoto University.
- Ichikawa K, Tsutsumi C, Akamatsu T, Arai N, Shinke T, Hara T, Adulyanukosol K. 2009.
 Preliminary estimation of detection rate of dugong acoustical observation. Pages 47-50. Proceedings of the 4th International Symposium on SEASTAR2000 and Asian Bio-logging Science (The 8th SEASTAR2000 workshop), Kyoto University.
- Ichikawa K, Akamatsu T, Shinke T, Arai N, Adulyanukosol K. 2012. Clumped distribution of vocalising dugongs (*Dugong dugon*) monitored by passive acoustic and visual observations in Thai waters. Acoustics 2012 Fremantle, Fremantle, Australia.
- IPCC. 2019. Summary for Policy Makers in Shukla PR, et al., editors. Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems Intergovernmental Panel on Climate Change.

- Irvine AB. 1983. Manatee metabolism and its influence on distribution in Florida. Biological Conservation **25**:315-334.
- IUCN. 2021. The IUCN Red List of Threatened Species, Version 2021-3. https://www.iucnredlist.org. Accessed 09 December, 2021.
- IWC. 1990. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters in Hammond PS, Mizroch SA, and Donovan GP, editors. Symposium and Workshop on Individual Recognition and the Estimation of Cetacean Population Parameters. International Whaling Commission, Cambridge.
- Jaine FRA, Rohner CA, Weeks SJ, Couturier LIE, Bennett MB, Townsend KA, Richardson AJ. 2014. Movements and habitat use of reef manta rays off eastern Australia: offshore excursions, deep diving and eddy affinity revealed by satellite telemetry. Marine Ecology Progress Series **510**:73-86.
- James MC, Andrea Ottensmeyer C, Myers RA. 2005. Identification of high-use habitat and threats to leatherback sea turtles in northern waters: New directions for conservation. Ecology Letters **8**:195-201.
- Jiménez-López ME, Palacios DM, Jaramillo Legorreta A, Urbán R J, Mate BR. 2019. Fin whale movements in the Gulf of California, Mexico, from satellite telemetry. PLoS One **14**.
- Johnston DW, Read AJ. 2007. Flow-field observations of a tidally driven island wake used by marine mammals in the Bay of Fundy, Canada. Fisheries Oceanography **16**:422-435.
- Kastelein RA, Mosterd P, van Santen B, Hagedoorn M, de Haan D. 2002. Underwater audiogram of a Pacific walrus (*Odobenus rosmarus divergens*) measured with narrow-band frequency-modulated signals. The Journal of the Acoustical Society of America **112**:2173-2182.
- Kastelein RA, Hagedoorn M, Au WWL, de Haan D. 2003. Audiogram of a striped dolphin (*Stenella coeruleoalba*). The Journal of the Acoustical Society of America **113**:1130-1137.
- Keith-Diagne LW, Barlas ME, Reid JP, Hodgson AJ, Marsh H. 2022. Chapter 3: Diving and foraging behaviors in Marsh H, editor. Ethology and Behavioral Ecology of Sirenia. Springer.
- Ketten DR. 2000. Cetacean ears in Au WWL, Popper AN, and Fay RR, editors. Hearing by whales and dolphins. Springer-Verlag, New York.
- Klinesmith DE, McCuen RH, Albrecht P. 2007. Effect of Environmental Conditions on Corrosion Rates. Journal of Materials in Civil Engineering 19:121–129.
- Knip DM, Heupel MR, Simpfendorfer CA. 2012a. Mortality rates for two shark species occupying a shared coastal environment. Fisheries Research **125–126**:184-189.
- Knip DM, Heupel MR, Simpfendorfer CA. 2012b. Evaluating marine protected areas for the conservation of tropical coastal sharks. Biological Conservation **148**:200-209.
- Kuhn CE, Costa DP. 2014. Interannual variation in the at-sea behavior of California sea lions (*Zalophus californianus*). Marine Mammal Science **30**:1297-1319.
- Laist DW, Reynolds JE. 2005a. Florida manatees, warm-water refuges, and an uncertain future. Coastal Management **33**:279-295.
- Laist DW, Reynolds JE. 2005b. Influence of power plants and other warm-water refuges on Florida manatees. Marine Mammal Science **21**:739-764.
- Laist DW, Shaw C. 2006. Preliminary evidence that boat speed restrictions reduce deaths of Florida manatees. Marine Mammal Science **22**:472-479.

- Langtimm CA, Beck CA, Edwards HH, Fick-Child KJ, Ackerman BB, Barton SL, Hartley WC. 2004. Survival estimates for Florida manatees from the photo-identification of individuals. Marine Mammal Science **20**:438-463.
- Lanyon JM. 2003. Distribution and abundance of dugongs in Moreton Bay, Queensland, Australia. Wildlife Research **30**:397-409.
- Lanyon JM, Sneath HL, Kirkwood JM, Slade RW. 2002. Establishing a mark-recapture program for dugongs In Moreton Bay, Southeast Queensland. Australian Mammalogy **24**:51-56.
- Lanyon JM, Johns T, Sneath HL. 2005. Year-round presence of dugongs in Pumicestone Passage, south-east Queensland, examined in relation to water temperature and seagrass distribution. Wildlife Research **32**:361-368.
- Lanyon JM, Newgrain K, Alli TSS. 2006. Estimation of water turnover rate in captive dugongs (*Dugong dugon*). Aquatic Mammals **32**:103-108.
- Lanyon JM, Sneath HL, Long T, Bonde RK. 2010. Physiological response of wild dugongs (*Dugong dugon*) to out-of-water sampling for health assessment. Aquatic Mammals **36**:46-58.
- Lanyon JM, Horgan P, Booth D, Nichols C. 2015. Reply to the Comment of Owen et al. on "Insulative capacity of the integument of the dugong (*Dugong dugon*): Thermal conductivity, conductance and resistance measured by in vitro heat flux" by Horgan, Booth, Nichols and Lanyon (2014). Marine Biology **162**:1147-1149.
- Lanyon J, Noad M, Meager J. 2019a. Chapter 5: Ecology of the marine mammals of Moreton Bay. Pages 415-430 in Tibbetts IR, Rothlisberg PC, Neil DT, Homburg TA, Brewer DT, and Arthington AH, editors. Moreton Bay *Quandamooka* & Catchment: *past, present, and future*. The Moreton Bay Foundation, Brisbane, Australia.
- Lanyon JM, Noad M, Meager J. 2019b. Chapter 6 Management of Megafauna in Estuaries and Coastal Waters: Moreton Bay as a Case Study. Pages 87-101 in Wolanski E, Day JW, Elliott M, and Ramachandran R, editors. Coasts and Estuaries. Elsevier.
- Lanyon JM, Athousis C, Sneath HL, Burgess EA. 2021. Body scarring as an indicator of social function of dugong (Dugong dugon) tusks. Marine Mammal Science **37**: 962-981.
- Laplanche C, Marques TA, Thomas L. 2015. Tracking marine mammals in 3D using electronic tag data. Methods in Ecology and Evolution **6**:987-996.
- Lascelles B, Di Sciara, GN, Agardy T, Cuttelod A, Eckert S, Glowka L, Hoyt E, Llewellyn F, Louzao M, Ridoux V, Tetley MJ. 2014. Migratory marine species: their status, threats and conservation management needs. Aquatic Conservation: Marine and Freshwater Ecosystems 24:111-127.
- Lee KA, Huveneers C, Duong T, Harcourt RG. 2017. The ocean has depth: two- versus three-dimensional space use estimators in a demersal reef fish. Marine Ecology Progress Series **572**:223-241.
- Lee Long WJ, Coles RG, McKenzie LJ. 1996. Deepwater seagrasses in northeastern Australia – how deep, how meaningful? Pages 41–50 in Kuo J, Phillips RC, Walker DI, and Kirkman H, editors. Seagrass Biology: Proceedings of an International Workshop, University of Western Australia, Perth.
- Levin SA. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943.
- Lidgard DC, Bowen WD, Iverson SJ. 2020. Sex-differences in fine-scale home-range use in an upper-trophic level marine predator. Movement Ecology **8**:11-11.
- Limpus CJ. 1992. Estimation of tag loss in marine turtle research. Wildlife Research **19**:457-469.

- Lipscombe, RS, Spaet, JLY, Scott, A, Lam, CH, Brand, CP, & Butcher, PA. 2020. Habitat use and movement patterns of tiger sharks (*Galeocerdo cuvier*) in eastern Australian waters. ICES Journal of Marine Science, 77(7-8), 3127-3137.
- Luczkovich JJ, Sprague MW, Krahforst CS, Corbett DR, Walsh JP. 2012. Passive acoustics monitoring as part of integrated ocean observing systems. The Journal of the Acoustical Society of America **132**:1915-1915.
- Lusseau D. 2005. Residency pattern of bottlenose dolphins *Tursiops spp*. in Milford Sound, New Zealand, is related to boat traffic. Marine Ecology Progress series (Halstenbek) **295**:265-272.
- Lyons MB, Roelfsema CM, Phinn SR. 2013. Towards understanding temporal and spatial dynamics of seagrass landscapes using time-series remote sensing. Estuarine, coastal and shelf science **120**:42-53.
- MacLeod M, Arp HPH, Tekman MB, Jahnke A. 2021. The global threat from plastic pollution. Science 373:61–65
- Maitland RN, Lawler IR, Sheppard JK. 2006. Assessing the risk of boat strike on dugongs (*Dugong dugon*) at Burrum Heads, Queensland, Australia. Pacific Conservation Biology **12**:321-326.
- Malone TC. 2003. The coastal component of the U.S. Integrated Ocean Observing System. Environmental Monitoring and Assessment **81**:51-62.
- Marsh H. 2000. Evaluating mangement intitiatives aimed at reducing the mortality of dugongs in gill and mesh nets in the Great Barrier Reef World Heritage Area. Marine Mammal Science **16**:684-694.
- Marsh H. 2008. Dugong: *Dugong dugon*. Pages 332-335 in Perrin WF, Würsig B, and Thewissen JGM, editors. Encyclopedia of Marine Mammals (Second Edition). Academic Press, London.
- Marsh H. 2022. Dugong in Australia. Error! Hyperlink reference not valid. In Trebilco R, Fischer M, Hunter C, Hobday AJ, Thomas L, Evans K (2021). Marine. In: *Australia state of the environment 2021*, Australian Government Department of Agriculture, Water and the Environment, Canberra, In Press. Marsh H, Kwan D. 2008. Temporal variability in the life history and reproductive biology of female dugongs in Torres Strait: The likely role of sea grass dieback. Continental Shelf Research **28**:2152-2159.
- Marsh H, Rathbun GB. 1990. Development and application of conventional and satellite radio tracking techniqes for studying dugong movements and habitat use. Australian Wildlife Research **17**:83-100.
- Marsh H, Sinclair D. 1989. An experimental evaluation of dugong and sea turtle aerial survey techniques. Wildlife Research **16**:639-650.
- Marsh H, Sobtzick S. 2015. *Dugong dugon. The IUCN Red List of Threatened Species* 2015. e.T6909A43792211. http://dx.doi.org/10.2305/IUCN.UK.2015-
 - 4.RLTS.T6909A43792211.en. Downloaded on 02 November, 2018.
- Marsh H, Gardner BR, Heinsohn GE. 1981. Present-day hunting and distribution of dugongs in the Wellesley Islands (Queensland): Implications for conservation. Biological Conservation **19**:255-267.
- Marsh H, Harris ANM, Lawler IR. 1997. The sustainability of the indigenous dugong fishery in Torres Strait, Australia/Papua New Guinea. Oceanographic Literature Review **45**:1062-1063.
- Marsh H, Eros C, Corkeron P, Breen B. 1999. A conservation strategy for dugongs: implications of Australian research. Marine and Freshwater Research **50**:979-990.

- Marsh H, De'ath G, Gribble N, Lane B. 2000. Four decades of decline in dugong numbers off the urban coast of Queensland: Evidence from the Queensland Shark Control Program. Townsville, Queensland.
- Marsh H, Penrose H, Eros C, Hugues J. 2002. Dugong: Status Report and Action Plans for Countries and Territories.
- Marsh H, De'ath G, Gribble N, Lane B. 2005. Historical marine population estimates: triggers or targets for conservation? The dugong case study. Ecological Applications **15**:481-492.
- Marsh H, O'Shea TJ, Reynolds III JE 2011. Ecology and conservation of the Sirena: Dugongs and manatees. . Cambridge University Press, New York.
- Marsh H, Grech A, McMahon K. 2018. Dugongs: Seagrass Community Specialists. Pages 629-661 in Larkum AWD, Kendrick GA, and Ralph PJ, editors. Chapter 24: Seagrasses of Australia: Structure, Ecology and Conservation. Springer International Publishing AG, Switzerland.
- Marsh H, Hagihara R, Hodgson A, Rankin R, Sobtzick S. 2019. *Monitoring dugongs within the Reef 2050 Integrated Monitoring and Reporting Program: final report of the Dugong Team in the Megafauna Expert Group*. Townsville, Queensland.
- Marsh H, Albouy C, Arraut E, Castelblanco-Martínez DN, Collier C, Edward H, James C, Keith–Diagne L. 2022. Chapter 8: How might climate change affect the ethology and behavioral ecology of dugongs and manatees? in Marsh H, editor. Ethology and Behavioral Ecology of Sirenia. Springer.
- Marshall CDM, Sarko DKS, Reep RLR. 2022. Chapter 2: Morphological and sensory innovations for an aquatic lifestyle in Marsh H, editor. Ethology and Behavioral Ecology of Sirenia. Springer.
- Martin KJ, Alessi SC, Gaspard JC, Tucker AD, Bauer GB, Mann DA. 2012. Underwater hearing in the loggerhead turtle (*Caretta caretta*): a comparison of behavioral and auditory evoked potential audiograms. The Journal of Experimental Biology **215**:3001-3009.
- Matthiopoulos J. 2003. The use of space by animals as a function of accessibility and preference. Ecological Modelling **159**:239-268.
- Mazzoldi, C, Bearzi, G, Brito, C, Carvalho, I, Desiderà, E, Endrizzi, L, Freitas, L, Giacomello, E, Giovos, I, Guidetti, P, Ressurreição, A, Tull, M, MacDiarmid, A. 2019. From sea monsters to charismatic megafauna: Changes in perception and use of large marine animals. PLOS ONE 14:e0226810.
- McConnell BJ, Chambers C, Fedak MA. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarctic Science **4**:393-398.
- McKenzie LJ. 2014. Composite of coastal seagrass meadows in Queensland, Australia -November 1984 to June 2010. doi:10.1594/PANGAEA.826368. Supplement to: McKenzie, Len J; Yoshida, Rudolf L; Grech, Alana; Coles, Robert (2010): Queensland seagrasses. Status 2010 - Torres Strait and East Coast. Fisheries Queensland (DEEDI), Cairns, 6 pp, hdl:10013/epic.42902.d001.
- McKinzie MK, Jarvis ET, Lowe CG. 2014. Fine-scale horizontal and vertical movement of barred sand bass, Paralabrax nebulifer, during spawning and non-spawning seasons. Fisheries Research **150**:66-75.
- McMahon K. 2005. Recovery of subtropical seagrasses from natural disturbance. PhD thesis, Centre for Marine Studies. University of Queensland, Brisbane, Queensland.

- Meager JJ. 2016. Marine wildlife stranding and mortality database annual report 2013-2015: dugong. Queensland, Australia.
- Meager JJ, Limpus C. 2012. Marine wildlife stranding and mortality database annual report 2011: dugong. Queensland, Australia.
- Meager JJ, Limpus CJ, Sumpton W. 2013. A review of the population dynamics of dugongs in southern Queensland: 1830-2012. Brisbane.
- Millspaugh JJ, Nielson RM, McDonald L, Marzluff JM, Gitzen RA, Rittenhouse CD, Hubbard MW, Sheriff SL. 2006. Analysis of resource selection using utilization distributions. The Journal of Wildlife Management **70**:384-395.
- Moore SE, Reeves RR. 2018. Tracking arctic marine mammal resilience in an era of rapid ecosystem alteration. PLoS Biology **16**.
- Morrison ML, Marcot BG, Mannan RW 2006. Wildlife-habitat relationships: concepts and applications. Island Press, Washington, D.C.
- Nachtigall PE, Mooney TA, Taylor KA, Miller LA, Rasmussen MH, Akamatsu T, Teilmann J, Linnenschmidt M, Vikingsson GA. 2008. Shipboard measurements of the hearing of the white-beaked dolphin *Lagenorhynchus albirostris*. Journal of Experimental Biology **211**:642-647.
- Nakaoka M, Mukai H, Chunhabundit S. 2002. Impacts of dugong foraging on benthic animal communities in a Thailand sea grass bed. Ecological Research **17**:625-638.
- National Geographic. 2004. Dugongs. Crittercam documentary, produced by National Geographic. https://video.alexanderstreet.com/watch/dugongs.Mazzoldi C et al. 2019. From sea monsters to charismatic megafauna: Changes in perception and use of large marine animals. PLOS ONE 14:e0226810.
- Nelms S et al. 2021. Marine mammal conservation: over the horizon. Endangered Species Research **44**:291–325.
- Orgeret F, Thiebault A, Kovacs KM, Lydersen C, Hindell MA, Thompson SA, Sydeman WJ, Pistorius PA. 2022. Climate change impacts on seabirds and marine mammals: The importance of study duration, thermal tolerance and generation time. Ecology Letters **25**:218–239.
- Nowacek SM, Nowacek DP, Johnson MP, Wells RS. 2001. Manatee behavioral responses to vessel approaches: results of digital acoustic data logger tagging of manatees in Belize. Mote Technical Report 847, Sarasota, FL. 57 pp.
- O'Brien KR, Waycott M, Maxwell P, Kendrick GA, Udy JW, Ferguson AJP, Kilminster K, Scanes P, McKenzie LJ, McMahon K, Adams MP, Samper-Villarreal J, Collier C, Lyons M, Mumby PJ, Radke L, Christianen MJA, Dennison WC. 2018. Seagrass ecosystem trajectory depends on the relative timescales of resistance, recovery and disturbance. Marine Pollution Bulletin **134**:166-176.
- O'Connell CP, Andreotti S, Rutzen M, Meÿer M, Matthee CA. 2018. Testing the exclusion capabilities and durability of the Sharksafe Barrier to determine its viability as an eco-friendly alternative to current shark culling methodologies. Aquatic Conservation **28**:252-258.
- Orgeret F, Thiebault A, Kovacs KM, Lydersen C, Hindell MA, Thompson SA, Sydeman WJ, Pistorius PA. 2022. Climate change impacts on seabirds and marine mammals: The importance of study duration, thermal tolerance and generation time. Ecology Letters 25:218–239.
- O'Shea TJ, Beck CA, Bonde RK, Kochman HI, Odell DK. 1985. An analysis of manatee mortality patterns in Florida, 1976-81. The Journal of Wildlife Management **49**:1-11.

- Owen HC, Flint M, Limpus CJ, Palmieri C, Mills PC. 2013. Evidence of sirenian cold stress syndrome in dugongs *Dugong dugon* from southeast Queensland, Australia. Diseases of Aquatic Organisms **103**:1-7.
- Owen HC, Flint M, Limpus C, Palmieri C, Mills PC. 2015. Comment on "Insulative capacity of the integument of the dugong (*Dugong dugon*): Thermal conductivity, conductance and resistance measured by in vitro heat flux" by Horgan, Booth, Nichols and Lanyon (2014).
- Pabst DA, Rommel SA, McLellan WA. 1999. The functional morphology of marine mammals. Pages 15-72 in Reynolds III JE, and Rommel SA, editors. Biology of Marine Mammals. Smithsonian Institution Presss, Washington.
- Pantus FJ, Dennison WC. 2005. Quantifying and evaluating ecosystem health: a case study from Moreton Bay, Australia. Environmental Management (New York) **36**:757-771.
- Parsons ECM. 2017. Impacts of Navy sonar on whales and dolphins: now beyond a smoking gun? Frontiers in Marine Science.
- Parsons MJG, Holley D, McCauley RD. 2013. Source levels of dugong (Dugong dugon) vocalizations recorded in Shark Bay. The Journal of the Acoustical Society of America 134:2582–2588.
- Pendoley KL, Schofield G, Whittock PA, Ierodiaconou D, Hays GC. 2014. Protected species use of a coastal marine migratory corridor connecting marine protected areas. Marine Biology **161**:1455-1466.
- Pennisi E. 2005. Satellite tracking catches sharks on the move. Science **310**:32-33.
- Pillans RD, Bearham D, Boomer A, Downie R, Patterson TA, Thomson DP, Babcock RC. 2014. Multi-year observations reveal variability in residence of a tropical demersal fish, *Lethrinus nebulosus*: Implications for spatial management. PLoS ONE 9:e105507.
- Ponganis PJ. 2015. Thermoregulation. Pages 145-161. Diving physiology of marine mammals and seabirds. Cambridge University Press.
- Ponnampalam LS, Keith-Diagne L, Marmontel M, Marshall C, Reep RL, Powell J, Marsh H. 2022. Chapter 7: Historical and current interactions with humans in Marsh H, editor. Ethology and Behavioral Ecology of Sirenia. Springer.
- Popov VV, Supin AY, Pletenko MG, Tarakanov MB, et al. 2007. Audiogram variability in normal bottlenose dolphins (*Tursiops truncatus*). Aquatic Mammals **33**:24-33.
- Preen A. 1989. Observations of mating hehaviour in dugongs (*Dugong dugon*). Marine Mammal Science **5**:382-387.
- Preen A. 1992. Interactions between dugongs and seagrasses in a subtropical environment. PhD Thesis. James Cook University, Townsville.
- Preen A. 1995a. Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. Marine Ecology Progress Series **124**:201-213.
- Preen A. 1995b. Diet of dugongs: Are they omnivores? Journal of Mammalogy 76:163-171.
- Preen A. 2004. Distribution, abundance and conservation status of dugongs and dolphins in the southern and western Arabian Gulf. Biological Conservation **118**:205-218.
- Preen A, Marsh H. 1995. Response of dugongs to large-scale loss of sea grass from Hervey Bay, Queensland, Australia. Oceanographic Literature Review **43**:507-519.
- QDAF. 2016. Queensland Department of Agriculture and Fisheries Shark Control Program, Available from https://www.daf.qld.gov.au/fisheries/services/shark-controlprogram/shark-control-equipment-and-locations (accessed 20 January 2016).

- QLD Dept of Agriculture and Fisheries. 2017. Queensland Sustainable Fisheries Strategy 2017-2027.
- QLD Dept of Agriculture and Fisheries. 2020. Queensland Government Department of Shark Control Program Gear Locations, Available from https://www.daf.qld.gov.au/business-priorities/fisheries/shark-control-program/sharkcontrol-equipment (accessed September 22 2021).
- Queiroz N, Humphries NE, Noble LR, Santos AM, Sims DW. 2012. Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. PLoS ONE **7(2)**: e32374. doi:32310.31371/journal.pone.0032374.
- R Development Core Team. 2018. R: A Language and Environment for Statistical Computing in R Foundation for Statistical Computing, editor, Vienna, Austria.
- Rappucci GM, Keith EO, Hardigan PC. 2012. Tidal cycle effects on the occurrence of the Florida manatee (*Trichechus manatus latirostris*) at the Port Everglades Power Plant. Aquatic Mammals **38**:31-42.
- Rasheed MA, McKenna SA, Carter AB, Coles RG. 2014. Contrasting recovery of shallow and deep water seagrass communities following climate associated losses in tropical north Queensland, Australia. Marine Pollution Bulletin **83**:491-499.
- Rayment W, Dawson S, Slooten E. 2010. Seasonal changes in distribution of Hector's dolphin at Banks Peninsula, New Zealand: Implications for protected area design. Aquatic Conservation: Marine and Freshwater Ecosystems **20**:106-116.
- Raynor R. 2010. The US Integrated Ocean Observing system in a global context. Marine Technology Society Journal **44**:26-31.
- Read AJ. 2008. The looming crisis: Interactions between marine mammals and fisheries. Journal of Mammalogy **89**:541-548.
- Read AJ, Drinker P, Northridge S. 2005. Bycatch of marine mammals in U.S. and global fisheries. Conservation Biology **20**:163-169.
- Reeves RR, Berggren P, Crespo EA, Gales N, Northridge SP, di Sciara GN, Perrin WF, Read AJ, Rogan E, Smith BD, Van Waerebeek K. 2005. Global priorities for reduction of cetacean bycatch. Washington D.C. Available from http://cetaceanbycatch.org/pr.2005.06.09.cfm (accessed April 5, 2015).
- Reichmuth C, Holt MM, Mulsow J, Sills JM, Southall BL. 2013. Comparative assessment of amphibious hearing in pinnipeds. Journal of Comparative Physiology A **199**:491-507.
- Reid JP, Butler SM, Easton DE, Deutsch CJ. 2001. Fifteen years of success in tracking manatees with the Argos system: An overview of programs and techniques.
 Proceedings of the Argos International Users Conference, 23-25 April 2001, Annapolis, Maryland USA.
- Reijnders PJH, Aguilar A, Borrell A. 2009. Pollution and Marine Mammals. Pages 890-898. Elsevier Inc.
- Reubens J, Verhelst P, van der Knaap I, Wydooghe B, Milotic T, Deneudt K, Hernandez F, Pauwels I. 2019. The need for aquatic tracking networks: the Permanent Belgian Acoustic Receiver Network. Animal Biotelemetry **7**.
- Reyier EA, Franks BR, Chapman DD, Scheidt DM, Stolen ED, Gruber SH. 2014. Regional-Scale Migrations and Habitat Use of Juvenile Lemon Sharks (Negaprion brevirostris) in the US South Atlantic. PLoS One **9**.
- Roberts DT, Udyawer V, Franklin C, Dwyer RG, Campbell HA. 2017. Using an acoustic telemetry array to assess fish volumetric space use: a case study on impoundments, hypoxia and an air-breathing species (*Neoceratodus forsteri*). Marine and Freshwater Research **68**:1532-1543.

- Roelfsema CM, Phinn SR, Udy N, Maxwell P. 2009. An integrated field and remote sensing approach for mapping seagrass cover, Moreton Bay, Australia. Journal of Spatial Science **54**:45-62.
- Roelfsema CM, Lyons M, Kovacs EM, Maxwell P, Saunders MI, Samper-Villarreal J, Phinn SR. 2014. Multi-temporal mapping of seagrass cover, species and biomass: a semiautomated object based image analysis approach. Remote Sensing of Environment 150:172-187.
- Rojas-Bracho L, Reeves RR, Jaramillo-Legorreta A. 2006. Conservation of the vaquita *Phocoena sinus*. Mammal Review **36**:179-216.
- Ropert-Coudert Y, Kato A, Chiaradia A. 2009. Impact of small-scale environmental perturbations on local marine food resources: A case study of a predator, the little penguin. Proceedings: Biological Sciences **276**:4105-4109.
- Rutz C, Hays GC. 2009. New frontiers in biologging science. Biology Letters (The Royal Society) **5**:289-292.
- Rycyk AM, Deutsch CJ, Barlas ME, Hardy SK, Frisch K, Leone EH, Nowacek DP. 2018. Manatee behavioral response to boats. Marine Mammal Science **34**:924-962.
- Sattelberger DC, Kleen JM, Allen A-C, Flamm RO. 2017. Seasonal warm-water refuge and sanctuary usage by the Florida manatee (*Trichechus manatus latirostris*) in Kings Bay, Citrus County, Florida. GIScience & Remote Sensing **54**:1-19.
- Sayigh LS, Esch HC, Wells RS, Janik VM. 2007. Facts about signature whistles of bottlenose dolphins, *Tursiops truncatus*. Animal Behaviour **74**:1631-1642.
- Schoonyan A, Kraus RT, Faust MD, Vandergoot CS, Cooke SJ, Cook HA, Hayden TA, Krueger CC. 2017. Estimating incision healing rate for surgically implanted acoustic transmitters from recaptured fish. Animal Biotelemetry **5**.
- Schrope M. 2002. Whale deaths caused by US Navy's sonar. Nature 415:106.
- Seaman DE, Powell RA. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology **77**:2075-2085.
- Seddon JM, Ovenden JR, Sneath HL, Broderick D, Dudgeon CL, Lanyon JM. 2014. Fine scale population structure of dugongs (*Dugong dugon*) implies low gene flow along the southern Queensland coastline. Conservation Genetics **15**:1381-1392.
- Sheppard J. 2008. The spatial ecology of dugongs: applications to conservation management. PhD thesis; School of Earth and Environmental Sciences. James Cook University, Townsville, Queensland.
- Sheppard JK, Preen AR, Marsh H, Lawler IR, Whiting SD, Jones RE. 2006. Movement heterogeneity of dugongs, *Dugong dugon* (Müller), over large spatial scales. Journal of Experimental Marine Biology and Ecology **334**:64-83.
- Sheppard JK, Jones RE, Marsh H, Lawler IR. 2009. Effects of tidal and diel cycles on dugong habitat use. Journal of Wildlife Management **73**:45-59.
- Sheppard JK, Marsh H, Jones RE, Lawler IR. 2010. Dugong habitat use in relation to seagrass nutrients, tides, and diel cycles. Marine Mammal Science **26**:855-879.
- Shiffman D. 2014. Keeping swimmers safe without killing sharks is a revolution in shark control. Animal Conservation **17**:299-300.
- Shillinger GL, et al. 2008. Persistent leatherback turtle migrations present opportunities for conservation. PLoS Biology **6**:e171.
- Shimada T, Limpus C, Jones R, Hazel J, Groom R, Hamann M. 2016. Sea turtles return home after intentional displacement from coastal foraging areas. Marine Biology **163**:1.

- Shipley ON, Brownscombe JW, Danylchuk AJ, Cooke SJ, Owen ROS, Brooks EJ. 2018. Fine-scale movement and activity patterns of Caribbean reef sharks (*Carcharhinus perezi*) in the Bahamas. Environmental Biology of Fishes **101**:1097-1104.
- Shorter KA, Shao Y, Ojeda L, Barton K, Rocho-Levine J, Hoop J, Moore M. 2017. A day in the life of a dolphin: using bio-logging tags for improved animal health and well-being. Marine Mammal Science 33:785-802.
- Simmonds MP, Eliott WJ. 2009. Climate change and cetaceans: concerns and recent developments. Journal of the Marine Biological Association of the United Kingdom **89**:203-210.
- Simpfendorfer CA, Heupel MR, Hueter RE. 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Canadian Journal of Fisheries and Aquatic Sciences **59**:23-32.
- Simpfendorfer CA, Heupel MR, Collins AB. 2008. Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. Canadian Journal of Fisheries and Aquatic Sciences **65**:482-492.
- Simpfendorfer CA, Heupel MR, Moland EM. 2012. Three-dimensional kernel utilization distributions improve estimates of space use in aquatic animals. Canadian Journal of Fisheries and Aquatic Sciences **69**:565-572.
- Simpkins MA, Kelly BP, Wartzok D. 2001. Three-dimensional analysis of search behaviour by ringed seals. Animal Behaviour **62**:67-72.
- Skilleter GA, Cameron B, Zharikov Y, Boland D, McPhee DP. 2006. Effects of physical disturbance on infaunal and epifaunal assemblages in subtropical, intertidal seagrass beds. Marine Ecology Progress Series **308**:61-78.
- Slone DH, Reid JP, Kenworthy WJ. 2013. Mapping spatial resources with GPS animal telemetry: Foraging manatees locate seagrass beds in the Ten Thousand Islands, Florida, USA. Marine Ecology Progress Series **476**:285-299.
- Slooten E, Dawson SM. 2010. Assessing the effectiveness of conservation management decisions: likely effects of new protection measures for Hector's dolphin (*Cephalorhynchus hectori*). Aquatic Conservation: Marine and Freshwater Ecosystems **20**:334-347.
- Sobtzick S, Hagihara R, Grech A, Marsh H. 2012. Aerial survey of the urban coast of Queensland to evaluate the response of the dugong population to the widespread effects of the extreme weather events of the summer of 2010-11.
- Sobtzick S, Cleguer C, Hagihara R, Marsh H. 2017. Distribution and abundance of dugong and large marine turtles in Moreton Bay, Hervey Bay and the southern Great Barrier Reef: A report to the Great Barrier Reef Marine Park Authority. University JC, Publication 17/21, James Cook University, Townsville.
- Sousa A, Alves F, Dinis A, Bentz J, Cruz MJ, Nunes JP. 2019. How vulnerable are cetaceans to climate change? Developing and testing a new index. Ecological Indicators **98**:9-18.
- Southall BL, Schusterman RJ, Kastak D. 2003. Acoustic communication ranges for nothern elephant seals (*Mirounga angustirostris*). Aquatic Mammals **29**:202-213.
- Southard J. 2021. Chapter 4: Flow in channels. in Introduction to Fluid Motions and Sediment Transport. Massachusetts Institute of Technology.
- Sprogis KR. 2008. Small-scale habitat use and movements of dugongs (*Dugong dugon*) with respect to tides, foraging time and vessel traffic on the eastern banks areas of Moreton Bay. School of Integrative Biology. Honours thesis. Bachelor of Marine Studies. University of Queensland, Brisbane.

- Sprogis KR, Raudino HC, Rankin R, MacLeod CD, Bejder L. 2016. Home range size of adult Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in a coastal and estuarine system is habitat and sex-specific. Marine Mammal Science **32**:287-308.
- Stirling I, Calvert W, Spencer C. 1987. Evidence of sterotyped underwater vocalizations of male Atlantic walruses (*Odobenus rosmarus rosmarus*). Canadian Journal of Zoology 65:2311-2321.
- Sumpton WD, Taylor SM, Gribble NA, McPherson G, Ham T. 2011. Gear selectivity of largemesh nets and drumlines used to catch sharks in the Queensland Shark Control Program. African Journal of Marine Science **33**:37-43.
- Sweatman JL, Layman CA, Fourqurean JW. 2017. Habitat fragmentation has some impacts on aspects of ecosystem functioning in a sub-tropical seagrass bed. Marine Environmental Research **126**:95-108.
- Szesciorka AR, Calambokidis J, Harvey JT. 2016. Testing tag attachments to increase the attachment duration of archival tags on baleen whales. Animal Biotelemetry 4:18.
- Takeshita R, Sullivan L, Smith C, Collier T, Hall A, Brosnan T, Rowles T, Schwacke L. 2017. The Deepwater Horizon oil spill marine mammal injury assessment. Endangered Species Research **33**:95-106.
- Taylor HA, Rasheed MA. 2011. Deepwater seagrass dynamics in the Torres Strait Dugong Sanctuary - Interim Report. March & November 2010. DEEDI Publication. Fisheries Queensland, Cairns, 21pp.
- Telonics Inc. USA. 2007. Telonics Data Converter Version 2.13. Telonics, Inc., Mesa Arizona USA.
- Tol SJ, Coles RG, Congdon BC. 2016. *Dugong dugon* feeding in tropical Australian seagrass meadows: implications for conservation planning. PeerJ.
- Tomkiewicz SM, Fuller MR, Kie JG, Bates KK. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. Philosophical Transactions of the Royal Society B **365**:2163-2176.
- Tracey JA, Sheppard J, Zhu J, Wei F, Swaisgood RR, Fisher RN. 2014. Movement-based estimation and visualization of space use in 3D for wildlife ecology and conservation. PLoS ONE **9**.
- Tubelli A, Zosuls A, Ketten D, Mountain D. 2012. Prediction of a Mysticete audiogram via finite element analysis of the middle ear. Pages 57-59 in Popper A, and Hawkins A, editors. The Effects of Noise on Aquatic Life. Springer New York.
- Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. Science (American Association for the Advancement of Science) **359**:466-469.
- Turnbull MB. 2007. Determination regarding including World Heritage Places in the National Heritage List in Resources MftEaW, editor. Commonwealth of Australia.
- Tyack PL. 2009. Human-generated sound and marine mammals. Physics today 62:39-44.
- Udyawer V, Simpfendorfer CA, Heupel MR. 2015. Diel patterns in three-dimensional use of space by sea snakes. Animal Biotelemetry **3**:29.
- Udyawer V, Groom RA, Griffiths A, Thums M. 2019. Quantifying dive behaviour and threedimensional activity space of dugongs in the Gulf of Carpentaria. Report prepared for The Department of Environment and Natural Resources. Australian Institute of Marine Science, Darwin NT. (22pp).
- UNESCO. 1981. Great Barrier Reef: Outstanding Universal Value.

- UNESCO. 2021. Australian Properties described on the World Heritage List 1976-2021, Available from https://whc.unesco.org/en/statesparties/au (accessed January 15, 2022).
- Vander Wal E, Rodgers AR. 2012. An individual-based quantitative approach for delineating core areas of animal space use. Ecological Modelling **224**:48-53.
- Vemco. 2012. V16-4H Transmitters. Vemco, Bedford, Nova Scotia Canada.
- Vemco. 2021. V16-4H Transmitters. Vemco, Bedford, Nova Scotia Canada.
- Vianna GMS, Meekan MG, Meeuwig JJ, Speed CW. 2013. Environmental influences on patterns of vertical movement and site fidelity of grey reef sharks (Carcharhinus amblyrhynchos) at aggregation sites. PloS One **8**:e60331-e60331.
- Wang W-J, Peng W-Q, Huai W-X, Katul GG, Liu X-B, Qu X-D, Dong F. 2019. Friction factor for turbulent open channel flow covered by vegetation. Scientific Reports **9**:5178.
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- Wartzok D, Ketten DR. 1999. Marine Mammal Sensory Systems in Reynolds III J, and Rommel S, editors. Biology of Marine Mammals. Smithsonian Institution Press.
- Waycott M, Longstaff BJ, Mellors J. 2005. Seagrass population dynamics and water quality in the Great Barrier Reef region: a review and future research directions. Marine Pollution Bulletin **51**:343-350.
- Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams SL. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences **106**:12377-12381.
- Welch DW, Melnychuk MC, Rechisky ER, Porter AD, Jacobs MC, Ladouceur A, McKinley RS, Jackson GD. 2009. Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a largescale acoustic telemetry array. Canadian Journal of Fisheries and Aquatic Sciences 66:736-750.
- Wells RS. 2009. Identification Methods. Pages 593-599 in Perrin WF, Würsig B, and Thewissen JGM, editors. Encyclopedia of Marine Mammals (Second Edition). Academic Press, London.
- Westphal MM. 2020. IMatch Software for Photo ID, Usingen Germany. Available from https://www.photools.com/imatch/ (accessed January 18 2022).
- Whiting SD. 2002. Rocky reefs provide foraging habitat For dugongs in the Darwin region of northern Australia. Australian Mammalogy **24**:147-150.
- Whiting SD. 2008. Movements and distribution of dugongs (*Dugong dugon*) in a macro-tidal environment in northern Australia. Australian Journal of Zoology **56**:215-222.
- Williams-Grove LJ, Szedlmayer ST. 2017. Depth preferences and three-dimensional movements of red snapper, Lutjanus campechanus, on an artificial reef in the northern Gulf of Mexico. Fisheries Research **190**:61-70.
- Wilson K, Littnan C, Read AJ. 2017. Movements and home ranges of monk seals in the main Hawaiian Islands. Marine Mammal Science **33**:1080-1096.
- Winn HE, Goodyear JD, Kenney RD, Petricig RO. 1995. Dive patterns of tagged right whales in the Great South Channel. Continental Shelf Research **15**:593-611.
- Wirsing AJ, Heithaus MR, Dill LM. 2007. Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. Animal Behaviour **74**:93-101.

- Wood SN 2017. Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC.
- Wooldridge SA. 2017. Preventable fine sediment export from the Burdekin River catchment reduces coastal seagrass abundance and increases dugong mortality within the Townsville region of the Great Barrier Reef, Australia. Marine Pollution Bulletin 114:671-678.
- York PH, Carter AB, Chartrand K, Sankey T, Wells L, Rasheed MA. 2015. Dynamics of a deep-water seagrass population on the Great Barrier Reef: annual occurrence and response to a major dredging program. Scientific Reports (Nature Publisher Group) 5:13167.
- Young PC, Kirkman H. 1975. The seagrass communities of Moreton Bay, Queensland. Aquatic Botany **1**:191-202.
- Zakowski K, Narozny M, Szocinski M, Darowicki K. 2014. Influence of water salinity on corrosion risk—the case of the southern Baltic Sea coast. Environmental Monitoring and Assessment 186:4871–4879.
- Zeh DR, Heupel MR, Limpus CJ, Hamann M, Fuentes MMPB, Babcock RC, Pillans RD, Townsend KA, Marsh H. 2015. Is acoustic tracking appropriate for air-breathing marine animals? Dugongs as a case study. Journal of Experimental Marine Biology and Ecology **464**:1-10.
- Zeh DR, Heupel MR, Hamann M, Limpus CJ, Marsh H. 2016. Quick Fix GPS technology highlights risk to marine animals moving between protected areas. Endangered Species Research **30**:37-44.
- Zeh DR, Heupel MR, Hamann M, Jones R, Limpus CJ, Marsh H. 2018. Evidence of behavioural thermoregulation by dugongs at the high latitude limit to their range in eastern Australia. Journal of Experimental Marine Biology and Ecology **508**:27-34.
- Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution **1**:3-14.

Appendix Chapter 3

Appendix 3.1: Tagging details for dugongs fitted with GPS and acoustic transmitters in 2012 and 2013.

The number of days indicate total monitoring period (i.e., date from first detection to last). During 2012 the acoustic array was removed for six months from December 2012.

							Total	Total	Max	
					Days	Days	data	data	distance	21 day
	Maturity		Size	Date	tracked	tracked	points	points	GPS	analysis
Tag ID	stage ¹	Sex	(cm)	tagged	GPS	Acoustic	GPS	Acoustic	(km)	period
QA30696	Adult	F	312	4-Sep-12	32	55	242	40	27.2	4-Sep to 25-Sep
QA30723	Adult	М	288	24-Jul-12	57	56	690	74	31.9	24-Jul to 14-Aug
QA30677	Juvenile	F	216	4-Sep-12	38	32	420	44	2.3	4-Sep to 25-Sep
QA30541	Juvenile	Μ	200	4-Sep-12	62	73	701	123	1.3	7-Sep to 28-Sep
QA30710	Adult	Μ	298	24-Aug-12	41	21	254	39	15.4	28-Aug to 14-Sep
QA30676	Juvenile	F	239	4-Sep-12	34	32	268	46	6.4	4-Sep to 25-Sep
QA30712	Subadult	Μ	248	24-Aug-12	23	27	210	41	7.3	28-Aug to 14-Sep
QA2685	Subadult	Μ	245	24-Aug-12	8	48	368	32	3	-
QA30694	Juvenile	F	209	4-Sep-12	55	54	459	107	21.9	4-Sep to 25-Sep
QA30709	Subadult	F	257	24-Aug-12	61	60	599	71	31.9	28-Aug to 14-Sep
QA18400	Adult	F	290	7-Dec-13	35	263	176	18	280	-
QA183913 2,3	Adult	Μ	286	7-Dec-13	3	262	14	153	0	-
QA333223 ^{2,3}	Subadult	F	253	7-Aug-13	6	265	30	203	18	-
No tag ²	Subadult	Μ	250	7-Aug-13	108	1	388	4	320	-
QA334003 ^{2,3}	Subadult	F	250	7-Aug-13	4	266	72	232	19.7	-
QA18399	Juvenile	Μ	239	7-Dec-13	32	140	850	277	29.4	12-Jul to 2-Aug
QA33313	Subadult	Μ	247	7-Aug-13	16	40	102	41	6.8	-
K88240	Adult	Μ	297	7-Aug-13	34	74	452	75	16.9	11-Jul to 1-Aug
T71561	Adult	Μ	279	7-Aug-13	80	121	554	131	3.1	8-Jul to 29-Jul
QA33315	Adult	Μ	285	7-Nov-13	38	105	301	31	1.4	11-Jul to 1-Aug
QA33314 ³	Adult	Μ	292	7-Nov-13	42	256	22	497	10.1	-
				mean	38.5	107.2	341.5	108.5	40.7	
				SD	26.0	94.6	241.0	115.7	87.1	
				median	35	60	301	71	15.4	

¹based on Lanyon et al. (2010) and Burgess et al. (2012).

²excluded from Moreton Bay Region analyses due to limited GPS tracking records.

³transmitter still active at the date of latest acoustic download, April 2014.

Appendix 3.2: Assumptions considered for tracking methods and scenarios: Tagging assumptions

- 10 dugongs tracked.
- GPS tracked animals assumed to transmit data for 3 months; acoustic- one year.
- Acoustic arrays have 30 receivers.
- Acoustic downloads every three months taking 5 days on water and requiring certified divers.
- Costs do not account for new GPS or acoustic battery changes (annual expense).

- Field gear not costed (safety, wetsuits, hats, etc.).
- The capital cost of the array is included as an equipment cost only for the sites without an
- existing array.

Scenario 1 (Moreton Bay trips)

- Assume personnel are local / no accommodation or travel cost.
- Assume local personnel used for acoustic data download and array establishment.
- Catching 9 people (2 skippers + 4 catchers + 1 veterinarian + 1 data recorder + 1 extra).
- 5 people (4 divers + 1 skipper) to set up array and download dat.
- 2 vessels for catching; one vessel to set up array and download data (assume JCU vessels.
- 5 days catching; 5 days establish array; 5 days download data.
- No plane charter.
- Array set up based on costs in Moreton Bay in May 2013 (prices and material may vary).

Scenario 2 (Townsville trips)

- Assume local personnel / no accommodation or travel cost.
- Catching 9 people (2 skippers + 4 catchers + 1 veterinarian + 1 data recorder + 1 extra).
- 5 people (4 divers + 1 skipper) to set up array and download data.
- 2 vessels for catching; one vessel to set up array and to download data (assume JCU vessels).
- 10 days catching; 5 days set array; 5 days download data.
- Plane charter is necessary to spot dugongs.
- Array set up based on costs in Moreton Bay in May 2013 (prices and material may vary).

Scenario 3 (Torres Strait trips)

- Assume personnel are from Townsville.
- Catching 9 people (4 catchers + 2 skippers + 1 Vet + 2 ranger/locals).
- 5 people (4 divers + 1 skipper) to set up array and download data.
- 3 vessels (1 JCU + 2 local boats).
- No in kind support from Torres Strait Regional Authority.

- 20 days catching; 5 days set array; 5 days download data.
- Assume out of the 20 days, in the water catching for only 10 days.
- No plane charter necessary.
- Array set up based on costs in Moreton Bay in May 2013 + 10% of costs to account for more expensive material in Torres Strait (prices and material may vary).
- Assumes gear sent to Torres Strait with JCU boat to reduce freight costs.

Appendix 3.3: Breakdown of costs associated with each tracking method and scenario



Eq: Equipment cost, Tr: Travel cost (catching only), Sa: Salary cost (catching only), Op: Operations cost

Breakdown of costs associated with each tracking method for each scenario: Scenario 1- easy catching and accessible location (e.g., Moreton Bay); Scenario 2 difficult catching and accessible location (e.g., Townsville); and Scenario 3 - difficult catching and remote location (e.g., Boigu, Torres Strait). Percentages relate to overall cost. The capital cost of the array is included as an equipment cost only for sites without an existing array.

Appendix Chapter 5

Appendix Table 5.1: A, B, C – Individual Depth and Space Use Compared

A. Mean Dep	th			Mean Depth per Individual				
Females (5)	Size	Start Yr-Mo	End Yr-Mo	No. of Months	Mean depth per month (m/mo)	Mean max depth /mo (m/mo)		
13006	262	2014-04	2014-08	5	-2.1	-9.7		
13010	285	2014-05	2014-08	4	-6.1	-11.9		
14240	257	2012-08	2012-10	3	-2.6	-14.5		
14244	253	2013-07	2014-12	6	-7.3	-19.9		
14248	250	2013-07	2014-04	10	-3.4	-15.4		
All	F =>	2012-08	2014-12	28	-4.3	-14.3		
				Range	-2.1 to -7.3	-9.7 to -19.9		
Males (6)								
13004	292	2014-04	2014-07	4	-2.5	-8.9		
14236	288	2012-07	2012-09	3	-1.7	-13.3		
14242	292	2013-07	2014-11	6	-2.9	-12.2		
14258	297	2013-07	2013-09	3	-3.0	-15.3		
14260	279	2013-07	2013-11	5	-3.0	-9.6		
14270	239	2013-07	2013-11	5	-3.3	-12.2		
All	M =>	2012-07	2014-11	26	-2.8	-11.9		
				Range	-1.7 to -3.3	8.9 to -15.3		
All (F + I	M) =>	2012-07	2014-12	54	-3.50	-13.00		

B. Mean Spa	ce Use	<u>e</u>			Mean Space Use per Individual					
		Start	End	No. of						
Females (5)	Size	Yr-Mo	Yr-Mo	Months	A50 (km²)	A95 (km²)	V50 (km³)	V95 (km ³)		
13006	262	2014-04	2014-07	4	9.1	126.5	0.02	0.8		
13010	285	2014-05	2014-06	2	6.5	82.9	0.06	0.6		
14240	257	2012-08	2012-10	3	2.9	62.9	0.02	0.4		
14244	253	2013-07	2014-11	6	9.6	66.5	0.05	0.8		
14248	250	2013-07	2014-04	6	10.0	82.5	0.03	0.8		
AI	F =>	2012-08	2014-11	35	8.9	78.5	0.04	0.7		
				Median =	9.1	82.5	0.03	0.8		
					2.9 to	62.9 to	0.02 to	0.4 to		
				Range =	10.0	126.5	0.06	0.8		
Males (6)										
13004	292	2014-04	2014-07	4	13.2	72.0	0.03	0.3		
14236	288	2012-07	2012-09	3	4.2	78.5	0.01	0.3		
14242	292	2013-07	2014-10	15	6.9	97.4	0.02	0.5		
14258	297	2013-07	2013-07	1	10.5	123.4	0.02	0.7		
14260	279	2013-07	2013-10	4	8.8	56.1	0.03	0.4		
14270	239	2013-07	2013-11	5	2.5	65.2	0.03	0.4		
All	M =>	2012-07	2014-10	32	7.1	83.1	0.02	0.5		
				Median =	7.8	75.3	0.02	0.4		
					2.5 to	56.1 to	0.01 to	0.3 to		
				Range =	13.2	123.4	0.03	0.8		
All (F +	M) =>	2012-07	2014-11	67	8.10	80.70	0.03	0.60		

C. Mean Sp	ace Us	e Overlap			Mean Space Use Overlap per Individual					
Females		Start	End	No. of Overlap	A50 (%)	A95 (%)	V50 (%)	V95 (%)		
(5)	Size	Yr-Mo	Yr-Mo	Months	Mean	Mean	Mean	Mean		
13006	262	2014-04	2014-07	3	8.7%	82.7%	1.0%	62.5%		
13010	285	2014-05	2014-06	1*	1.0%	88.6%	1.6%	50.4%		
14240	257	2012-08	2012-10	2	1.7%	9.9%	41.2%	20.7%		
14244	253	2013-07	2014-11	14	51.4%	62.8%	37.9%	58.4%		
14248	250	2013-07	2014-04	9	44.6%	65.1%	44.0%	72.0%		
А	ll F =>	2012-08	2014-11	29	39.7%	62.8%	35.0%	60.2%		
					1.0% to	9.9% to	1.0% to	20.7% to		
				Range	51.4%	8.6%	44.0%	72.0%		
				* Not a mea	an => only one monthly overlap					
Males (5)					·	-				
13004	292	2014-04	2014-07	3	20.7%	62.5%	1.9%	53.5%		
14236	288	2012-07	2012-09	2	1.8%	54.6%	16.3%	67.3%		
14242	292	2013-07	2014-10	13	52.2%	71.5%	47.9%	70.8%		
14260	279	2013-07	2013-10	3	0.4%	19.9%	2.3%	28.0%		
14270	239	2013-07	2013-11	4	26.0%	55.3%	60.5%	53.0%		
Α	II M =>	2012-07	2014-10	25	34.0%	60.3%	36.4%	60.4%		
					0.4% to	29.9% to	1.9% to	28.0% to		
				Range	52.2%	71.5%	60.5%	70.8%		
All (F +	· M) =>	2012-07	2014-11	54	37.0%	61.7%	35.6%	60.3%		

					-	Variation for data > 10 m				
ID	Sex	Season	n	Ν	рс (%)	Mean	Median	SD	Max	Min
14240_12	F	1-Spring	5	383	1.3%	15.4	15.2	3.2	18.8	10.6
14244_1314	F	1-Spring	139	840	16.5%	13.9	13.0	3.1	21.5	10.0
14248_1314	F	1-Spring	19	625	3.0%	11.4	11.2	1.0	13.5	10.2
14236_12	Μ	1-Spring	2	119	1.7%	18.7	-	-	18.8	18.7
14242_1314	Μ	1-Spring	2	2202	0.1%	11.0	-	-	18.8	15.2
14260_13	Μ	1-Spring	8	240	3.3%	11.6	11.7	0.5	12.4	10.9
14270_13	М	1-Spring	14	624	2.2%	10.8	10.7	0.8	12.9	10.0
14244 1314	F	2-Summer	234	1523	15.4%	15 1	15.6	37	24.9	24.9
14244_1314	F	2-Summer	57	1308	10.4%	15.1	14.3	۵.7 ۸ ع	25.0	10.2
14240_1014	1	2-Ourniner	57	1000	т.т /0	10.0	14.0	4.0	20.0	10.2
13006_14	F	3-Autumn	18	821	2.2%	14.1	13.3	2.8	19.3	10.2
13010_14	F	3-Autumn	35	142	24.6%	13.8	12.7	2.9	20.6	10.3
14244_1314	F	3-Autumn	88	635	13.9%	14.5	13.8	3.6	23.7	10.0
14248_1314	F	3-Autumn	27	517	5.2%	17.1	17.1	1.4	19.6	11.7
13004 14	N/	3 Autumn	2	3/18	0.6%	10.2			10.5	10.0
13004_14		2 Autumn	2 1	340 25	0.070	10.2	-	-	10.5	10.0
14242_1314	IVI	5-Autumn	I	20	4.0%	10.5	-	-	-	-
13010 14	F	4-Winter	1	39	2.6%	10.5	-	-	-	-
14244_1314	F	4-Winter	166	789	21.0%	16.0	16.1	2.9	22.0	10.0
14248_1314	F	4-Winter	4	280	1.4%	12.3	12.3	2.0	14.6	10.0
14026 10	Ν.4	4 Mintor	1	260	0.20/	11 0				
14230_12		4-Winter	1	500	0.370	11.0	-	-	-	-
14242_1314		4-vvinter	0	525 469	Z.1%	17.1	17.4	3.9	22.4	10.0
14258_13		4-vvinter	ŏ ⊿	168	4.8% 0.0%	10.3	0.01	3.0	20.0	12.3
14260_13	IVI	4-vvinter	1	400	0.2%	11.1	-	-	-	-
142/0_13	IVI	4-Winter	3	815	0.4%	12.9	11.8	3.4	16.7	10.2
n = number of records > 10 m										

Appendix Table 5.2: Individual Depth Variation by Season – 11 dugongs

N = total number of records

			Resid	ency Index	Attenda	_	
		Days			Number of		
		Tracked	Days	Residency	Consecutive	Attendance	Acoustic
ID	Sex	(Monitored)	Detected	Index	Days	Index	Detections
13006_14	F	84	57	0.679	14	0.167	822
13010_14	F	49	26	0.531	7	0.143	181
14240_12	F	61	38	0.623	10	0.164	433
14244_1314	F	265	194	0.732	33	0.125	3787
14248_1314	F	267	214	0.801	42	0.157	2730
13004_14	Μ	86	63	0.733	14	0.163	1007
14236_12	Μ	57	36	0.632	7	0.123	479
14242_1314	Μ	256	210	0.820	77	0.301	3101
14258_13	Μ	74	43	0.581	8	0.108	285
14260_13	Μ	121	74	0.612	14	0.116	706
14270_13	Μ	140	109	0.779	25	0.179	1439
			Median =	0.679	Median =	0.157	
			Range =	0.531 to 0.820	Range =	0.108 to 0.301	

Appendix Table 5.3: Residency and Attendance Indices
Appendix	Table	5.4: 2D	Activity	Space	Com	nparisons
				-		

			A50 (km²)		A95 (km²)			
Approx.		-			-		Days	
Latitude	Location (M or F)	M/F-n	Median	Range (km ²)	Median	Range (km ²)	Tracked	Source
-27° 14' S	Moreton Bay	F-5	9.12	2.89 to 10.01	82.46	62.89 to 126.48	48 to 153	This chapter
-27° 14' S	Moreton Bay	M-6	7.85	2.53 to 13.24	75.26	56.09 to 123.44	56 to 155	This chapter
-27° 15 S	Moreton Bay	F-5	5.60	2.9 to 6.8	22.50	16.7 to 46.5	21	Zeh et al. 2015
-27° 15 S	Moreton Bay	M-8	6.65	2.5 to 85	51.00	16.7 to 81.5	21	Zeh et al. 2015
-25° 12' S	Burrum Heads	-	-	-	26.3±12.4 ^A	-	15 to 551 ^B	Sheppard et al., 2006
-22° 25' S	Shoalwater Bay	F-4, M-1	18.7	2.6 to 21.3	49.5	264.3 to 1269.2	6 to 141	Gredzens et al., 2014
-22° 25' S	Shoalwater Bay	F-1	114.4	-	1444.6	-		Gredzens et al., 2014
-20° 54' S	New Caledonia	F-5	17.4	12.3 to 47.2	206.0	74.1 to 455.8	12 to 40	Cleguer et al., 2020
-20° 54' S	New Caledonia	M-4	3.1	1.0 to 5.0	29.2	12.4 to 82.1	16 to 192	Cleguer et al., 2020
-19.25 S	Cleveland Bay	2	3.3 ^{A,D}	1.3 to 7.0	11.8 ^{A,D}	5.2 to 23.1	63 to 483	Marsh and Rathbun, 1990
-18° 13' S	Hinchinbrook Island	-	-	-	82.6±17.9 ^A	-	15 to 551 ^B	Sheppard et al., 2006
-16°5' S	Borroloola	-	-	-	280.3±122.3 ^A	732.5	15 to 551 ^B	Sheppard et al., 2006
								Marsh and Rathbun,
-14. 50°S	Starcke River	M-2	4.45 ^{A,C}	1.9 to 7.0	15.55 ^{A,C}	8.0 to 23.1	32 to 94	1990
-10° 36' S	Torres Strait	F-3, M-3	112.6	168.5	1042.9	1004.9	7 to 79	Gredzens et al., 2014
-10° 36' S	Torres Strait	M-6	74.45	37.3 to 130.3	453.2	258.5 to 928.7		Cleguer et al., 2016
**********	Haruku Bay, Lease							
-0° 48' S	Islands, East Indonesia	F-3	2.70	0.18 to 12.67	24.01	20.22 to 127.89	41 to 285	De longh et al., 1998
	Haruku Bay, Lease							
-0° 48' S	Islands, East Indonesia	M-1	0.95	-	1.65	-	53	De longh et al., 1998
	Manatees - Chetumal							Castelblanco-Martínez
18.5 N	Bay, Mexico	F-3	26.14	662.66	267.79	4954.73	4 to 301	et al., 2013
	Manatees - Chetumal							Castelblanco-Martínez
18.5 N	Bay, Mexico	M-5	320.56	633.35	2,637.71	3063.38		et al., 2013

^A The value given is a mean
 ^B The number of days tracked covers Burrum Heads, Hinchinbrook Island, and Borroloola.

^C Guaranteed locations only

^D Guaranteed and non-guaranteed locations

Appendix Chapter 6





Appendix Figure 6.1: Water temperatures inside the Eastern Banks inside Moreton Bay and the oceanic waters immediately outside Moreton Bay during the periods between 2012 and 2014 when dugongs were tracked. Note that in all three years the range of temperature values inside the bay is substantially larger than the range outside. In particular, temperatures inside the bay drop much lower during Autumn and Winter but may be higher during spring. (Monitoring periods did not include summer.).

Appendix 6.1.1: Equations estimating acoustic temperature from sea surface temperature.

For all results below, Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

6.1.1 Both inside and outside the bay

```
acoustic.all = lm(acoustic ~ SST*IN.OUT*theYear, data=Temps)
anova(acoustic.all)
```

Analysis of Variance Table

Response: acoustic

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
SST	1	960.29	960.29	3167.2377	< 2.2e-16 ***
IN.OUT	1	13.21	13.21	43.5837	1.746e-10 ***
theYear	2	3.20	1.60	5.2717	0.005602 **
SST:IN.OUT	1	0.12	0.12	0.4047	0.525149
SST:theYear	2	6.18	3.09	10.1835	5.196e-05 ***
IN.OUT:theYear	2	0.13	0.07	0.2164	0.805495
SST:IN.OUT:theYear	2	0.81	0.40	1.3283	0.266425
Residuals	312	94.60	0.30		

6.1.2 Inside the bay only

acoustic.in = lm(acoustic ~ SST*theYear,

data=Temps[Temps\$IN.OUT=="IN",])

anova(acoustic.in)

Analysis of Variance Table

Response: acoustic

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
SST	1	749.36	749.36	2370.0697	< 2.2e-16 ***
theYear	2	4.65	2.33	7.3558	0.0007888 ***
SST:theYear	2	5.49	2.74	8.6799	0.0002275 ***
Residuals	247	78.1	0.32		

summary(acoustic.in)

Residuals:

Min	1Q	Median	3Q	Max
-2.7062	-0.3243	0.0005	0.2839	3.2245

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	2.47961	0.69287	3.579	0.000415 ***
SST	0.8864	0.0345	25.691	< 2e-16 ***
theYear2013	-1.96103	1.19095	-1.647	0.10091
theYear2014	-4.23003	0.94397	-4.481	1.14e-05 ***
SST:theYear2013	0.09461	0.06061	1.561	0.119807
SST:theYear2014	0.20166	0.04843	4.164	4.32e-05 ***

Residual standard error: 0.5623 on 247 degrees of freedom (67 observations deleted due to missingness) Multiple R-squared: 0.9068 Adjusted R-squared: 0.9049 F-statistic: 480.4 on 5 and 247 DF, p-value: < 2.2e-16

6.1.3 Outside the bay only

acoustic.out = lm(acoustic ~ SST*theYear,

```
data=Temps[Temps$IN.OUT=="OUT",])
```

anova(acoustic.out)

Analysis of Variance Table

Response: acoustic

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
SST	1	99.773	99.773	393.0136	<2e-16 ***
theYear	2	0.1	0.05	0.1962	0.8224
SST:theYear	2	0.164	0.082	0.323	0.7251
Residuals	65	16.501	0.254		

Residuals:

Min	1Q	Median	3Q	Max
-1.28651	-0.33	0.01129	0.37606	1.00122

Coefficients:

	Estimate S	Std. Error	t value	Pr(> t)
(Intercept)	-0.3146	1.05129	-0.299	0.766
SST	0.9935	0.04903	20.264	<2e-16 ***

Residual standard error: 0.4929 on 69 degrees of freedom (249 observations deleted due to missingness) Multiple R-squared: 0.8561, Adjusted R-squared: 0.8541 F-statistic: 410.6 on 1 and 69 DF, p-value: < 2.2e-16

Appendix 6.2: Models describing dugong behaviour

6.2.A.1 Factors associated with the probability on any monitored day of an outgoing trip from Moreton Bay through South Passage to oceanic waters – full dataset.

Logistic regression and mixed effects logistic regression with individual dugong as a random effect. Fixed effects included the difference in temperature between oceanic water and the inside of the bay, year, Quarter of the year, and the interaction between Quarter and the temperature difference. Other interaction terms are not estimable, because only Quarter 3 data were available in all years (Quarter 2 data were available only in 2014, and Quarter 4 data were available only in 2012.). Note also that because only one individual dugong was monitored in more than one year, this mixed-effects model is underpowered to detect differences between years, which were indicated in a logistic regression not including the random effect.

<u>6.2.A.1.1</u>

mod.glm = glm(p.trip ~ combined.diff*QTR+theYear, weight=active, family = "binomial", data=zeh.all) Anova(mod.glm)

Analysis of Deviance Table (Type II tests)

Response: p.trip

LR	Chisq	Df	Pr(>Chisq)
combined.diff	43.294	1	4.710e-11 ***
QTR	27.095	2	1.307e-06 ***
theYear	8.888	2	0.0117469 *
combined.diff:QTR	17.12	2	0.0001916 ***

summary(mod.glm)

Call:glm(formula = trip ~ combined.diff * QTR +
 theYear, family = binomial(), data = zeh.ind)

Deviance Residuals:

	Min	1Q	Median	3Q	Max
-1	.3906 -	-0.5453	-0.3	-0.1992	2.9069

Coefficients:

	Estimate S	td. Error	z value	Pr(> z)
(Intercept)	-0.7751	0.5855	-1.324	0.185509
combined.diff	0.4745	0.1777	2.671	0.007573 **
QTR3Q	-2.5166	0.6358	-3.958	7.56e-05 ***
QTR4Q	-2.9993	0.7818	-3.837	0.000125 ***
theYear2013	-0.6592	0.347	-1.9	0.057431 .
theYear2014	-0.4598	0.419	-1.097	0.272488
combined.diff:QTR3Q	0.2845	0.2146	1.326	0.184869
combined.diff:QTR4Q	-1.2196	0.4117	-2.962	0.003053 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 (Dispersion parameter for binomial family taken to be 1)

Null deviance: 1134.52 on 1231 degrees of freedom Residual deviance: 875.75 on 1224 degrees of freedom AIC: 891.75 Number of Fisher Scoring iterations: 6

summary(glht(ptrip.glm, linfct=mcp(theYear = "Tukey"))) Linear Hypotheses:

	Estimate S	Std. Error	z value	Pr(> z)
2013 - 2012 == 0	-0.6489	0.3433	-1.8900	0.1400
2014 - 2012 == 0	0.2198	0.3963	0.5550	0.8430
2014 - 2013 == 0	0.8686	0.3293	2.6370	0.0225 *

<u>6.2.A.1.2</u>

```
mod.glmm = glmer(trip~combined.diff*QTR+theYear +
    (1|ID), family=binomial, data=zeh.ind,
    control = glmerControl(optimizer="Nelder_Mead"))
Anova(mod.glmm)
```

Analysis of Deviance Table (Type II Wald chisquare tests)

Response: trip

	Chisq	Df	Pr(>Chisq)
combined.diff	35.0615	1	3.195e-09 ***
QTR	40.2210	2	1.846e-09 ***
theYear	0.8303	2	0.6602335
combined.diff:QTR	16.0222	2	0.0003318 ***

summary(mod.glmm)

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['gImerMod'] Family: binomial (logit) Formula: trip ~ theYear + combined.diff * QTR + (1 | ID) Data: zeh.ind Control: gImerControl(optimizer = "Nelder_Mead")

AIC	BIC	logLik	deviance	df.resid
870.5	916.6	-426.3	852.5	1223
Scaled residuals: Min	1Q	Median	3Q	Max
-1.6738	-0.386	-0.198	-0.1224	6.7766

Random effects:

Groups Name			Variance	Std.Dev.
	ID	(Intercept)	0.4191	0.6474
Numb	er of	obs: 1232		
groups	: ID	, 22		

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.8859	0.6521	-1.359	0.174281
theYear2013	-0.3961	0.5150	-0.769	0.441836
theYear2014	-0.4722	0.5778	-0.817	0.413756
combined.diff	0.5199	0.1837	2.830	0.004658 **
QTR3Q	-2.6260	0.6545	-4.012	6.01e-05 ***
QTR4Q	-2.9354	0.7987	-3.675	0.000238 ***
combined.diff:QTR3Q	0.2645	0.2215	1.194	0.232498
combined.diff:QTR4Q	-1.2796	0.4105	-3.117	0.001824 **

Appendix 6.2.A.2: Factors associated with the probability on any monitored day of an outgoing trip from Moreton Bay through South Passage to oceanic waters – 3rd Quarter all years.

This analysis repeats those of Appendix 6.2.A.1 but using only data collected in Quarter 3 where all years are represented, in order to examine potential interactions between Year and the temperature difference between the inside and outside of the bay. No such interactions were identified.

<u>6.2.A.2.1</u>

```
mod.glmQ3 = glm(p.trip ~ combined.diff*theYear,
    weight=active, family = "binomial", data=zeh.allQ3)
Anova(mod.glmQ3)
```

Analysis of Deviance Table (Type II tests)

Response: p.trip

	LR Chisq	Df	Pr(>Chisq)
combined.diff	41.092	1	1.452e-10 ***
theYear	8.888	2	0.01175 *
combined.diff:theYear	1.618	2	0.44521

<u>6.2.A.2.2</u>

mod.glmmQ3 = glmer(trip~combined.diff*theYear +
 (1|ID), family=binomial, data=zeh.indQ3)
Anova(glmmQ3)

Analysis of Deviance Table (Type II Wald chisquare tests) Response: trip

	Chisq	Df	Pr(>Chisq)
combined.diff	37.0446	1	1.155e-09 ***
theYear	0.5468	2	0.7608
combined.diff:theYear	3.1282	2	0.2093

Appendix 6.2.A.3: Investigating the effects of dugong size and sex.

These analyses add (one at a time, because of data balance limitations) a measure of dugong length and sex to the mixed-effects model examined in Appendix 6.2.A.1. Neither variable had a significant effect. The mixed-effects model in Appendix 6.2.A.1 was therefore used to estimate the impact of temperature differences between inside and outside the bay on the probabilities of making a trip from inside to outside.

<u>6.2.A.3.1</u>

```
mod.size = glmer(trip~ combined.diff*QTR +theYear +
    scale(size.cm) + (1|ID), family=binomial, data=zeh.ind)
Anova(mod.size)
```

Analysis of Deviance Table (Type II Wald chisquare tests) Response: trip

	Chisq	Df	Pr(>Chisq)
combined.diff	34.5513	1	4.152e-09 ***
QTR	39.9004	2	2.166e-09 ***
theYear	1.0779	2	0.5833607
scale(size.cm)	0.7959	1	0.3723206
combined.diff:QTR	16.1952	2	0.0003043 ***
<u>6.2.A.3.2</u>			
			1.55+0==

Analysis of Deviance Table (Type II Wald chisquare tests) Response: trip

	Chisq	Df	Pr(>Chisq)
combined.diff	35.0938	1	3.142e-09 ***
QTR	40.2946	2	1.779e-09 ***
theYear	0.8346	2	0.6588216
Sex	0.2785	1	0.5976725
combined.diff:QTR	16.1632	2	0.0003092 ***

Appendix 6.2.B: Factors associated with the direction of travel for dugongs moving between the Eastern Banks of Moreton Bay and the oceanic waters outside South Passage.

Mixed-effects logistic regression with individual dugong as a random effect, to investigate the effects of quarter, tide, and time of day on the direction of travel by dugongs moving through South Passage between the Eastern Banks inside Moreton Bay and the adjacent oceanic waters.

<u>6.2.B.1</u>

```
direction.logit = glmer(Travel ~ (QTR+Period+Tide)^2 +
   (1|Animal.ID), family=binomial(), data=t.trips3)
Anova(direction.logit)
```

Analysis of Deviance Table (Type II Wald chisquare tests)

Response: Travel

	Chisq	Df	Pr(>Chisq)
QTR	2.8541	2	0.2400188
Period	97.3565	1	< 2.2e-16 ***
Tide	58.7423	3	1.091e-12 ***
QTR:Period	18.1328	2	0.0001155 ***
QTR:Tide	5.2745	5	0.3833106
Period:Tide	2.9463	3	0.3999747

summary(direction.logit)

Generalized linear mixed model fit by maximum likelihood

Family: binomial (logit) Formula: Travel ~ (QTR + Period + Tide)^2 + (1 | Animal.ID) Data: t.trips3

AIC	BIC	logLik	deviance	df.resid
429.3	508.5	-196.7	393.3	585
Scaled residuals:				

Min	1Q	Median	3Q	Мах
-8.1911	-0.3391	0.0002	0.2891	5.3767

Random effects:

Groups Name	Variance	Std.Dev.
Animal.ID (Intercept)	0.05208	0.2282
Number of obs: 603		
groups: Animal.ID, 21		

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	1.1883	0.398	2.986	0.002825 **
QTRQ3	-0.8127	0.4948	-1.642	0.100518
QTRQ4	-18.2057	367.8319	-0.049	0.960525
PeriodPM	-4.5057	0.5899	-7.638	2.20e-14 ***
TideNHigh	3.2417	0.873	3.713	0.000205 ***
TideNLow	-1.8243	0.7251	-2.516	0.011866 *
TideOut	3.1432	0.9531	3.298	0.000974 ***
QTRQ3:PeriodPM	2.7894	0.6551	4.258	2.06e-05 ***
QTRQ4:PeriodPM	-10.0368	581.5946	-0.017	0.986231
QTRQ3:TideNHigh	-1.1124	0.8279	-1.344	0.179071
QTRQ3:TideNLow	1.1685	0.8791	1.329	0.183794
QTRQ4:TideNLow	3.3069	512.0004	0.006	0.994847
QTRQ3:TideOut	-0.9903	0.9323	-1.062	0.288107
QTRQ4:TideOut	30.7882	520.1936	0.059	0.952804
PeriodPM:TideNHigh	-0.7546	0.7407	-1.019	0.308293
PeriodPM:TideNLow	-0.1651	0.7697	-0.215	0.830137
PeriodPM:TideOut	-1.2507	0.802	-1.560	0.118869

Appendix 6.2.C: Factors associated with the duration of visits by dugongs to oceanic waters outside Moreton Bay.

Here I examine whether the same factors tested in examining the probability of undertaking a trip are also associated with the length of time (hours) spent outside the bay when a trip occurs. The data are strongly right-skewed, so residuals were normalized via a natural-log transform. Tidal state and the time of day when outward travel occurred (AM or PM) were also included as potential covariates. The addition of sex and body length as explanatory variables did not improve the model.

<u>6.2.C.1</u>

```
TimeOutside1.lmer = lmer(log(TimeOutside+1) ~ Year +
    combined.diff*QTR + Period*Tide + (1|Animal.ID),
    data=t.trips3)
Anova(TimeOutside1.lmer)
```

Analysis of Deviance Table (Type II Wald chisquare tests) Response: log(TimeQutside1 + 1)

	Chisq	Df	Pr(>Chisq)				
Year	21.2052	2	2.485e-05 ***				
combined.diff	27.3825	1	1.669e-07 ***				
QTR	14.8394	2	0.0005993 ***				
Period	0.2591	1	0.610723				
Tide	4.6274	3	0.201201				
combined.diff:QTR	3.0636	2	0.216147				
Period:Tide	2.6705	3	0.445266				

summary(TimeOutside.Imer)

```
Linear mixed model fit by REML ['ImerMod']
Formula: log(TimeOutside1 + 1) ~ Year+combined.diff*QTR +
Period*Tide + (1 | Animal.ID)
Data: t.trips3
```

REML criterion at convergence: 519.2

Appendix Table 6.2.C.2: The tidal alignment and timing of outgoing and incoming trips in each field season. Note the tidal alignment of 66 unidirectional trips (11.1% of 595 total trips) was inconclusive. No trip was recorded in which the movement was against the tide.

		2012 - 2014	
Direction	Period	Total All	% of all trips
Outgoing	12 am - 12 pm	220	84.6%
	12 pm - 12 am	40	15.4%
Incoming	12 am - 12 pm	54	20.1%
	12 pm - 12 am	215	79.9%
	Trips matching tides	529	88.9%
	Total trips	595	

Scaled residuals: Median Min 1Q 3Q Max -3.1505 -0.5103 0.1143 0.6498 2.675 Random effects: Groups Name Variance Std.Dev. Animal.ID (Intercept) 0.109 0.3301 Residual 0.4471 0.6686 Number of obs: 241 groups: Animal.ID, 19 Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	1.86382	0.38279	4.869
Year2013	0.82255	0.29325	2.805
Year2014	-0.48805	0.31878	-1.531
combined.diff	0.17320	0.08900	1.946
QTRQ3	-1.06339	0.35646	-2.983
QTRQ4	-0.64638	0.52736	-1.226
PeriodPM	-0.07618	0.23866	-0.319
TideNHigh	0.04551	0.14323	0.318
TideNLow	-0.12006	0.22440	-0.535
TideOut	0.16239	0.14221	1.142
combined.diff:QTRQ3	0.17794	0.11297	1.575
combined.diff:QTRQ4	-0.07979	0.23291	-0.343
PeriodPM:TideNHigh	0.16717	0.32519	0.514
PeriodPM:TideNLow	-0.64363	0.49943	-1.289
PeriodPM:TideOut	-0.05303	0.33959	-0.156

Appendix 6.3: Details of dugongs making trips outside Moreton Bay including the number of trips and total tracking days per each dugong for the field season.

Size was defined to be the straight-line body length from the tip of the snout to the fluke notch (see Heinsohn 1981).

			Size	Trips	Tracking		
ID	Maturity ¹	Sex	(cm)	out	days	Start	End
12_109775	Adult	F	312	4	38	4-Sep	5-Oct
12_109776	Adult	Μ	288	21	92	24-Jul	23-Oct
12_109777	Juvenile	F	216	1	57	4-Sep	30-Oct
12_109778	Juvenile	Μ	200	2	62	4-Sep	4-Nov
12_112593	Adult	Μ	298	2	49	24-Aug	11-Oct
12_112595	Subadult	Μ	248	4	28	24-Aug	19-Sep
12_112597	Subadult	Μ	245	1	73	24-Aug	4-Nov
12_112598	Juvenile	F	209	3	61	4-Sep	3-Nov
12_112601	Adult	F	257	2	81	24-Aug	12-Nov
13_043650	Adult	М	286	1	35	12-Jul	14-Jul
13_112597 ²	Adult	F	250	2	4	10-Jul	11-Jul
13_112598	Subadult	Μ	239	3	77	12-Jul	26-Sep
13_112599	Subadult	Μ	247	1	16	11-Jul	23-Jul
13_112600	Adult	Μ	297	2	61	11-Jul	6-Sep
13_112601	Adult	Μ	279	5	80	11-Jul	25-Sep
13_112602	Adult	Μ	285	9	38	11-Jul	17-Aug
13_112603	Adult	Μ	292	2	4	11-Jul	14-Jul
14_043619	Adult	Μ	254	27	84	29-Apr	20-Jul
14_112594 ²	Adult	F	262	44	104	30-Apr	11-Aug
14_112598	Subadult	Μ	231	45	105	29-Apr	11-Aug
14_112599	Adult	F	278	66	137	29-Apr	11-Sep
14_112600	Subadult	F	245	18	107	30-Apr	14-Aug

¹ based on criteria from Lanyon (2003) and Burgess et al. (2012).

² IDs 13_112597 and 14_112594 are the same animal tagged in different years.

Appendix 6.4: Odds of a dugong making a trip from the Eastern Banks of Moreton Bay to the oceanic waters outside of South Passage calculated from model 1D3.

A	∆ dog⁰C	expression	initial	diff/°C expression	diff/°C	A (revised	B (1 + A)	Prob
Qu	A deg C	(intercept)	ouus	(combined.din)	value	ouusj	(I + A)	
2nd	0	exp(-0.8859)	0.412		NA	0.412	1.412	0.292
2nd	1		0.412	x exp(0.520)	1.682	0.694	1.694	0.410
2nd	2		0.412	x exp(0.520) ²	2.829	1.167	2.167	0.538
2nd	3		0.412	x exp(0.520) ³	4.759	1.962	2.962	0.662
2nd	4		0.412	x exp(0.520) ⁴	8.004	3.300	4.300	0.767
B Qtr	∆ deg°C	expression (QTR3Q)	value (QTR3Q)	2nd QTR (revised odds)	diff/°C (QTR3Q)	A (3rd QTR odds)	B (1 + A)	Prob (A/B)
3rd	0	exp(-0.8859- 2.6263)	0.0298		NA	0.0298	1.030	0.029
3rd	1	,	0.0298	x exp(0.520+0.2645)	2.191	0.0654	1.065	0.061
3rd	2		0.0298	x exp(0.520+0.2645) ²	4.802	0.1432	1.143	0.125
3rd	3		0.0298	x exp(0.520+0.2645) ³	10.522	0.3139	1.314	0.239
3rd	4		0.0298	x exp(0.520+0.2645) ⁴	23.058	0.6878	1.688	0.408
C Qtr	∆ deg°C	expression (QTR4Q)	value (QTR4Q)	2nd QTR (revised odds)	diff/°C (QTR4Q)	A (4th QTR odds)	B (1 + A)	Prob (A/B)
4th	0	exp(-0.8859-	0.0210		NIA	0.0210	1 022	0.021
4(1)	U	2.9339)	0.0219			0.0219	1.022	0.021
4th	1		0.0219	x exp(0.520-1.2800)	0.468	0.0102	1.010	0.010
4th	2		0.0219	x exp(0.520-1.2800) ²	0.219	0.0048	1.005	0.005
4th	3		0.0219	x exp(0.520-1.2800) ³	0.102	0.0022	1.002	0.002
4th	4		0.0219	x exp(0.520-1.2800) ⁴	0.048	0.0010	1.001	0.001

Appendix 6.5: The effect of water temperature change on internal temperature.

The overall heat transfer from body core to the skin expressed by Newton's Law of Cooling:

$$H = Ak(T_c-T_a)$$

Where H = heat produced, transferred through the circulation from core to surface, A = surface area, k = heat transfer coefficient, T_c = deep body temperature and T_a = water temperature

Let the change in water temperature be represented by ΔT

Let the original heat produced be shown as H_o and the final heat produced as H_f , then: $H_f - H_o = Ak(T_c-T_f) - Ak(T_c-T_o)$

where T_f is the final water temperature and T_o is the original water temperature

Let $T_f = T_o + \Delta T$, then: $H_f - H_o = Ak(T_c - (T_o + \Delta T)) - Ak(T_c - T_o)$

 $H_f - H_o = - \Delta T Ak$

	Flipper			Size		Acoustic
Year	Tag ID	Maturity	Sex	(cm)	Sattag ID	Transmitter
2012	QA2685	Subadult	Μ	245	112597	14228
2012	QA30541	Juvenile	Μ	200	109778	14238
2012	QA30676	Subadult	F	239	112594	14234
2012	QA30677	Juvenile	F	216	109777	14232
2012	QA30694	Juvenile	F	209	112598	14226
2012	QA30696	Adult	F	312	109775	14230
2012	QA30709	Adult	F	257	112601	14240
2012	QA30710	Adult	Μ	298	112593	14242
2012	QA30712	Subadult	Μ	248	112595	14244
2012	QA30723	Adult	Μ	288	109776	14236
2013	K88240	Adult	Μ	297	112600	14258
2013	No tag ID	Subadult	Μ	250	112595	14272
2013	QA18391	Adult	Μ	286	43650	14232
2013	QA18399	Subadult	Μ	239	112598	14270
2013	QA18400	Adult	F	290	43619	14264
2013	QA33313	Subadult	Μ	247	112599	14266
2013	QA33314	Adult	Μ	292	112603	14242
2013	QA33315	Adult	Μ	285	112602	14250
2013	QA33322	Adult	F	253	112594	14244
2013	QA33400	Subadult	F	250	112597	14248
2013	T71561	Adult	Μ	279	112601	14260
2014	K88308	Adult	Μ	292	112596	13004
2014	K88389	Subadult	Μ	231	112598	12998
2014	QA33400	Adult	F	262	112594	13006
2014	QA44101	Adult	Μ	290	43718	13012
2014	QA44111	Adult	F	304	112597	13014
2014	QA44112	Adult	F	278	112599	13000
2014	QA44113	Adult	F	285	112602	13010
2014	QA44116	Subadult	F	245	112600	13008
2014	QA44117	Adult	Μ	254	43619	13002

Appendix 7.0: Table of all dugongs tracked and tracking device IDs