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Linking wildlife tracking data with environmental features to improve understanding of dugong diving ecology and population size estimates

Thesis submitted by

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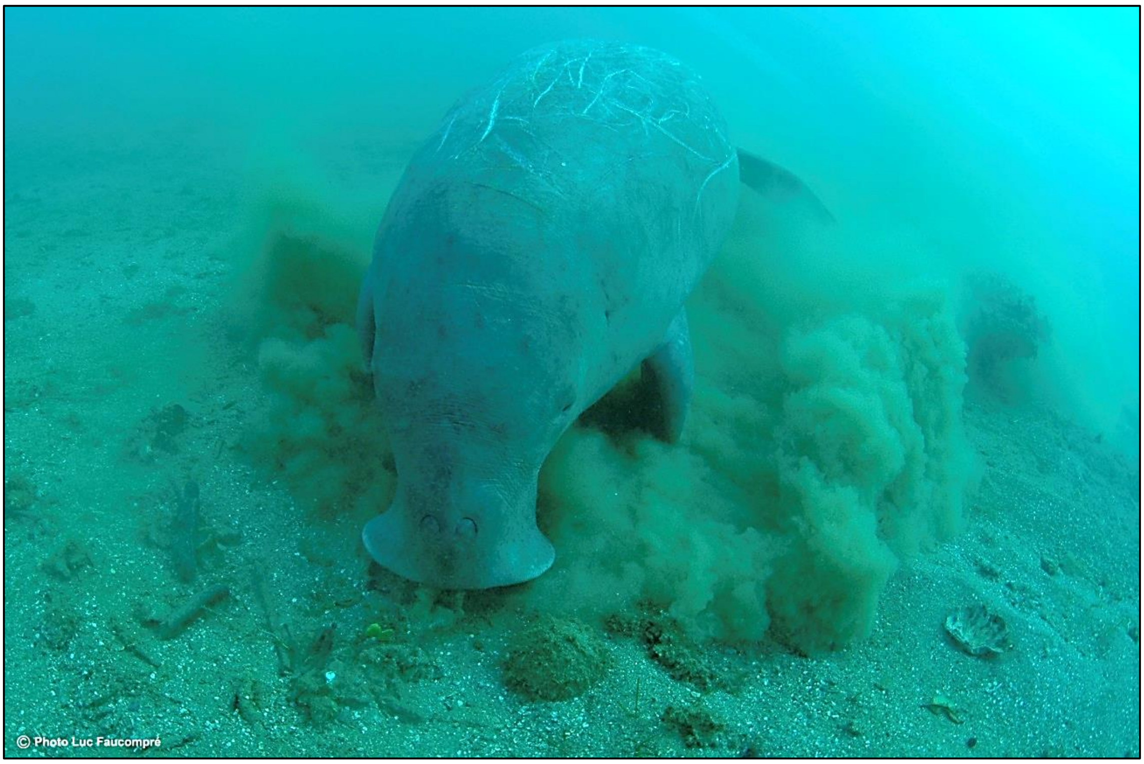

Frontispiece. A dugong feeding on low biomass seagrass in New Caledonia. Dugongs feed on both above- and below-ground seagrass such as leaves and rhizomes, often by causing sediments plumes as depicted on this picture. This feeding mode is referred as excavating (*sensu* Wirsing *et al.* 2007a) and target underground seagrass parts. (Photograph by Luc Faucompré).

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Consultancies

- **Aerial marine megafauna observer**. Project investigating dugong distribution and abundance around Wheatstone LNG Project off Onslow, Western Australia. Employed by Murdoch University, 2012............................$8,750
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Abstract

The dugong (*Dugong dugon*) is a coastal marine mammal of conservation concern with a sub-tropical and tropical range extending from East Africa to the Solomon Islands and Vanuatu. Australia is the dugong's stronghold and the site of most modern research. Compared to the research on the dugong's horizontal space use and movement patterns, little is known of the dugong's diving behaviour. Application of behavioural information to large-scale monitoring studies of population abundance has been minimal. My research combined data collected from a variety of technologies and platforms (satellite/GPS wildlife tracking, remote and benthic sensing, aerial survey) to study dugong diving behaviour and improve aerial survey estimates of dugong abundance.

The objective of this thesis was to maximise the usage of wildlife tracking data to improve fine-scale knowledge of the dugong diving ecology and to apply this information to improve the methodology to estimate dugong abundance. I achieved these objectives by: 1) developing an empirical procedure to maximise the correct identification of dives recorded by time-depth recorders (TDRs); 2) advancing understanding of fine-scale dugong diving behaviour by linking dive records with fine-scale spatial movement data and habitat descriptions; and 3) improving aerial survey estimates of dugong population size by accounting for their heterogeneous diving and surfacing behaviours. Details of my results follow.

Aim 1: Develop an empirical procedure to identify dives in shallow-diving aquatic wildlife such as the dugong

Dives from coastal aquatic animals can be difficult to interpret because the shallow nature of their dives relative to the resolution of TDRs often precludes the reliable identification of the different phases of a dive (*e.g.*, descent, bottom, and ascent). I developed an empirical procedure to determine the thresholds for: 1) the zero-offset correction (ZOC) for surface calibration; and 2) the maximum dive depth (dive threshold (DT)). This empirical approach increased the reliability of dive identification and was essential to subsequent interpretations of dugong diving behaviour (*Aim 2*).

Aim 2: Advance insights into fine-scale dugong diving ecology

I used statistical models based on dive parameters identified using the methodology developed for *Aim 1*. Dugongs are benthic feeders that primarily consume seagrass. Thus dugongs reaching in the vicinity of the seafloor where seagrass is present are more likely to be feeding on seagrass than the seafloor where no seagrass is present. However, behavioural inference from dives *per se* was not attempted because several behaviours can occur over seagrass meadows.

Using 8 dive metrics (descent rate, bottom time, vertical displacement, maximum depth, ascent time, ascent rate, asymmetry and ascent rate divided by descent rate), I performed a series of logistic regression models to predict dives that achieved the two criteria: a) mid-water dives that did not provide the dugong with access to the seafloor and dives that did; and b) dives that enabled the dugong to access the seafloor in areas with seagrass and without seagrass. These criteria were determined from a bathymetric model, tidal records, and a seagrass model from shallow banks of Moreton Bay, The logistic regression models showed that compared to dives that had a high likelihood of accessing the seafloor (seafloor dives), dives that had a high likelihood of not reaching the seafloor (mid-water dives) were characterised by shorter bottom times, a larger degree of vertical displacement (presumably the result of active tail movements) during the bottom phase, and slower ascent rates. The profiles of these mid-water dives included U-, V- and other shapes (Fig.1).

The dugongs that had a high likelihood of accessing the seafloor in locations supporting seagrass transited quickly between the surface and the seafloor and maximised the time spent on the substratum, presumably maximising nutrient return. The profiles of such dives were mostly classified as square-shaped and less frequently U-shaped. Dugongs undertaking seafloor dives in locations without seagrass also spent a long time on the bottom but were sluggish in all phases of the dive, including the transits between the surface and the bottom. These dives generally had U-shaped profiles (with some square profiles). The dive shapes in the three groups overlapped supporting my assumption that inferences about dive function on a broad classification of dive shapes given the data I examined is not possible.

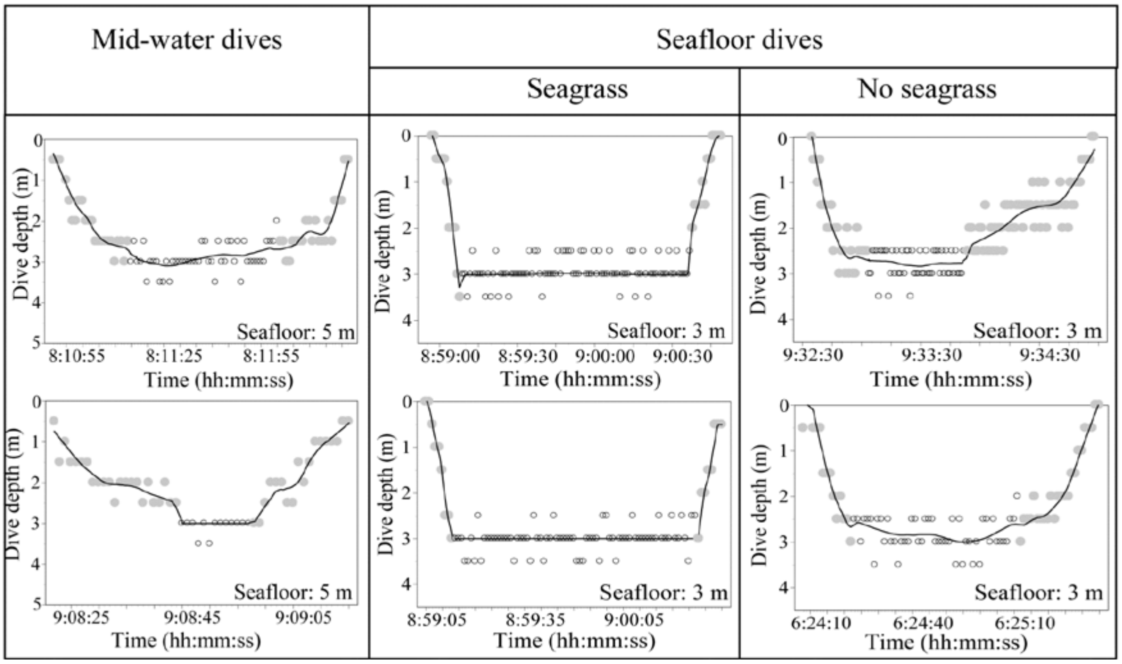

Figure 1 Examples of dive profiles.

Aim 3: Estimate dugong population size that is more robust by accounting for their heterogeneous diving and surfacing behaviours

The current aerial survey methodology used to estimate dugong population sizes at extensive spatial scales accounts for availability bias (animals that are present in survey transects but not visible) due to water turbidity and sea state but assumes constant dugongs' diving and surfacing patterns. To improve availability bias estimates (availability detection probabilities), particularly to account for heterogeneous availability bias, I first estimated availability detection probability by combining data from dugongs fitted with TDRs, GPS satellite tracking units, and fine-scale bathymetric models (Chapter 5). I found availability detection probabilities varied with water depth. All dugongs in clear shallow water (*e.g.*, <1 m) are presumed to be available for detection and the availability bias in these shallow waters was not estimated experimentally. The probability of a dugong being available was next highest in water up to 5 m deep (0.60 to 0.87), followed by water ≥25 m deep (0.58 to 0.85), and lowest in water 5 to 25 m deep (0.34 to 0.69). These depth-specific availability corrections should be more accurate and increasing the likelihood of detecting actual change in a population size.

Using correction factors that incorporated the dugong depth-specific availability detection probabilities, I improved estimates of dugong population abundance over three survey regions (Chapter 6). In Moreton Bay, the abundance estimates based on depth-independent (constant) and depth-specific availability detection probabilities were similar because a high proportion of dugongs were sighted in clear shallow water where all animals were potentially available for detection. In Hervey Bay, the abundance estimate based on the depth-specific availability detection probabilities was lower than the estimate using the constant availability detection probabilities, because more than 50% of dugongs were sighted in clear deep water where the estimated depth-specific availability detection probabilities were higher than the depth-independent estimates. In Torres Strait, the difference in the estimated abundance between the two methodologies was large (>3500 dugongs; 28%). Many dugongs were sighted in waters 5-25 m deep in this region and the depth-specific availability estimates were smaller than the estimates independent of water depth, leading to the larger abundance estimate.

Summary

The results of my research have not only significantly improved understanding of the diving behaviour of dugongs and led to improved estimates of dugong abundance in heterogeneous environments but have also demonstrated methodological advances that should have wider application to shallow-diving aquatic wildlife whose studies are often hampered by coarse resolution of TDRs and affinity of the animals to shallow waters.

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Chapter 1: Linking wildlife tracking data with fine-scale environmental features to improve understanding of dugong diving ecology and population size estimates

Understanding the behavioural ecology of free-ranging animals requires complementary information on both the animals and their environment. Such information is not only valuable for understanding animal ecology but can also inform conservation planning and management practices. In this chapter, I provide the rationale for using an approach in which animal data are linked with environmental information to improve fine-scale insights into dugong diving ecology and the methodology for estimating abundance. I conclude this chapter by outlining the aims of my thesis and its structure.

Chapter 1: Linking animal tracking data with fine-scale environmental features to improve understanding of dugong diving ecology and population size estimates

1.1 Introduction

Studying the behaviour of aquatic vertebrates is logistically challenging. The animals typically spend most of their time submerged. In addition, some species perform long distance migrations, making extended visual observations difficult or impossible (Rutz and Hays 2009; Bograd *et al.* 2010). Technological advances and the development of a range of small-sized sensing units that can be attached to individual animals have enabled free-ranging animals to be studied in their natural environments over vast spatial and temporal scales (Wilson *et al.* 2002; Shillinger *et al.* 2012). This use of wildlife telemetry or biologging sensors has expanded our understanding of the physiology, behaviour, habitat use, and social interactions of marine taxa from coelenterates to cetaceans (*e.g.*, jelly fish: Hays *et al.* 2012; fish: Domeier and Nasby-Lucas 2008; birds: Culik *et al.* 1996; marine turtles: Rice and Balazs 2008; and mammals: Kooyman 1965; Sommerfeld *et al.* 2015). The invaluable insights obtained from wildlife tracking studies have been well summarised in comprehensive reviews (*e.g.* Wilson *et al.* 2002; Boyd *et al.* 2004; Cooke et al. 2004; Kooyman 2004; Naito 2004; Block 2005; Ropert-Coudert and Wilson 2005; Burger and Shaffer 2008; Cooke 2008; Hart and Hyrenbach 2009; Ropert-Coudert *et al.* 2009; Bograd *et al.* 2010; Costa *et al.* 2010; Evans *et al.* 2013; McIntyre 2014; Kraska *et al.* 2015),

Additional insights into animal ecology and habitat use can be obtained when remotely sensed wildlife tracking data are linked with complementary information about the tracked animals and their immediate environment. For instance, several studies have identified prey species by combining location data collected from geolocators or Platform Transmitter Terminals (PTTs) and diet information obtained from stable isotope analysis (Furness *et al.* 2006; Phillips *et al.* 2007). Banks *et al.* (2014) attached Satellite Relayed Data Loggers (SRDLs) to the southern elephant seals (*Mirounga* *leonina*), and also collected fatty acid signature from the seals. They found that animals foraging in different regions in Southern Oceans consumed different prey types (predominantly squid compared with a mixed diet of fish and squid). The diets changed annually, presumably responding to prey availability.

Similar approaches have also been used to provide information applicable to conservation and management. For example, Cooke *et al.* (2006) described the underlying reasons for migration failure in a commercially and recreationally important species, the sockeye salmons (*Lncorhynchus nerka*). Based on examination of physiological and somatic conditions and blood samples, and the use of radio transmitters attached to the salmons, these authors found the fish that failed to reach spawning sites had lower somatic energy and higher levels of stress hormones such as cortisol than the fish that reached their final destination. By combining data from GPS tracking and scats in declining populations of South American sea lions (*Otaria flavescens*) , Riet-Sapriza *et al.* (2013) showed variable levels of spatial and resource overlap between the sea lions and artisanal and commercial trawl fisheries. The results lead to recommendations concerning changed management arrangements for each of the two fisheries.

When the study objective is to understand animal behaviour, ecology, or physiology at fine scales, the information on their environment should be collected at correspondingly fine scales. Animals modify their behaviour at fine spatio-temporal scales in response to biotic and abiotic processes that also vary at these scales resulting in fine-scale heterogeneity in resource distribution and density (Mori 1998; Bradshaw *et al.* 2003; Lea and Dubroca 2003; Bailleul *et al*. 2007). Improvements in the quality and quantity of data collected from contemporary tracking units allow animal data to be documented with high spatial accuracy (*e.g.*, <10 m) and at short time intervals (*e.g*., 1 s) using Global Positioning System (GPS) and biologging units such as time-depth recorders (TDRs).

Nonetheless, the fine-scale interpretation of remotely sensed animal data such as a single dive in the context of the environment is difficult as the environmental information is often sparse, absent or available at inappropriate spatial or temporal scales. Environmental data collected at broad spatio-temporal scales (*e.g.*, kilometres) limits our capacity to interpret fine scale movement data collected at metre resolutions. Despite these limitations, invaluable insights into foraging behaviour and habitat requirements have been obtained by combining wildlife tracking and oceanographic data (*e.g.*, Georges *et al.* 2000; Hyrenbach *et al.* 2002; Lea and Dubroca 2003; Shaffer *et al.* 2006; Bailleul *et al.* 2007; Howell *et al.* 2010; Sommerfeld *et al.* 2015). For instance, Raymond *et al.* (2014) identified overlapping critical habitats of penguins and otariid and phocid seals (Raymond *et al.* 2014) by using tracking data to conduct multi-species modelling of habitat utilisation and applying the results to marine protected area planning.

Although many marine studies have examined fine-scale spatio-temporal data (*e.g.*, Schofield *et al.* 2007; Hazel 2009; Preston *et al.* 2010), fewer studies have combined fine-scale spatio-temporal information on the target species with similarly fine-scale environmental features (but see *e.g.*, Sheppard *et al.* 2010; Jessop *et al.* 2013). The advantages of this approach are illustrated by Sheppard *et al.* (2007, 2010) who combined GPS location data with a nutrient map of a 24 km^2 seagrass bed to document a strong association between the dugong (*Dugong dugon*) and seagrass with relatively high starch and nitrogen concentrations at 200 m resolution. Both starch and nitrogen are important dietary requirements for dugongs (Lanyon 1991; Marsh *et al.* 2011b). This study showed that dugongs also exploited intertidal areas during high tides and at night, possibly to seek seagrass rhizomes that are high in carbohydrate and at times when boating activities are little (Sheppard *et al.* 2010).

As the above examples illustrate, wildlife tracking data are best exploited by amalgamating complementary fine-scale information on both animals their environment. Although the cost of electronic tags is dropping, wildlife tracking still incurs substantial financial and human resources. Researchers often work with threatened species, and the sample size is constrained by financial, logistical, and ethical considerations. The dugong, a species of conservation concern, provides an excellent model for such a framework of data maximisation. Its body size (~3 m length and ~> 400 kg weight of healthy adult dugongs, unpublished data) allows researchers to use a range of tag sizes and weights while addressing animal welfare concerns.

1.2 The dugong

1.2.1 High conservation values

The dugong is a species of high conservation value, which occurs over a huge range in the tropical and subtropical Indo-West Pacific Ocean from East Africa to the Solomon Islands and Vanuatu (Marsh *et al.* 2011b). The dugong has high evolutionary value as the only extant herbivorous mammal that is strictly marine, the only extant species in the family Dugongidae and one of only four extant species in the order Sirenia. The order Sirenia includes another extant family, the Trichechidae, with three species of manatees (Amazonian *Trichechus inunguis*; West Indian manatee *T. manatus*; West African manatees *T. senegalensis*), that variously occur in both freshwater and saltwater systems (Boyd *et al.* 1999; Marsh *et al.* 2011b). Two subspecies of the West Indian manatee are recognised: the Florida manatee (*T. manatus latirostris*) and the Antillean manatee (*T. manatus manatus*). In addition, the dugong's closest relative, Steller's sea cow (*Hydrodamalis gigas*: Dugongidae), was hunted to extinction in the 18th century, some 27 years after being rediscovered by sealers (Stejneger 1887). This extinction has highlighted the vulnerability of sirenia to human-induced mortality.

The dugong also has high intrinsic and cultural values throughout its range. Australia is the dugong's stronghold and dugong hunting is an important expression of Indigenous identity (Smith and Marsh 1990; McNiven and Bendingfield 2008).

Dugongs are ecologically important to the tropical and sub-tropical seagrass communities that provide nursery grounds for commercially important juvenile fishes and invertebrates (*e.g*. prawns and shrimps; Young and Kirkman 1975). Dugongs often feed by uprooting whole seagrass plants thereby aerating sediments (Anderson and Birtles 1978). This feeding mode called excavating (*sensu* Wirsing *et al.* 2007a, see Chapter 4 for details) is thought to promote nitrogen fixation (Perry and Dennison 1999). Dugong foraging on seagrass has also been found to increase seagrass productivity and nitrogen content. McMahon (2005) reported that seagrass meadows intensively foraged by dugongs are twice as productive in summer and 1.5 times as productive in winter compared with areas undisturbed by dugongs. These findings have been replicated experimentally by removing pioneer seagrass species in a manner that simulates dugong feeding, resulting in a 35% increase of nitrogen concentration in *Halohila ovalis* and 25% in *Halodule uninervis* (Aragones *et al.* 2006).

Dugongs are of conservation concern as they face direct threats from entanglement in fishing gear, vessel strikes, Indigenous hunting, and indirect threats from sediment and nutrients loads from catchments, land reclamation, dredging, cyclones, floods, and climate change (Abal and Dennison 1996; Preen and Marsh 1995; Marsh *et al.* 2011b; Sobtzick *et al.* 2012). Dugongs are not wilderness animals and occur in major port areas such as Singapore, and Gladstone and Townsville in Queensland, Australia (Marsh *et al.* 2011b). Projected port expansions in many parts of the dugong's range impose additional threats to coastal ecosystems including seagrass and dugongs.

Several international and domestic conventions and regulations aim to conserve dugongs. The International Union for Conservation of Nature (IUCN) lists the species as "vulnerable" (IUCN 2015). At the national level in Australia, the *Environmental Protection and Biodiversity Conservation Act 1999* (EPBC Act) provides the legal framework to protect "matters of national environmental significance" which includes "migratory species" such as dugongs. The listing of the dugong as a migratory species regulates actions that impose harm and such actions require approval from the federal environment minister. The *Great Barrier Reef Marine Park Act* 1975 also obliges the Great Barrier Reef Marine Park Authority (GBRMPA) to protect dugongs within the Great Barrier Reef Marine Park (GBRMP). In addition, one of the reasons for the World Heritage listing of the GBRMP is its large populations of dugongs (GBRMPA 1981). The species is also protected under Queensland state regulation *Nature Conservation Act 1992* which lists the species as "vulnerable".

In the next section I will explain the research gaps I identified from the literature and how I will address them using the dugong as my study animal.

1.3 Research gaps

1.3.1 Dive profiling

Due to technological advances, a large volume of data collected from time-depth recorders (TDRs) has led to the development of dive analysis software which constructs dives from a series of two-dimensional depth readings using user-defined parameters. Nonetheless, the method of determining the thresholds of these parameters has received relatively little attention. Researchers adjust the surface level either manually or using a zero-offset correction (ZOC) function embedded in the dive software (*e.g*. Gordos and Franklin 2002; Bodkin *et al.* 2004; Hays *et al.* 2007; Witt *et al.* 2010). How the ZOC values are chosen is often not described. Some studies do not mention the process of surface adjustments at all (*e.g*. Boveng *et al.* 1996; Arnould and Hindell 2001; Fossette et al. 2008). In addition, relatively few dive studies have discussed what factors might be considered in selecting a Dive Threshold (DT) – a minimum depth below which a vertical movement is considered to be a “dive” – (see Bengtson and Stewart 1997; Arnould and Hindell 2001; Gordos and Franklin 2002; Bodkin *et al.* 2004; Chilvers *et al.* 2004; Hays *et al.* 2007). The DT is often arbitrarily specified as twice the resolution of the TDR used (Hooker and Baird 2001). Shallow diving animals such as dugongs feed in shallow coastal communities sometimes <1 m deep (Hodgson 2004). Robust and objective methods need to be developed to optimise the choice of these parameters for shallow-diving species such as the dugong because the existing arbitrary methodology is likely to miss shallow dives – an important component of their feeding ecology.

1.3.2 Dugong ecology

Due to the challenges associated with studying wild dugongs, most information on their behavioural ecology has been collected from short visual observations from terrestrial vantage points, swimmers, and vessels (Anderson and Birtles 1978; Hartman 1979; Reynolds 1981a,b; Anderson 1989; Whiting 2002; Wirsing *et al.* 2007a,b,c; D’souza and Patankar 2009). Large populations of dugongs and manatees (especially West African and Amazonian manatees) inhabit remote, turbid waters where field observations are logistically difficult (Marsh *et al.* 2011b). Sirenians spend their entire life in the water unlike semi-aquatic animals such as seals, sea lions, and turtles. As sirenians surface for only a few seconds to breathe (Anderson and Birtles 1978; Hartman 1979) they are categorised as “surfacers” rather than “divers” (Kramer 1988). The window of opportunity for surface observations is very short and turbidity generally precludes observation of underwater behaviour (Anderson and Birtles 1978). Florida manatees are easier to observe than dugongs as some populations reside in clear freshwaters or industrial canals close to human habitation (Hartman 1979; Reynolds 1981a,b; Edwards *et al.* 2007). In addition, the apparent lack of unique markings on dugongs’ bodies makes individual identification very difficult, in contrast to some species of whales, dolphins, and Florida manatees with persistent markings that can be used to recognise individuals in longitudinal studies (*e.g.*, Reid *et al.* 1991; Baird and Whitehead 2000).

The technological advances in wildlife tracking discussed earlier have enabled remote observations of sirenian behaviour in the wild. Marsh and Rathbun (1990) developed a dugong satellite tracking mechanism using a tether system and PTT, that was based on the system developed for manatees (Rathbun *et al.* 1990; Deutsch *et al.* 1998; see Chapter 2). This technique has consistently shown that dugongs exhibit individualistic movement patterns. For instance, Sheppard *et al.* (2006) tracked 70 dugongs fitted with GPS transmitters. Some of these animals performed long large-scale movements of >100 km during the tracking period, whereas other animals were relatively sedentary. Gredzens *et al.* (2014) fitted fast acquisition GPS satellite transmitters to dugongs and green turtles (*Chelonia mydas*) in two regions Shoalwater Bay and Torres Strait in Queensland. The home-ranges of the two species significantly overlapped in both locations, and the authors recommended that dugongs and turtles to be managed together. Nonetheless there were regional differences within species. Dugongs in Torres Strait had much larger home ranges (median: 1042.9 km^2) than dugongs in Shoalwater Bay (median: 49.5 km^2). Torres Strait dugongs also favoured slightly deeper waters (5-15 m) than Shoalwater Bay dugongs (< 5 m). Both species used existing protection areas in Shoalwater Bay, but only one dugong used the existing protection area in Torres Strait. Gredzens *et al.* (2014) concluded that the protected area in Shoalwater Bay was sufficient, while that in Torres Strait needed to be extended to provide adequate protection.

Acoustic transmitters have been deployed on dugongs (Zeh *et al.* 2015) to compare the efficacy of acoustic and GPS satellite transmitters for estimating home range. The study demonstrated that both technologies provided similar information on habitat and depth use within the acoustic array boundary but that the selection of the more appropriate tracking devices should depend on the research question and whether an acoustic array is already in place as array instalment is expensive. Acoustic transmitters have been also attached to Florida manatees (Aven *et al.* 2014). The authors attested to their usage as an alternative to GPS transmitters which frequently detach, leading to the loss of valuable information.

Compared with the advances in our understanding of sirenian horizontal space use revealed by these studies, our understanding of their diving behaviour in relation to their environment is limited. Hodgson (2004, 2007) developed a blimp-cam (a video camera attached to a helium balloon) to remotely observe dugong behaviour under natural settings. She used this technique to obtain the data required to describe detailed behavioural repertoires and develop an ethogram for dugongs feeding in shallow clear waters in winter, when the water was calm. However, this technique has limited application for studying dugongs in turbid or rough waters, which consist of the majority of dugong habitats.

TDRs have provided limited information on the diving behaviour of wild sirenians. Using TDRs and GPS satellite transmitters, Chilvers *et al.* (2004) estimated dive statistics, categorised dive shapes based upon visual inspection into four main dive types (Square, U-shaped, Erratic and Resting, and V-shaped dives), and examined environmental influences on the dive shapes from which behaviours were inferred. Because location fixes were rarely obtained from these transmitters, it was impossible to correlate dive shapes and environmental features and validate presumed behaviours. Sheppard *et al.* (2006) documented deep consecutive dives >21 m deep and maximum dive depth of 36.5 m, but the location of these deep dives was unknown due to a lack of location data. Castelblanco-Martínez *et al.* (2015) used GPS units and salt water sensors (SWSs) attached to wild West Indian manatees to categorise sequences of dives called bouts into four behavioural types (travelling, surface, bottom feeding, bottom resting). This categorisation was based on three criteria: travel distance between two GPS fixes, number of dives in a bout, and total dive duration. Bottom behaviour occurred frequently over habitats with known subaquatic plants while the manatees tended to travel across open waters. The categorisation however did not utilise information on environment, and the dives were identified from the records of salt water sensors installed on satellite units. As the satellite unit is attached to manatees via a tether, similar to the one for dugongs, these dives may not represent actual dives, especially when animals are swimming and a satellite unit is dragged underwater.

As described above, fine-scale insights into sirenian ecology can be obtained when fine scale remotely sensed animal data are combined with relevant environmental information collected at similar spatial and temporal scales. The distribution and abundance of the dugong's primary food resource, sub-tropical and tropical seagrass, also vary in space and time at fine scales (Bell *et al.* 1999; Turner *et al.* 1999; Robbins and Bell 2000; Frederiksen *et al.* 2004; Sheppard *et al.* 2007). As discussed above, Sheppard *et al*. (2007, 2010) used this approach combining GPS location data with seagrass nutrient maps generated using marine videography and near-infrared spectroscopy to explore the dugong's food preferences .

A weakness of Sheppard's study was the lack of information on the dugong's diving behaviour at his study site. Sheppard *et al.* (2007, 2010) could not confirm whether the dugongs they studied had dived to the seafloor where seagrass occurred and consumed the seagrass modelled at that location. Our understanding of dugong behavioural and foraging ecology would be enhanced by linking fine-scale seagrass distribution and bathymetry maps with behavioural data on both the vertical and horizontal spatial use of dugongs equipped with TDRs and fast acquisition GPS transmitters.

1.3.3 Dugong aerial surveys as a management tool

Australia has international and domestic obligations to protect and conserve dugongs as explained above in Section 1.2.1. Since the 1980s, the distribution and abundance of Australia's dugong populations have been monitored using a time-series of aerial surveys using a methodology developed by Marsh and Sinclair (1989a,b) and Pollock *et al.* (2006). These aerial surveys have provided a cost-effective method of monitoring dugongs along extensive coastlines in over 20 countries including the Arabian region (see review by Preen *et al.* 2012), New Caledonia (Garrigue *et al.* 2008), and Mozambique (line transect design: Cockcroft *et al.* 2008; Provancha and Stolen 2008).

In Australia, the results of these surveys have provided the basis for dugong conservation and management. Dugong aerial survey data have been used to assess the risks to dugongs from commercial fishing, vessel traffic, and terrestrial runoff at regional scales (Grech and Marsh 2008; Grech *et al.* 2008), and traditional hunting (Heinsohn *et al.* 2004; Marsh *et al.* 2004; Grayson 2011). The surveys have catalysed management responses including the declaration of Dugong Protection Areas (Marsh 2000) and other regulations to modify netting practices (Fernandes *et al.* 2005; Dobbs *et al.* 2008; GBRMPA 2014).

Monitoring changes in population size requires robust population abundance estimates. Despite the expense of the monitoring program, the statistical power to detect population trends from aerial survey population estimates is relatively low at the current survey interval (*ca*. every 5 years) (Marsh *et al.* 2004). A contributing factor is that not all animals are available for detection during population census. Abundance estimated from aerial or boat-based surveys are generally underestimates (Buckland and Turnock 1992; Laake *et al.* 1997). Hence the proportion of animals that is unavailable for detection needs to be estimated for obtaining robust abundance estimates (Buckland *et al.* 2004; Pollock *et al.* 2004) and for conservation and management applications.

Availability detection probabilities can be reduced by the capacity of the observers, environmental conditions (*e.g.*, turbidity, sea state, glare, cloud cover) and various physical and the behavioural traits of the target animals (*e.g.*, body colour and size, group size, vertical and horizontal spatial distribution) (Bayliss 1986; Marsh and Sinclair 1989b; Anderson 2001; Buckland *et al.* 2004; Pollock *et al.* 2006; Edwards *et al.* 2007). Marsh and Sinclair (1989b) classified these biases into two categories: availability bias (animals that are unavailable for detection due to the factors described above); and perception bias (animals that are available but not sighted by observers). Dugong aerial survey methodology attempts to correct for both types of bias (see Chapters 5 and 6). Although environmental variability (water turbidity and sea state) in sighting conditions is accounted for dugong estimation methodology (Pollock *et al.* 2006), the vertical displacement patterns of dugongs are assumed to be homogeneous across environmental conditions. Changes in availability bias resulting from both environmental and animal traits need to be quantified to estimate dugong population abundance that is more robust.

Studies employing aerial and boat-based surveys on other aquatic species have generally assumed that environmental features and animal behaviour are homogeneous (*e.g.*, Barlow *et al.* 1988; Schweder *et al.* 1991a,b; Laake *et al.* 1997; Skaug *et al.* 2004; Slooten *et al.* 2004), and have focused on improving the precision of abundance estimates by rigidly standardising survey protocols and increasing survey frequency in order to improve the power to detect trends (Gerrodette 1987). Nonetheless, changes in relative abundance, which inherently assume homogeneous sighting conditions, do not always reflect changes in absolute abundance (Link and Nichols 1994b; Conroy 1996; Gibbs *et al.* 1998; Larsen *et al.* 2001; Wilson *et al.* 2011). Heterogeneity in environmental conditions and animal behaviour reduces the statistical power to detect changes in population size (Forney 2000). Accounting for heterogeneity in the availability of a target species such as a dugong should improve the accuracy of abundance estimates. Along with improved precision, improved accuracy will increase the likelihood of detecting a trend in dugong abundance (Gerrodette 1987; Taylor and Gerrodette 1993).

1.4 Thesis objective

In response to the research gaps identified above, the objectives of my thesis were to maximise the outcomes wildlife tracking by linking fine-scale dive records with spatial data from remotely-sensed animals and fine-scale habitat models to improve: (a) fine-scale knowledge of the diving ecology of coastal wildlife, and (b) methodologies to estimate their population abundance.

To achieve these objectives, I identified the following aims:

1. To develop empirical methods to identify dives in shallow diving aquatic wildlife such as the dugong; and

by linking fine-scale dive records with spatial data from remotely-sensed dugongs and fine-scale habitat models,

2. To advance insights into the fine-scale diving ecology of dugongs; and

3. To estimate dugong population abundance that is more robust by accounting for their heterogeneous diving and surfacing behaviours.

Aim 1: Develop an empirical procedure to identify dives in shallow diving aquatic wildlife such as the dugong

Quantitative methodology is required to assist in determining zero-offset correction (ZOC) and dive threshold (DT) and maximise the correct identification of shallow dives. I address this need in Chapter 3 using depth measurements collected from shallow diving dugongs.

Aim 2: Advance insights into fine-scale diving ecology of dugongs

In Chapter 4, I advance understanding of dugong diving ecology by linking fine-scale behavioural data (depth records and GPS location fixes) with a bathymetry model (± 100 m spatial resolution) and a seagrass map (± 10 m spatial resolution) generated from high resolution satellite imageries and ground truthing. I use logistic regression models based on the dives identified in Chapter 3 to estimate probabilities of dives achieving 3 criteria: a) dives that did not provide the dugong with access to the seafloor; b) dives that enabled the dugong to access the seafloor in areas where seagrass is present; and c) dives that enabled the dugong to access the seafloor in areas where seagrass is absent. I will then examine the dives that had high likelihoods of achieving these criteria in order to draw insights into the dugong diving behaviour.

Aim 3: Estimate dugong population abundance that is more robust by accounting for their heterogeneous diving and surfacing behaviours

I estimate dugong population abundance by accounting for their heterogeneous diving and surfacing patterns. In Chapters 5 and 6, I estimate the availability detection probabilities for different water depths using depth measurements collected from satellite-tracked dugong. In Chapter 6, I then re-estimate population abundance using improved availability detection probabilities. The detection probabilities are estimated by: 1) repeating the Pollock *et al*.'s (2006) experiment using dugong replicas (Dugong Secchi Disks) to improve the estimates of detection zones (*sensu* Pollock *et al.* 2006) with higher resolution TDRs; and 2) incorporating measurements of heterogeneous diving behaviour with respect to water depth into estimates of the detection probability based on the improved detection zones. The aerial survey data were collected in 2011 in Moreton Bay, Hervey Bay, and Torres Strait.

1.5 Thesis outline

This thesis comprises seven chapters: an introductory chapter, a methodology chapter, four data chapters and a final discussion chapter (Fig. 1.1). Chapters 3 and 4 focus on the diving ecology of dugongs. Chapters 5 and 6 provide studies that contribute to the aerial survey methodology, a management tool for monitoring their distribution and abundance over time. Chapter 7 provides a general discussion of my key findings together with suggestions for future research.

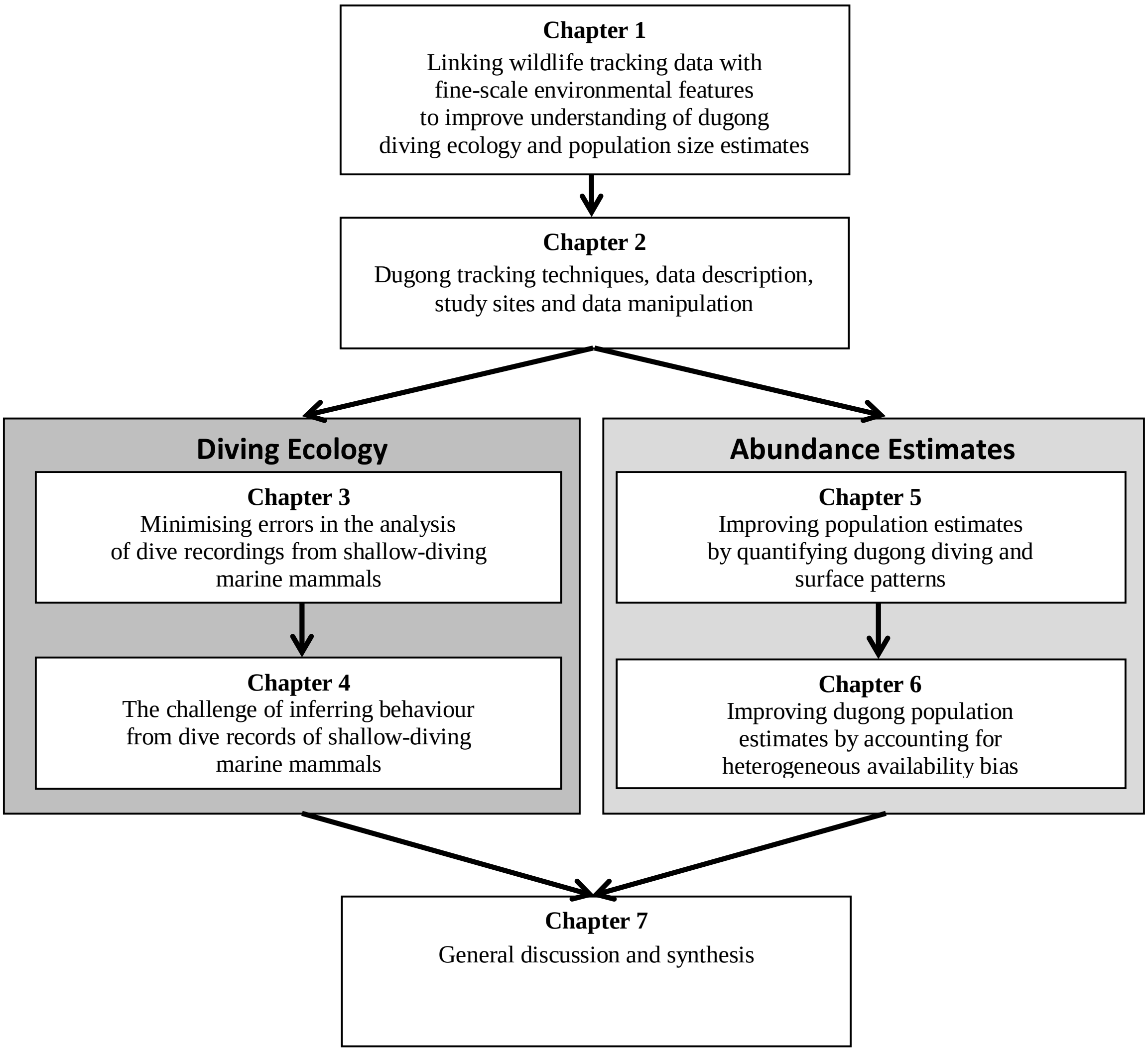
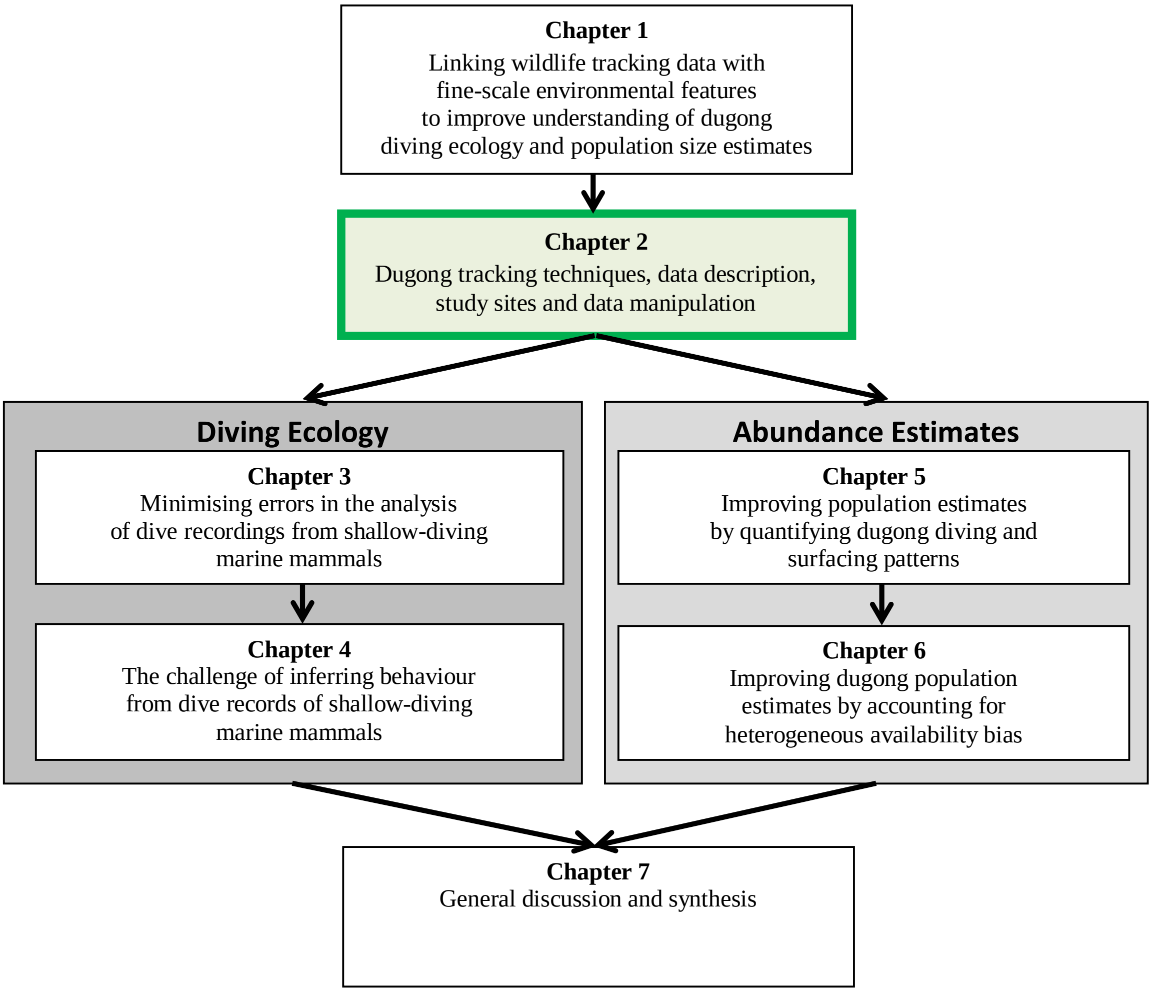


Figure 1.1 Structure of this thesis.

Chapter 2: Dugong tracking techniques, data description, study sites and data manipulation



Wildlife tracking (*i.e.*, biologging) enable researchers to remotely observe animals and their environment using electronic devices and provide valuable information for understanding physiology, ecology, and habitat use and for management application. Dugong satellite tracking has been conducted for almost 30 years and the use of GPS units and time-depth recorders (TDRs) has provided detailed information on their spatial use and diving behaviours. Here, I describe the dugong tracking methodologies, data collected from the tracking, and descriptions of the study sites, plus some generic information on the data manipulation techniques used in this thesis.

Chapter 2: Dugong tracking techniques, data descriptions, study sites and data manipulation

2.1 Dugong tracking

2.1.1 Tracking apparatus

The dugong tracking apparatus used largely reflects the design developed by Marsh and Rathbun (1990), Sheppard *et al.* (2006), Holley (2006), and Lanyon *et al.* (2006). The apparatus consisted of a GPS (Global Positioning System) satellite unit Telonics Inc., Mesa, Arizona, USA), a time-depth recorder (TDR) (Wildlife Computers Woodinville, WA, USA), a 3-m tether, and a peduncle belt (Fig. 2.1). GPS units were painted with anti-foulant to reduce biosettlement (Fig. 2.1B). A TDR was attached to each tether near the dugong's tail (Fig. 2.1A,C).

To maximize successful uplink opportunities (communication between ground devices and orbiting satellites), the GPS unit was housed in a slightly buoyant cylinder which was connected to a tailstock harness via a tether. When a telemetered dugong is within 3 m of the water surface and stationary or swimming slowly, the unit breaks the water surface (Sheppard *et al.* 2006). The salt water sensor installed on the GPS unit detects air, turning the unit on. The unit receives radio signals from nearby GPS satellites and calculates the location based on the signals and archives the data (Cooke 2008). When the surfacing time is sufficient, the archived location data are transmitted to Argos satellites for data retrieval.

This dugong tracking apparatus has several features to prevent or minimize harm to the tagged dugongs. To prevent abrasion of the dugong's skin, the tailstock belt is covered with a latex tube. To minimise the impact on the animal from the apparatus and hence the dugong being entangled in corals, mangroves or attacked by sharks, the attachment includes a weak link mechanism, which was designed to break off when a force of *ca*. >270 lb (122.5 kg) is applied (Ocean Industries, WA, Australia). This strength on trace wire was determined from experimental trials (Sheppard 2008). The weak link also needs to be strong enough to endure dugong's normal tail movements.

The author found all tags with 150 lb trace wires were released from animals within hours. Hence the use of a stronger breaking strain in the weak link was required. The weak link is also corrodible, which ensures the release of the apparatus after a planned period of deployment (usually several months).

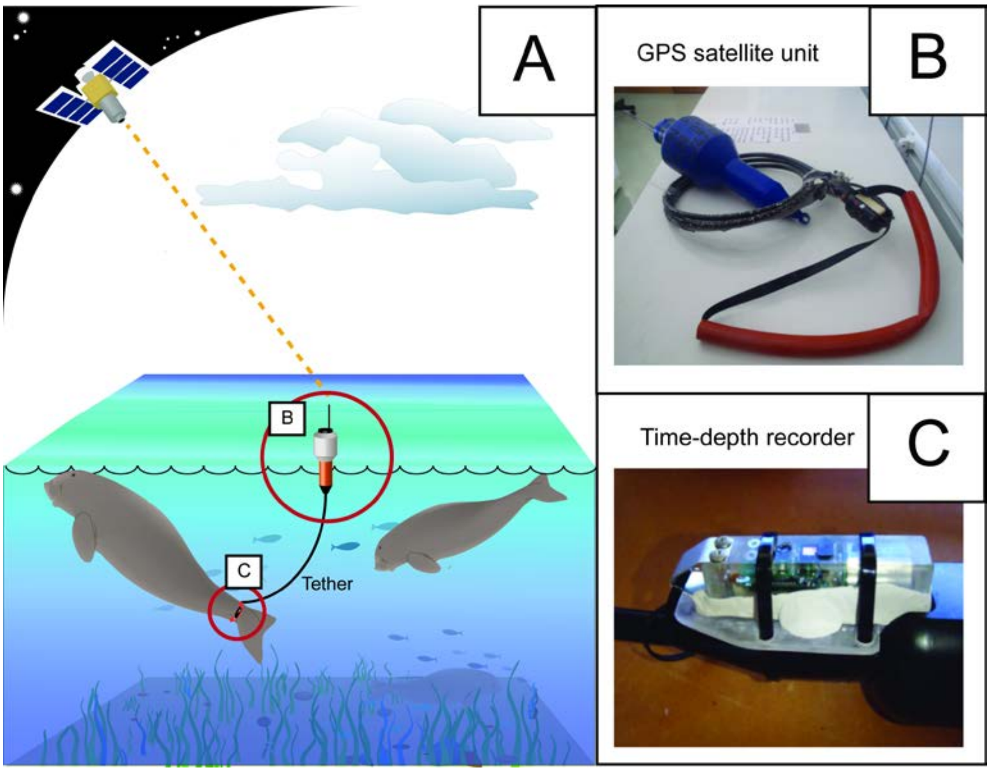


Figure 2.1 Diagram of dugong tracking apparatus: A) an overall schematic drawing of the dugong tracking mechanism; B) a GPS satellite unit painted with blue anti-foulant and a 3-m tether covered with a latex tube; and C) a time-depth recorder (TDR) attached close to the dugong’s tailstock.

2.1.2 Capture technique

Dugongs were captured using the rodeo technique described in Appendix 2.1.

2.1.3 Recovery of the tracking apparatus

Whenever possible, the entire tracking apparatus was retrieved after the planned deployment periods, following the procedure described in Sheppard *et al.* (2006). The tagged dugong was first relocated based on its most recent GPS fixes. A recovery team then searched for the dugong from the water using VHF radio tracking and antennae (Telonics Inc., Arizona, USA). Once the relocated animal was within 150 m of the vessel, tag release was initiated by a hand-held trigger (Telonics Inc., Arizona, USA) which sends signals to a tether. Upon receipt of signals, the weak link installed in the tether initiates corrosion, released the apparatus from the dugong after *ca*. 10 min. If this technique was unsuccessful, the animal was captured using the rodeo technique (Lanyon *et al.* 2006), and the belt removed manually.

Some tags were released prematurely, often at the weak-link. Premature release was indicated by successive hourly uplinks over extended period (*e.g.*, > 1 day), uplinks from the same locations, or continuous straight-line movements (Gredzens *et al.* 2014). The released apparatus was recovered by research staff, local rangers, boaters, fishers, or local residents induced by a reward.

2.2 Data description

I examined tracking data from 21 free ranging dugongs (Table 2.1). The data from four dugongs tracked in 2011 (MB 1-4) were obtained for my PhD thesis. The remainder of the data originated from studies by Sheppard (2008) in which five dugongs were tracked in Hervey Bay 2003/2004 and Gredzens *et al.* (2014) in which three dugongs were tracked in Shoalwater Bay 2012. I also used tracking data collected by Zeh (Zeh *et al.* 2015) who tagged nine dugongs in Moreton Bay 2012.

Satellite data

The sampling intervals of the GPS transmitters (Telonics Inc., Mesa, Arizona, USA) were 20 min, 30 min, or 1 h (Table 2.1). The location data from the GPS units were accessed via the Argos website (http://www.argos-system.org), and decoded using software *Telonics Data Converter* provided by manufacturer (Telonics Inc., Mesa, Arizona, USA). GPS fixes obtained in 2003/2004 over Hervey Bay had an accuracy 2–10 m (Telonics 2009) but required a surfacing time of >30 s. GEN4 GPS models used in dugong tracking in 2011 and 2012 provided, in addition to the GPS fixes, Quick Fix Pseudoranging (QFP) positions which required only <5 s of surfacing time for fix generation (Telonics 2011). This quick uplink capability was a significant advance for aquatic species such as the dugong that surfaces for only a few seconds (Anderson and Birtles 1978).

Including the GPS and QFP fixes, five types of location fixes were available for inspection and were labelled with the following quality indicators: 1) GPS (accuracy <10 m); 2) Resolved QFP (accuracy of ≤75 m); 3) Resolved QFP Uncertain (accuracy of >75 m); 4) Unresolved QFP (accuracy unknown); and 5) Failed QFP. These classes were determined by the number of GPS signals received, geometry of the satellites, and residual errors in the positioning mathematics (pers. comm., Telonics 2011). I used GPS and Resolved QFP fixes based on their positioning accuracy. The use of resolved QFP fixes in addition to GPS fixes resulted in 1.5–4.9 times more fixes for each dugong compared to GPS fixes alone (Hagihara *et al.* 2014). Although GPS and Resolved QFP fixes have different spatial accuracy, the manufacture states 98.4% of resolved QFP fixes have < 30 m of the actual location (Gredzens et al. 2014). The incorporation of such differences in quality (*e.g.*, as weight) in statistical analyses will improve the analyses described in my thesis. However such attempt requires quantitative assessment on accuracy of GPS and QFP fixes. Thus I have treated GPS and Resolved QFP fixes equally here.

Table 2.1 Details of the 21 dugongs tracked with GPS satellite units and TDRs and specification of each type of tracking unit.

	Year	ID	Sex	Pregnancy status	Body length (m)	Satellite transmission interval	TDR recording interval (sec)	TDR Resolution (m)	No. of days with dive data	Data source
Hervey Bay	2004	HB 1	M	NA	3.0	1h	2	0.5	43	Sheppard (2008)
	2003	HB 2	F	*	2.9	1h	2	0.5	56	
	2003	HB 3	F	*	2.8	1h	2	0.25	42	
	2003	HB 4	M	NA	2.7	1h	2	0.25	50	
	2004	HB 5	M	NA	2.2	1h	2	0.5	44	
Moreton Bay	2011	MB 1	F	Not pregnant	2.8	1h	1	0.5	78	Hagihara *et al.* (2014)
	2011	MB 2	F	Pregnant	2.9	1h	1	0.5	77	
	2011	MB 3	F	Pregnant	2.9	1h	1	0.5	76	
	2011	MB 4	F	Not pregnant	2.7	1h	1	0.5	16	
Moreton Bay	2012	MB 5	M	NA	2.5	1	2	0.5	19	Zeh *et al.* (2015)
	2012	MB 6	M	NA	3.0	1	2	0.5	22	
	2012	MB 7	F	*	3.1	30min	2	0.5	27	
	2012	MB 8	F	*	2.2	30min	2	0.5	24	
	2012	MB 9	F	*	2.4	1h	2	0.5	28	
	2012	MB 10	F	*	2.1	1h	2	0.5	48	
	2012	MB 11	M	NA	2.0	1h	2	0.5	70	
	2012	MB 12	M	NA	2.9	30min	2	0.5	29	
	2012	MB 13	M	NA	2.5	1h	2	0.5	6	
Shoalwater Bay	2012	SWB 1	F	*	2.9	1h	2	0.5	50	Gredzens *et al.* (2014)
	2012	SWB 2	F	*	1.8	1h	2	0.5	31	
	2012	SWB 3	F	*	2.3	1h	2	0.5	50	

*Pregnancy status unknown

Depth records

All dugongs fitted with GPS units were also fitted with archival TDRs Mark 7 or Mark 9 TDRs (Wildlife Computers, WA, USA). The depth accuracy of the TDRs was either 0.25 m for Mark 7 or 0.5 m for Mark 9 (Table 2.1). TDRs attached to dugongs in Moreton Bay 2011 recorded depth every 1 s and 2 s for dugongs tracked in Hervey Bay 2003/2004, and Moreton Bay 2012, and Shoalwater Bay 2012 (Fig. 2.2). Temperature and light levels were recorded every 10 min. Depth data were retrieved using software *HexDecode* provided by the manufacturer.

Environmental data

Environmental data were obtained from other researchers or institutions. I used bathymetry models generated by Beaman (2010) (spatial resolution 100 m) for eastern Queensland and Lewis (2001) (spatial resolution 250 m) for Torres Strait. Tidal records were obtained from Maritime Safety Queensland (Department of Transport and Main Roads 2011, 2012) and National Tidal Centre (Bureau of Meteorology 2011). Tidal predictions replaced actual tidal heights when such data were unavailable (Twin Island, Torres Strait). Tidal heights were recorded in 10-min increments, and 6-min increments for tidal predictions. Bathymetry models in conjunction with tidal records were used to estimate water depth at the time of each location fixed by GPS units.

I used a GIS-based seagrass model to interpret dugong behaviour over seagrass meadows (Chapter 4). The model produced by Roelfsema *et al.* (2014) was generated using field sampling (video, snorkelling observations, and transect surveys) and high resolution satellite imagery taken in June 2011 (Roelfsema *et al.* 2009). This timing matched the period of four dugongs tracked in Moreton Bay (between May and August 2011; Table 2.1). The spatial accuracy of the seagrass model was ± 10 m. The spatial extent of the model (<3 m deep at low tides) was determined by the depth limits of Landsat 5 Thematic Mapper satellite imagery.

2.3 Dugong tagging sites

Moreton Bay, Hervey Bay, and Shoalwater Bay were selected as tagging sites because they consistently support relatively large, healthy dugong populations. Dugongs occur in clear shallow water over the Eastern Banks of Moreton Bay (Lanyon 2003; Sobtzick *et al.* 2014) and Burrum Heads of Hervey Bay (Sheppard 2008), and over shallow banks along the coastal areas of Shoalwater Bay. Shallow banks provide ideal environments to locate and capture dugongs for fitting tracking apparatus.

2.3.1 Moreton Bay

Moreton Bay (27.39°S; 153.32°E) is a large sub-tropical embayment located in southeast Queensland, Australia (Fig. 2.2A). The bay is designated as a Marine Park to protect its marine and coastal environments (Queensland Department of Environment and Resource Management 2012). Four elongated islands (Moreton, North and South Stradbroke, and Bribie) shelter the bay forming a wedge-shaped embayment. The bay is approximately 32 km wide and 74 km long and covers a total area of approximately 1,500 km^2. Most of Moreton Bay is <10 m deep with an average depth of 6.8 m (Lawrence 2010). The maximum tidal range is *ca.* 2.5 m (The State of Queensland, Department of Transport and Main Roads 2012).

2.3.2 Hervey Bay

Hervey Bay (-25.20°S; 152.45°E) is situated close to the southern border of the Great Barrier Reef World Heritage Area (GBRWHA) and forms part of the Great Sandy Marine Park (Fig. 2.2B). The funnel-shaped embayment is sheltered by Fraser Island to the east. About a quarter of the bay is <10 m deep, 50% in 10–20 m deep, and only 1% in >30 m deep (Beach Protection Authority 1989). The maximum depth of adjacent Great Sandy Strait is 4 m (Cagnazzi *et al.* 2011). The tidal range is 4.1 m (Bengtson Nash *et al.* 2005).

2.3.3 Shoalwater Bay

Shoalwater Bay (-22.20°S; 150.20°E) is within the Great Barrier Reef Marine Park (GBRMP) and GBRWHA. The bay has restricted access and reserved as the military training area since 1965, and is relatively undisturbed (Lee Long *et al.* 1997). Most of the bay is <10 m deep, and its maximum water depth is reported to be 11 m (Lee Long *et al.* 1997). The extensive inter-tidal and sub-tidal seagrass communities are subjected to a large tidal range of 7 m (Arthur *et al.* 2006).

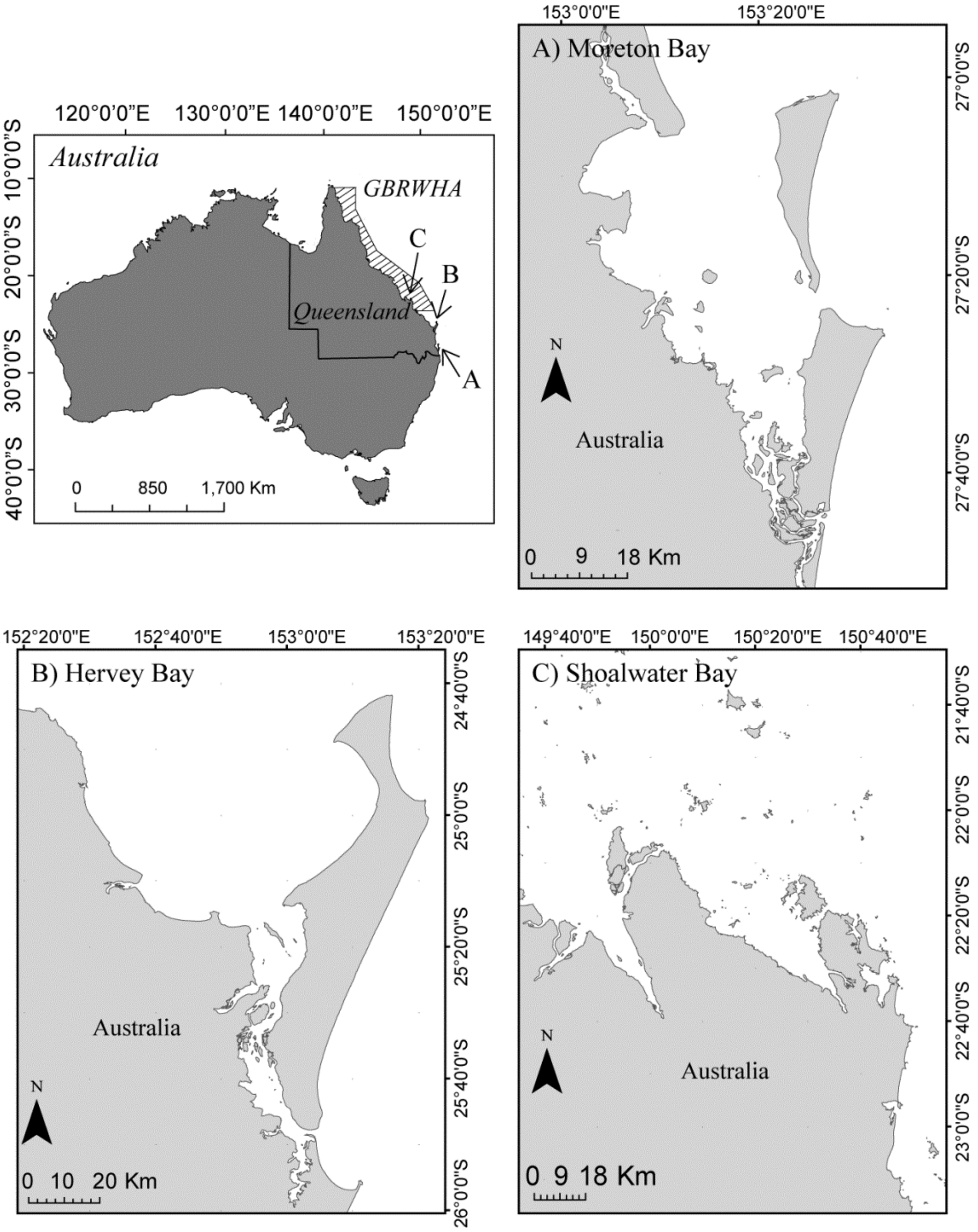


Figure 2.2 Three important dugong habitats in Queensland, Australia where dugongs were tracked: A) Moreton Bay; B) Hervey Bay; and C) Shoalwater Bay. Moreton and Hervey Bays are marine parks. Shoalwater Bay, a military training area mostly closed to the public, is situated within the Great Barrier Reef Marine Park (GBRMP) and World Heritage Area (GBRWHA).

2.4 Data manipulation

2.4.1 Initial data processing

The dive records were pre-processed using custom software *SpikeScrubber* developed by R. Jones (PhD supervisor), which executed the following three functions: 1) split the dive records sequence into manageable one-day recordings; 2) adjusted the water surface (zero-offset) by taking the minimum depth readings recorded during each 15-min interval; and 3) removed spikes, *i.e.*, biologically implausible rapid changes in depth (Fig. 2.3A; Hagihara *et al.* 2011). The duration for surface adjustment needed to be long enough to include at least one, and preferably several, surfacing events, but long enough so that little or no drift was contained in the adjusted depth records. Estimates of maximum dive duration for dugongs vary considerably between studies; the longest dive reported is 12.4 min (Chilvers *et al.* 2004). In my data set, there were normally at least 3 surfacing events during each 15-min interval.

Tracking data collected within 3 days of tag deployment were discarded to avoid any potential post-release behavioural responses. However, no apparent changes in diving patterns were observed in the three days after deployment. Capture and handling did not appear to trigger a flight response in most tagged dugongs and most dugongs stayed in the vicinity of the capture area (Sheppard *et al.* 2006; Hagihara *et al.* 2014). The number of days with both GPS fixes and dive records varied from 6 to 77 days for individual dugongs (mean = 42.2 days, SE = 21.0 days).

2.4.2 Subsequent data processing

I used the dive data in two different formats: dives profiled by the dive analysis package *diveMove* (ver 0.9.7) (Luque 2007) used in R Environment (Fig. 2.3B); and raw depth records (Fig. 2.3C). I chose *diveMove* on the basis of its open source status, flexibility, relative ease of use, and capacity to produce dive profiles and statistics. *diveMove* delineates the diving and surfacing phases of continuous behaviour based on user-defined thresholds, zero offset and dive threshold. Chapter 3 describes how I quantitatively determined the thresholds of these two parameters while minimizing the errors in dive reconstruction. Using the methodology described in Chapter 3, Chapter 4 examines dive parameters obtained from *diveMove* (*e.g.*, descent/ascent rate, bottom time, and maximum dive depth) to draw insights into dugong diving behaviour. I used raw depth records in Chapters 5 and 6 to estimate how long the dugongs spent at the surface for estimating availability bias and population abundance.

Linking location and depth records or dives

Data in both formats (dives and raw depth records) were sub-sampled around a GPS or QFP fix for a 10-min block (Fig. 2.3D). This technique ensured reasonably accurate association of external information (water depth, tide, and seagrass presence/absence) to dives or depth records to reflect environmental conditions experienced by tagged dugongs at the time of each satellite uplink. The beginning and ending of a dive often did not coincide with the onset and cessation of a 10-min block. Thus all dives that started after the start of the block were sub-sampled, which means a dive could end after a 10 min block (Fig. 2.3B). The raw depth records comprised individual depth records. Their subset was simply extracted from a 10-min block (Fig. 2.3C). This sub-sampling technique also reduced auto-correlation. For instance, a dive that was made at 10:00 probably has different nature to a dive made at 11:00. The sub-sampled data were associated with environmental features (water depth and seagrass attributes) using ArcGIS and custom software *DepthMatcher* (by R. Jones).

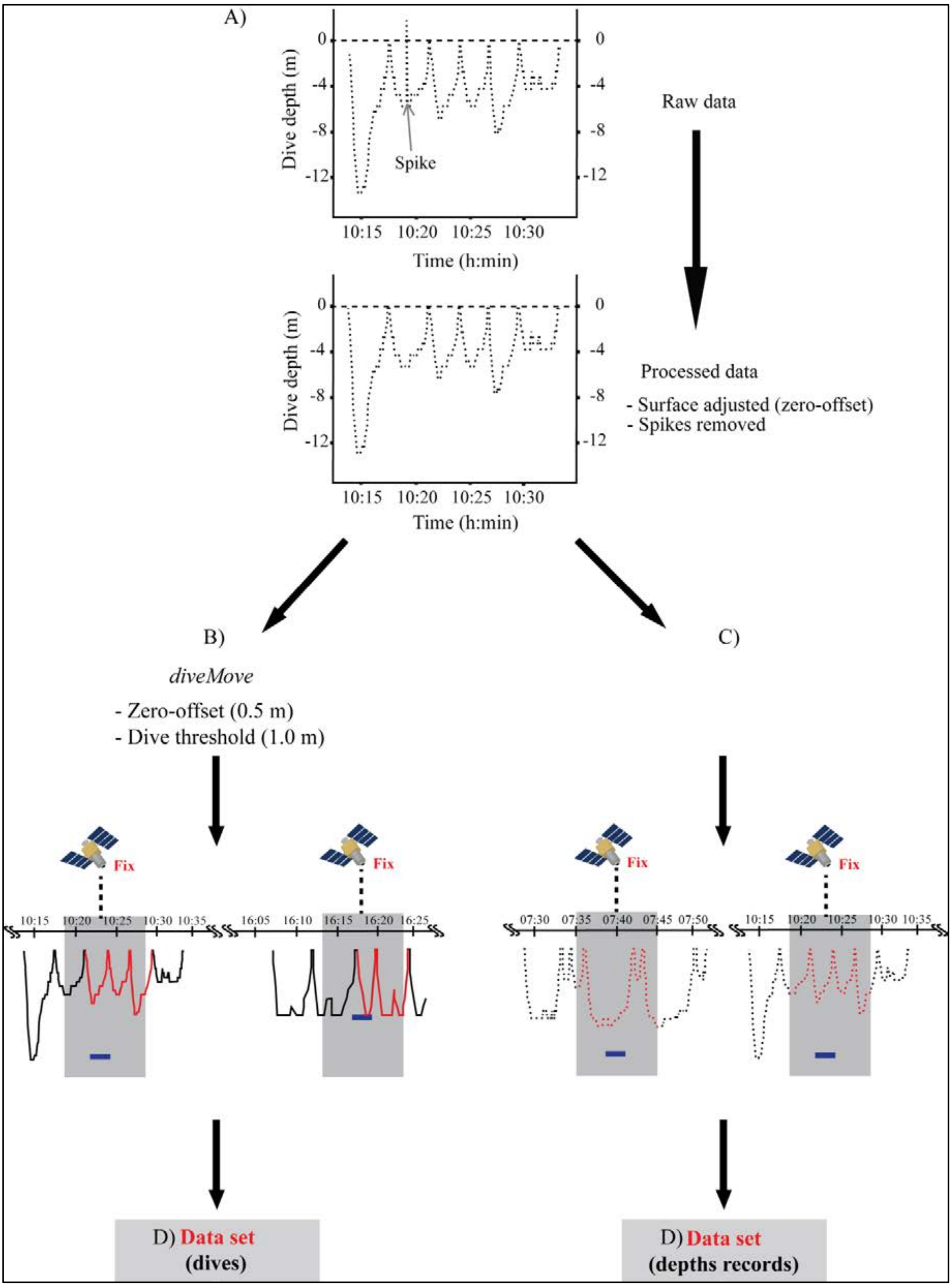
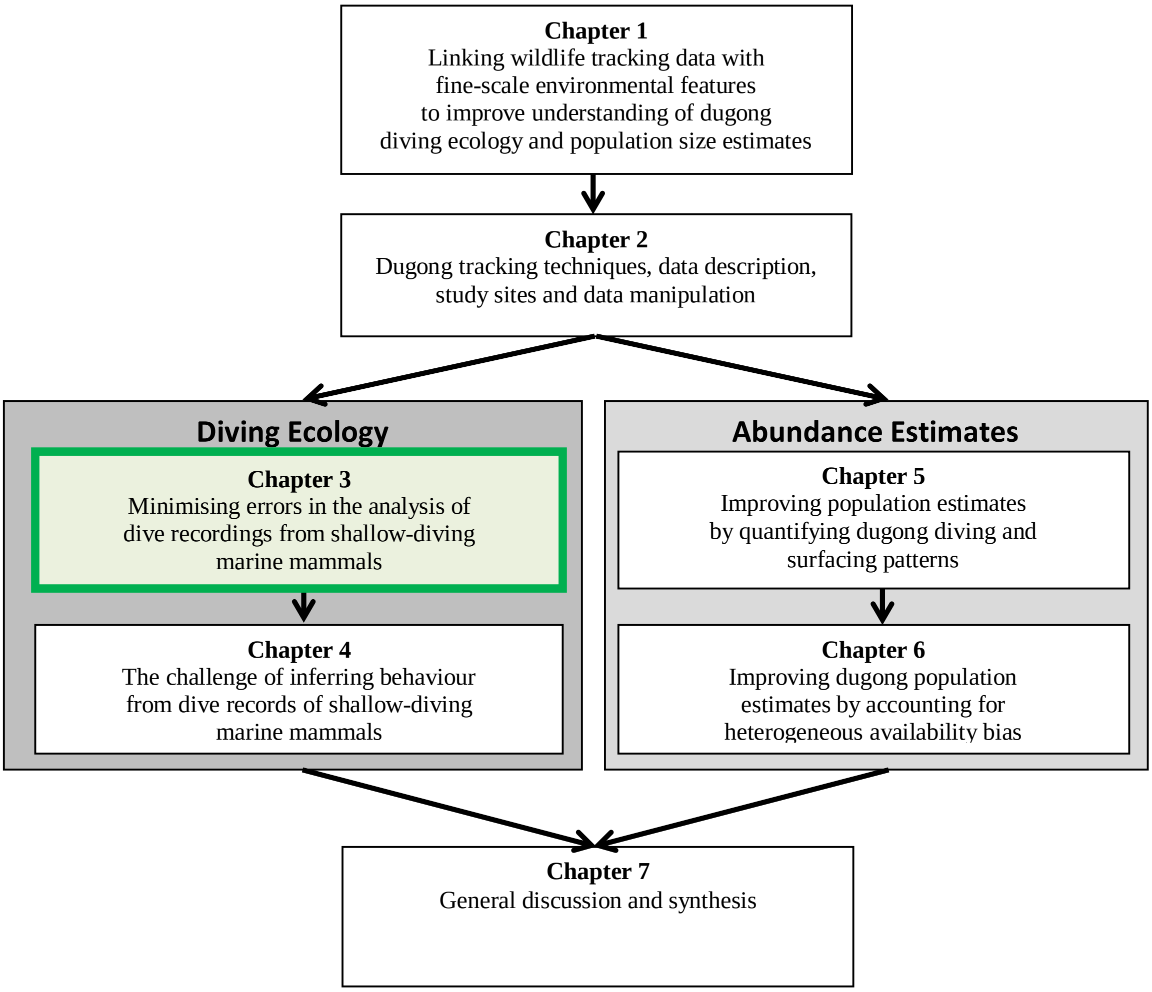


Figure 2.3 Schematic diagram of the data manipulation I undertook: A) depth data cleaned by correcting for zero-offset and removing spikes using custom software; B) dives profiled using *diveMove*; C) raw depth records; and D) sub-sampled data represented in red that are found within the 10 min block before and after each fix.

2.5 Chapter summary

- This thesis is based on data collected from GPS satellite transmitters and time-depth recorders (TDRs) fitted to dugongs caught using the rodeo technique in Moreton Bay, Hervey Bay, and Shoalwater Bay in eastern Queensland.
- These three embayments are important dugong habitats supporting extensive seagrass meadows and carry health dugong populations.
- Data external to the dugong tracking (bathymetry models, tidal records, and a seagrass model for Moreton Bay) were obtained from other researchers or institutions.
- The data manipulations common to all the data chapters in my thesis include:
    1. Splitting the dive recordings into manageable one-day recordings;
    2. Adjusting the water surface (zero-offset);
    3. Removing spikes; and
    4. Sub-sampling the data found within the 10 min block surrounding GPS fixes;
    5. Associating the sub-sampled dives or depth records with environmental features.

Chapter 3: Minimising errors in the analysis of dive recordings from shallow-diving marine mammals[1]



Knowledge of the diving behaviour of aquatic animals expanded considerably with the invention of time-depth recorders (TDRs) in the 1960s. The large volume of data acquired from TDRs can be analysed using dive analysis software, but the application of such software has received relatively little attention. This chapter presents an empirical procedure to select optimum values for the two parameters that are critical to obtaining reliable dive identification: the zero-offset correction (ZOC) and the dive threshold (DT). I use dive data from shallow-diving coastal dugongs and visual observations from an independent study to develop and test the procedure.

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[1] Chapter 3 has been published as Hagihara, R., R.E. Jones, J.K. Sheppard, A.J. Hodgson & H. Marsh. 2011. Minimizing errors in the analysis of dive recordings from shallow-diving animals. *Journal of Experimental Marine Biology and Ecology* 399:173-181.

Chapter 3: Minimizing errors in the analysis of dive recordings from shallow-diving marine mammals

3.1 Introduction

Since their invention in the 1960s, time-depth recorders (TDRs) have helped elucidate the diving behaviour of numerous aquatic animals in the wild. Technological advances have enabled the size and weight of the TDR to be reduced and the information the TDR can store to expand. As a result, TDRs have been deployed on a wide variety of animals including sharks (*e.g*., Graham *et al.* 2006), fish (*e.g*., Hobson *et al.* 2007), marine reptiles (*e.g*., Rice and Balazs 2008), birds (*e.g*., Culik *et al.* 1996), and marine mammals (*e.g*., Kooyman 1965, Biuw *et al.* 2009).

Researchers use commercially available or custom-made dive analysis programs to analyse the massive amount of dive data collected from either depth loggers that require their retrieval for data acquisition (*e.g*. Hays *et al.* 2007; Sheppard *et al.* 2006) or sophisticated on-board satellite relay data loggers (SRDLs) which compress and summarize data for signal transmission to ARGOS satellites (*e.g*. Burns and Castellini 1998; Hochscheid *et al.* 2005; Myers *et al.* 2006). The analysis program constructs a dive by taking a series of depth readings at pre-programmed intervals with user-defined parameters that are suitable for the study animal (Luque 2007). The use of these programs has greatly increased the efficiency of the analysis. Nonetheless, the application of the software has received surprisingly little attention.

The arbitrary choice of user-defined parameters can result in erroneous conclusions about dive parameters (*e.g*., descent and ascent times and rates), dive statistics (*e.g*. average number of dives per day, dive duration and maximum dive depth), and their interpretation (*e.g*., feeding frequency, energetics). Validation of such results is however extremely difficult or impossible without access to parallel information from other methods such as visual observations; this information is rarely available due to logistical constraints and/or the elusive nature of target species. Hence dive data requires caution in processing.

As explained in Chapter 2, before any analysis, dive recordings require initial processing to define the surface level. This surface adjustment is often known as the zero-offset correction (ZOC) and is necessary as the surface value recorded by TDRs may shift due to:

1. Drift in the surface reading as a result of changes in barometric pressure and temperature;
2. Wave action causing the TDR to be underwater even though the animal is at the surface; and/or
3. Animal behaviour (*e.g.*, the TDR may be fixed on a body part that remains underwater when the animal surfaces).

If the ZOC is set too small, the dive package may mistakenly identify noise produced by external factors as dives. In contrast, if the ZOC is set too large, the package will fail to identify actual shallow dives; too few dives will be identified. Dive depths will also be underestimated because the "start" of the dive will be too deep.

Many diving studies using TDRs correct water surface either manually choosing different values for different parts of the records or using the ZOC function (*e.g.* Gordos and Franklin 2002; Bodkin *et al.* 2004; Hays *et al.* 2007; Hazel 2009; Witt *et al.* 2010), without any indication of how and what ZOC values were chosen, or whether the resulting dive depths were consistent with bathymetry – that is, whether estimated dive depths remain within the water depth at the animal's location. Bathymetric validation is often impossible, either because the animal's location is unknown or because fine-scale bathymetry data are not available. Some studies do not mention the ZOC, although the surface level seems to be corrected (*e.g.*, Boveng *et al.* 1996; Arnould and Hindell 2001; Baechler *et al.* 2002; Fossette *et al.* 2008). Most dive software allows the user to manually set the ZOC at different values, however, when depth data have been collected every few seconds for a period of months, the resulting datasets make manual correction daunting.

Another key user-defined parameter is the dive threshold, which is generally applied after the ZOC (water surface) value has been set. The dive threshold defines the minimum depth below which a sequence of dugong depth estimates is considered a "dive". That is, a dive consists of a series of depth readings, starting at 0 m (surface), which is set using the ZOC, and progressing beyond a depth which is determined by the dive threshold, to a maximum depth, then returning back to 0 m (surface).

The choice of dive threshold also requires consideration. If the dive threshold is set too small (shallow), there will be numerous very shallow and short dives that are probably artefacts produced by the resolution of the TDRs, drift in the zero readings, wave action, *etc*. (Fig. 3.1A). In contrast, an excessive dive threshold (deep) will fail to identify actual shallow dives.

Hooker and Baird (2001) criticise the use of a dive threshold that is arbitrarily defined by many authors as twice the resolution of the TDRs. This practice seems to have originated from a company which makes dive analysis software (Hooker and Baird 2001). To my knowledge, relatively few dive studies have discussed what factors should be considered in selecting a dive threshold. Examples which do explain the choice of depth threshold include Bengtson and Stewart (1997), Arnould and Hindell (2001), Gordos and Franklin (2002), Bodkin *et al.* (2004), Chilvers *et al.* (2004), and Hays *et al.* (2007).

The arbitrary choice of the dive threshold value by many researchers probably stems from their study animals feeding in deep water and exhibiting dives many times deeper than the chosen dive threshold values (*e.g.*, northern *Mirounga angustirostris* (LeBouef *et al.* 1986) and southern (Hindell *et al.* 1991) elephant seals, and fin whales *Balaenoptera physalus* (Panigada *et al.* 1999)). Identification of shallow dives was not critical to these analyses, because the main interest was generally related to feeding behaviour, and the feeding dives of these species often occurred in deep waters. The arbitrary choice of these two parameter values for these animals is unlikely to have a substantial influence on the identification, characterisation, and interpretation of dives.

In studies of coastal/estuarine/riverine shallow-diving animals, such as sirenians, dolphins and turtles (see Elliott and Gaston 2009), the solid protocol for selecting user-defined parameters is more critical. Shallow dives (*e.g.* < 5 m) may comprise the majority of the diving behaviour of shallow-diving species and they often feed in shallow waters. For example, the dugong feeds in shallow intertidal seagrass beds, the depth of which is sometimes <1 m (Hodgson 2004). Such protocol may also be useful for some deep-diving animals which make shallow dives in different life stages (juvenile, adults), location, or season (Nolet and Kruuk 1993; Hays *et al.* 2001).

Here, I present an empirical procedure for selecting ZOC and dive threshold values by minimising errors in dive identification and characterisation. I believe this procedure is particularly applicable to the analysis of large volume of TDR data and to shallow-diving aquatic wildlife.

3.2 Materials and methods

3.2.1 Study animals, sites, and tracking units

The dugong is a relatively shallow-diving species that feeds amongst coastal seagrass communities (Heinsohn and Birch 1972; Marsh *et al.* 1982; Preen 1995b). Dugongs have been observed feeding on seagrass in waters <1 m deep (Hodgson 2004), and the deepest reported dugong dive is 36.5 m (Sheppard *et al.* 2006).

For this chapter, I used dive data collected from five dugongs tracked with TDRs in Hervey Bay, Australia between July 2003 and August 2004. The TDRs were programmed to record water pressure (depth) every 2 s. The resolution of the TDRs was either 0.1 or 0.25 m. In total, between 42 and 56 days of dive depth records were available for each dugong. Details of the tagging units/animals are given in Table 2.1.

Preliminary data processing is as described in Chapter 2 (Section 2.2 and 2.4). A total of 20 one-day (24 h) sub-samples (4 from each of the five animals) were then randomly chosen for further analysis. Dives were profiled from depth records as described in Section 2.4 using *diveMove* (ver. 0.9.7, Luque 2007) in R (ver. 2.15.3, R Development Core Team).

3.2.2 Terminology

I identified the following 4 types of dives made by dugongs (Fig. 3.1);

1. *Unrecognised dive (ZOC)* – a dive that the software failed to identify at the chosen ZOC, but was identified as a Plausible dive at a higher or lower ZOC value (Fig. 3.1A).

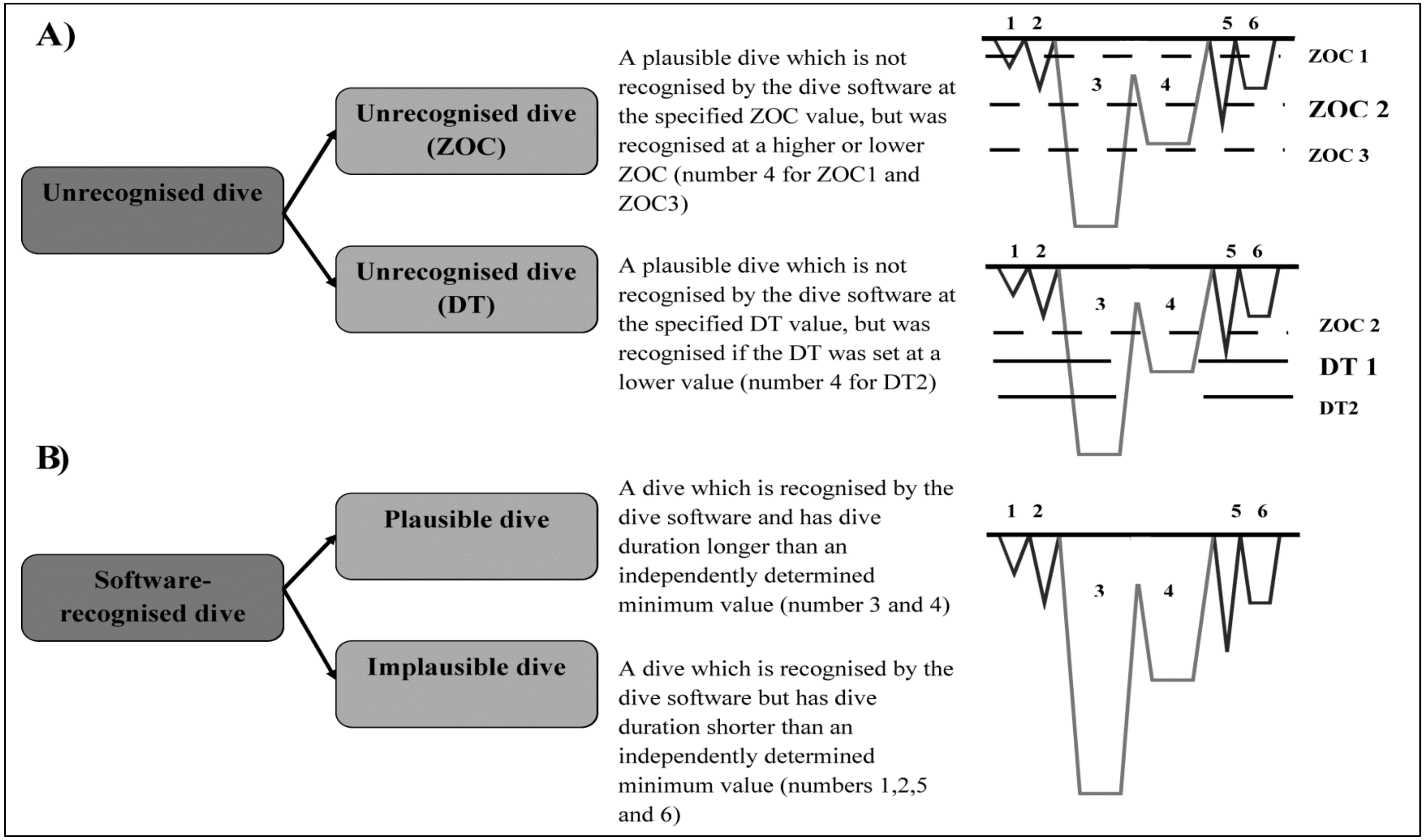
2. *Unrecognised dive (DT)* – a dive that the software failed to identify at the chosen dive threshold, but was identified as a Plausible dive at a higher or lower dive threshold (Fig. 3.1A).
3. *Plausible dive* – a dive recognised by the software that had a duration greater than the minimum dive duration “time threshold” determined from direct observation by Hodgson (2004) (see Section 3.2.4 and Fig. 3.1B).
4. *Implausible dive* – a dive recognised by the software of duration shorter than the time threshold above (Fig. 3.1B).

I used the following procedure for selecting appropriate parameter values for the ZOC and dive threshold to minimize the frequency of Implausible and Unrecognised dives and maximize that of Plausible dives.

3.2.3 Factors influencing depth readings

Five common sources of error in depth readings are (*e.g.*, Chilvers *et al.* 2004):

1. Drift in zero readings, caused by the sensitivity of the TDR pressure transducer. The transducer takes some time to adjust to rapid pressure or temperature changes after an animal equipped with a TDR makes a deep or fast dive;
2. Wave action, which varies in time and space with weather and sea conditions;
3. The depth resolution of the TDR;
4. Location of the TDR on the study animal’s body. A TDR is attached to the dugong’s tailstock (see (Sheppard 2008) for details), which can cause an error in dive identification because of the distance between the animal’s head and its tail. Based on an allometric study of dugong carcasses (Spain and Heinsohn 1975), the maximum possible difference in depth between the dugong’s head and the TDR was estimated to be approximately 2 m (2.4 m (mean body length of the 5 dugongs) – 0.33 m); and
5. The behaviour of study animals relative to the recording interval. The proportion of surfacing events recorded by a TDR will depend on the recording interval relative to the time the animal spends on the surface.



A plausible dive which is not recognised by the dive software at the specified ZOC value, but was recognised at a higher or lower ZOC (number 4 for ZOC1 and ZOC3)

A plausible dive which is not recognised by the dive software at the specified DT value, but was recognised if the DT was set at a lower value (number 4 for DT2)

A dive which is recognised by the dive software and has dive duration longer than an independently determined minimum value (number 3 and 4)

A dive which is recognised by the dive software but has dive duration shorter than an independently determined minimum value (numbers 1,2,5 and 6)

Figure 3.1 Definition of tentative dive classification using two parameters: zero-offset correction (ZOC) and dive threshold (DT) and hypothetical scenarios: A) At ZOC 1, 2 dives (numbers 3 and 4) are recognised as one dive while at ZOC 3, the dive number 4 becomes an Unrecognised dive (ZOC) because the surface level is set too deep. In this scenario, ZOC 2 is a more appropriate value. Using the ZOC 2 and DT 2, the dive number 4 becomes an Unrecognised dive (DT) because the dive threshold is set too deep. Thus DT 1 is the more appropriate; B) A Plausible dive has dive duration longer than the time threshold. Given time threshold of 16 s, the dive number 3 was 28 s long and dive number 4 was 36 s long, therefore both dives are Plausible dives. The dive numbers 1, 2, 5 and 6 are Implausible dives because they last only 4-8 s long.

I corrected the drift in zero readings (1 above) using custom software (see Section 2.4). All other sources of error except the depth resolution of TDRs (2 above) were the target of the second error minimisation described below.

3.2.4 Time threshold

A minimum time threshold was established as the basis for distinguishing Plausible from Implausible dives and was based on the dive duration obtained from 126 focal follows (mean duration = 12 min 32 s) of 56 individual dugongs in clear water <5 m deep using a blimp-cam – a video camera mounted in a blimp (Hodgson 2007). A total of 287 dives were used to estimate minimum dive duration. I used a bootstrap approach with 1,000 replications to estimate the values (95% confidence limits) above which 99% of observations were expected to fall in S-plus statistical package (TIBCO Software Inc., Seattle, USA).

3.2.5 Optimum zero-offset correction (ZOC)

The optimum ZOC is the value that consistently gives the largest proportion of Plausible dives (lasted longer than my time threshold) across dugongs and days. The proportion of Plausible dives was obtained using ZOC values of 0, 0.5, 1, 1.5, 2 and 2.5 m in *diveMove*. The count of Unrecognised dives (ZOC) was made visually for ZOC = 0 m and by sequential pair-wise comparisons thereafter. The dive threshold was kept constant as 1 m. A factorial ANOVA with unplanned comparisons ($\alpha = 0.05$) was used to compare the mean proportions at each ZOC value. The arcsin transformation was applied to normalise the response variable of proportion. Individual dugong was treated as a second explanatory variable to examine its contribution to the variable in the mean proportions.

The proportion of Plausible dives was calculated as:

$$Proportion\ of\ \ Plausible\ dives = \frac{PD_{ZOC_x}}{PD_{ZOC_x} + UD(ZOC)_{ZOC_x}}$$

Where,

PD_{ZOC_x} = the number of Plausible dives using a ZOC of x m

$UD(ZOC)_{ZOC_x}$ = the number of Unrecognised dives (ZOC) using a ZOC of x m

3.2.6 Optimum dive threshold

I used dive thresholds of 0.4, 0.9, 1.4 and 1.9 m to compensate for the different depth resolutions of the TDRs. These numbers were used because *diveMove* identifies a dive when the observed depths move beyond a specified dive threshold. For example, the 0.4-m dive threshold enabled me to identify dives $\geq$0.5 m for all resolutions. The range of the selected dive threshold values (0.4 to 1.9 m) covered 1.5 m which was the dive threshold used in Chilvers *et al.* (2004).

The proportion of Implausible dives was calculated as:

$$Proportion\,of\;\;implausible\;dives = \frac{ID_{DT_X}}{PD_{DT_X} + ID_{DT_X}}$$

Where,

$ID_{DT_x} =$ the number of Implausible dives using a dive threshold of x m

$PD_{DT_x} =$ the number of Plausible dives using a dive threshold of x m

The proportion of Unrecognised dives (DT) was calculated as:

$$Proportion\,of\;\;Unrecognized\;\;dives\;(DT) = \frac{PD_{DT_{\min}} - PD_{DT_X}}{PD_{DT_{\min}}}$$

Where,

$PD_{DT_{\min}} =$ the number of Plausible dives using a minimum dive threshold

$PD_{DT_X} =$ the number of Plausible dives using a dive threshold of x m

I determined the optimum dive threshold value that minimised the proportion of Implausible dives and Unrecognised dives (DT) and maximised that of Plausible dives;

that is where the two variables intersect (Reeb and Leavengood 1988). As the dive threshold increased, the number of Implausible dives decreased, but the number of Unrecognised dives increased

3.2.7 Supplemental cross-check

To cross-check the ZOC and dive threshold values determined above, I examined the frequency distributions of dive durations obtained from *diveMove* at the ZOC threshold selected above and three dive thresholds (0.4, 0.9, and 1.4 m) and compared them with the frequency distribution of the visual observation from the independent visual observational study of dugongs (Hodgson 2007).

3.3 Results

3.3.1 Time threshold

The bootstrap technique indicated a threshold submergence time of 16 s (95% CI = 12 to 20 s). Therefore a dive that had submergence time $\geq$16 s was classified as a Plausible dive, otherwise Implausible dive.

3.3.2 Optimum zero-offset correction (ZOC)

The total number of Plausible dives varied with ZOC values, dugong, and day, ranging from 44–647 dives (mean = 335.8 ± 149.7) per dugong per day. The total number of dives increased initially with increasing ZOCs, usually peaking around 1 m ZOC. The frequency of Unrecognised dives (ZOC) was minimised at the value of 1 m (mean = 47.2 ± 8.2 dives). The factorial ANOVA showed a significant difference among ZOCs in the mean proportions of Unrecognised dives (ZOC) ($F_{5,90}$ = 92.47, $p < 0.0001$). Post-hoc Tukey tests showed that all possible differences were significant, except between ZOC 0.5 and 1 m.

The proportion of Plausible dives was the highest at ZOC 0.5 m for “HB 1” and at 1 m for the rest of the animals with the mean dive number of 464.9 ± 23.0 dives at 1 m dive threshold (Fig. 3.2). The proportion of Plausible dives was the mirror of the proportion of Unrecognised dives (ZOC). The factorial ANOVA showed again a significant difference across ZOCs in the mean proportions ($F_{5,90} = 92.47$, $p < 0.0001$). Post-hoc Tukey tests indicated a significant difference in all combinations of the mean proportion, except between ZOC 0.5 and 1 m.

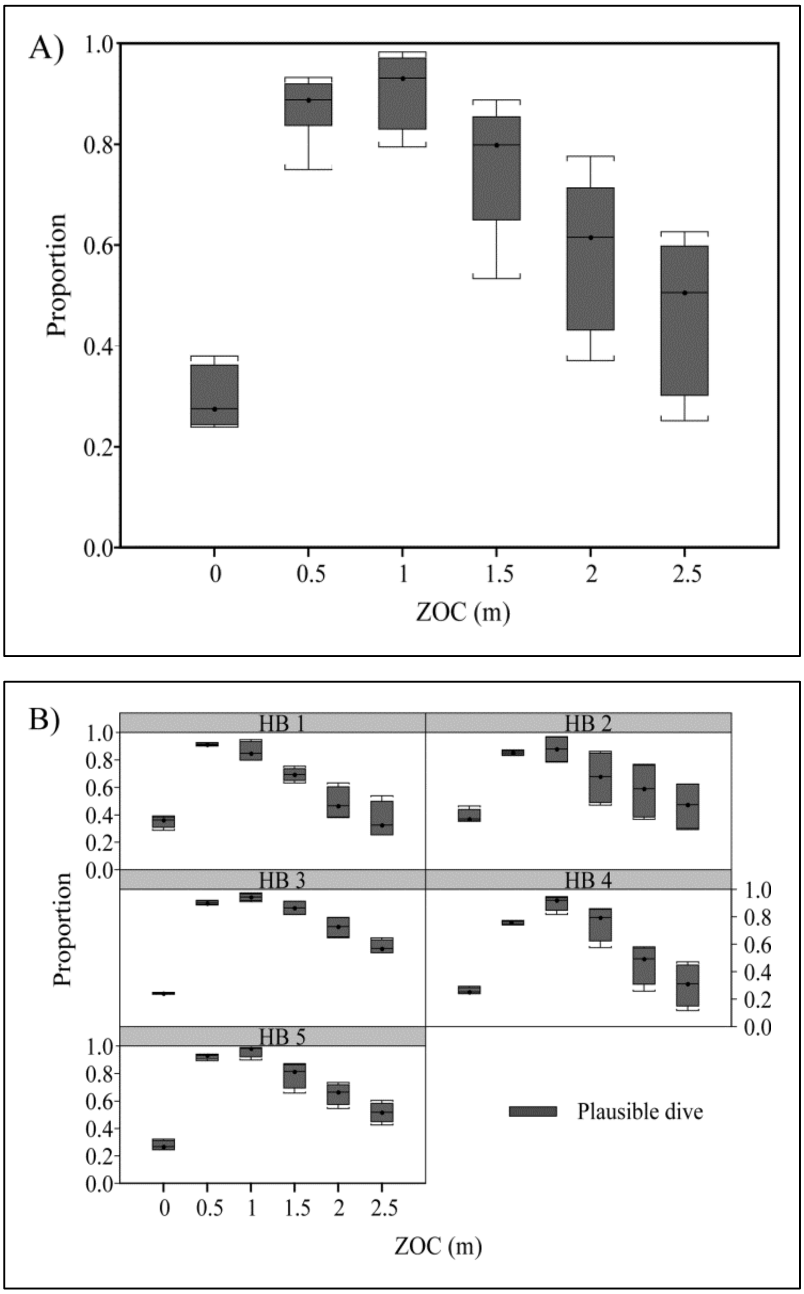


Figure 3.2 A box plot of the proportion of Plausible dives across different ZOC values (0, 0.5, 1, 1.5, 2 and 2.5 m) with all five dugongs combined (A) and individually (B) plotted. The graphs indicate that 1-m ZOC maximises the proportion of Plausible. The dots represent the median.

The effect of individual dugong was also significant ($F_{4, 90} = 6.28$, $p < 0.0002$), although there was no interaction between ZOC and individual dugong ($F_{20, 90} = 1.46$, $p = 0.11$). This means that although different dugongs had different numbers of dives each day, the effect of the ZOC value did not differ among dugongs. The ZOC of 1 m was therefore used for all animals in the subsequent sections.

3.3.3 Optimum dive threshold

The total number of Plausible dives varied from 111–913 dives per dugong per day (mean = 504.8 ± 194.3) and decreased as the dive threshold increased. The proportions of Implausible dives dropped sharply close to 0 at dive thresholds above 0.5 m for most dugongs, while the proportion of Unrecognised dives (DT) increased slowly (Fig. 3.3). The two lines of Implausible dives and Unrecognised dives (DT) intersected near a dive threshold of 0.75 m, which was the optimum value from Unrecognised dives + Implausible dives.

The dive threshold of 0.75 m was the optimum value; however 0.9 m was used to compensate for different resolutions of TDRs (0.25 and 0.5 m). If all TDRs had a similar resolution, for example 0.25 m, 0.75 m was used instead as the dive threshold, which would in practice have meant that submergence depths of 1 m or more were identified as dives.

3.3.4 Supplemental cross-check

The frequency distribution of dive durations using a dive threshold of 0.4 m (which identified dives $\geq$0.5 m) had very different patterns from those of the visual observations of dugong diving behavior (Fig. 3.4 A,B). With a 0.4 m-dive threshold, Implausible dives (*e.g.* $\leq$8 s) were over-represented (N = 15,064), indicating that using a dive threshold of 0.4 m, many of these dives identified are probably artifacts from noise. In contrast, the frequency distributions using a dive threshold of 0.9 and 1.4 m were similar (both of which identified dives with 1 and 1.5 m or more, respectively) to the one from visual observations. Using a dive threshold of 0.9 m, however, there were 2,500 dives more (N = 10,701, >30%) than when using a dive threshold of 1.4 m (N = 8,188).

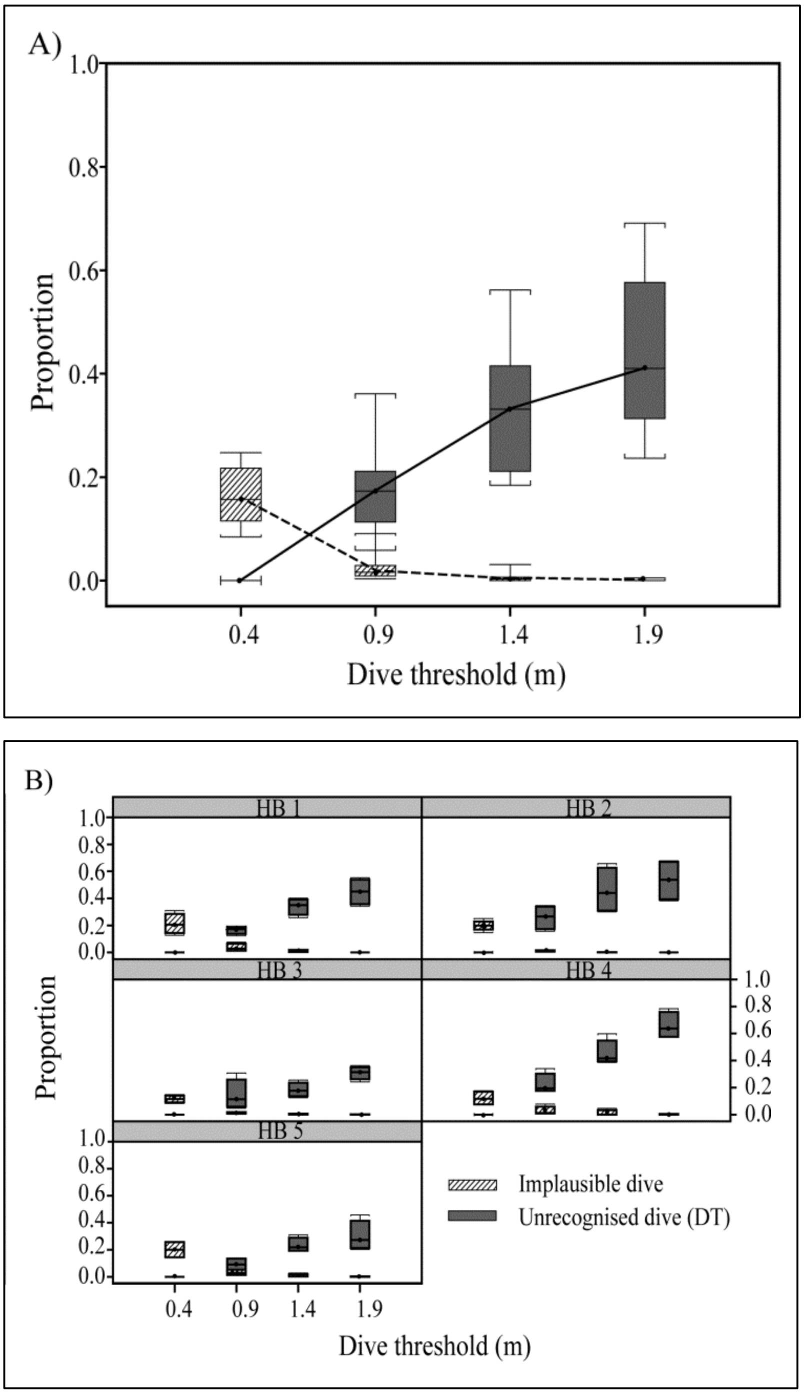


Figure 3.3 A box plot of the proportion of Implausible dives using various dive thresholds (0.4, 0.9, 1.4, and 1.9 m), combined (A) and individually (B) plotted. The two variables of Implausible dives and Unrecognised dives (DT) intersect at around 0.75 m, indicating the optimum minimum dive depth.

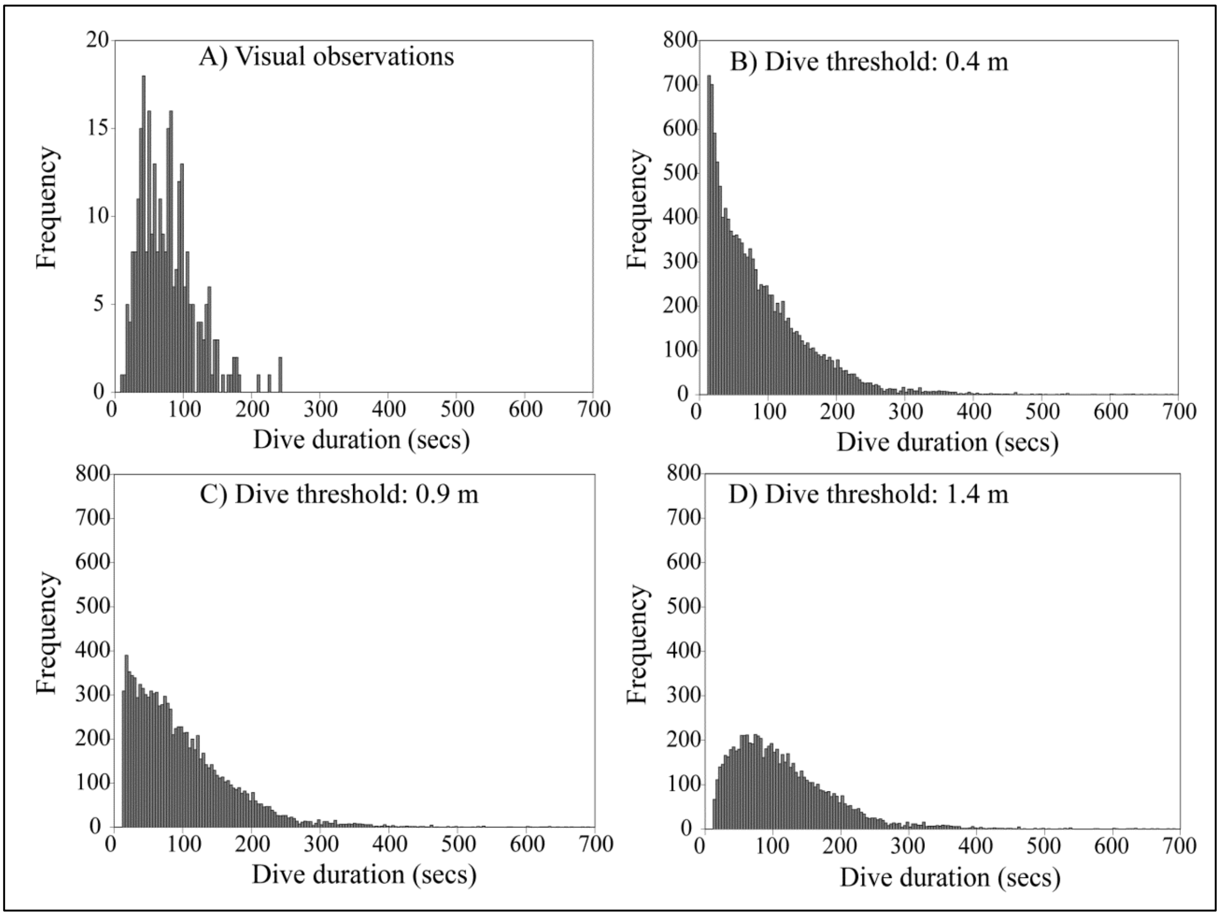


Figure 3.4 Frequency distribution of dive durations from: A) a blimp-cam observation of wild dugongs in ≤5 m (A. Hodgson unpublished data) (N = 247) and TDR data from five dugongs with ZOC 1 m; B) dive threshold 0.4 m (N = 15,064); C) 0.9 m (N = 10,701); and D) 1.4 m (N = 8,188). The figures represent only Plausible dives ≤5 m deep to correspond with the blimp-cam observations.

3.4 Discussion

3.4.1 Empirical approach

This chapter presented an empirical procedure for determining the optimum values for two fundamental user-defined parameters common to the analysis of animal depth data: the surface correction known as the zero-offset correction (ZOC) and the dive threshold (DT). I determined each optimum value by identifying Unrecognised dives (ZOC or DT), Plausible, and Implausible, and in the dive analysis output and choosing the values that maximised Plausible dives and minimized the sum of Implausible and Unrecognised dives.

The approach initially removed errors introduced by drift in the zero-reading using the custom software. The drift which is presumably caused by changes in barometric pressure and temperature was corrected for every 15-min of the deployment periods. The interval was long enough to capture ≥3 surfacing events. The second error minimisation involved the use of the open-source software *diveMove* and aimed to minimise errors that were introduced by wave action, location of TDRs on the study animal's body, and behaviour of the animal relative to the sampling interval. The procedure is summarized in Fig. 3.5.

Zero-offset correction (ZOC)

Using the methodology described here, the optimum ZOC value was 1 m, the value that resulted in the largest numbers of Plausible dives and smallest numbers of Unrecognised dives (ZOC) in most animals on most days. Individual animals differed in their average proportion of Unrecognised dives (ZOC). The interaction term between ZOC and individual dugong was however insignificant, indicating the common ZOC value was suitable for all animals. Consequently, I used the ZOC of 1 m for all five dugongs. If the data had indicated that different ZOC values were required for different animals, this could have been incorporated in the procedure.

1 Preliminary clean-up of TDR data

- Divide depth readings into one-day sampling units
- Remove spikes
- Calibrate surface depth to 0 m at 15-min interval

2 Identify potential factors

- Recognise factors *(e.g.*, position of TDRs on animal's body) and the range of error in depth readings

3 Establish time threshold

- Determine the minimum dive duration from visual observations of diving behaviour using bootstrap technique

4 Define dive types

- Classify dives into:
    - Plausible and Implausible dives based on the time threshold
    - Unrecognised dives (ZOC or DT)

5 Determine the zero-offset correction (ZOC)

- Count Plausible and Unrecognised dives (ZOC) and plot their proportions against ZOC values
- Identify the ZOC giving a maximum proportion of Plausible dives

6 Determine the dive threshold (DT)

- Count Plausible, Implausible and Unrecognised dives (DT) and plot their proportions against dive thresholds
- Identify the intersection of the proportions of Implausible and Unrecognised dives (DT)

7 Validate the ZOC and dive threshold with histogram

- Plot the histogram of dive durations obtained from the visual observations and depth readings from TDRs
- Identify which dive threshold value from TDRs gives a similar distribution pattern to the one from the visual observation

Figure 3.5 Sequence of analysing depth readings from shallow-diving dugongs. Visual observations used to determine the "time threshold" can be modified with depth data being examined by manually inspecting dive profiles. Additional parameters (*e.g.*, thresholds for speed or wet/dry period) appropriate to studies of other diving animals can also be included.

Dive threshold

The 0.9-m dive threshold was smaller than the value used in Chilvers *et al.* (2004) (1.5 m dive threshold, 0.25 and 0.4 m resolution of TDRs, 1 and 5 s sampling interval). Chilvers *et al.* (2004) manually examined dive profiles to determine the value while considering sources of errors in depth data. The discrepancies in the dive threshold chosen here and their study indicate that the smaller dive threshold value can be obtained with an empirical procedure. Some real shallow dives may have been missed in the previous studies.

The dive threshold identified here falls within the range of values used in other studies of shallow-diving animals, although a formal comparison cannot be made and is probably not meaningful: 0.2 m (American minks *Mustela vison*; Hays *et al.* 2007), 0.45 (freshwater turtles *Rheodytes leukops* and *Emydura macquarii*; Gordos and Franklin 2002), 1.5 m (green turtles; Seminoff *et al.* 2006), 2 m (common guillemots *Uria aalge*; Tremblay *et al.* 2003), 3 m (leatherback turtles *Dermochelys coriacea*; Fossette *et al.* 2008).

Cross-check

Using the 1-m ZOC and 0.9-m dive threshold, the frequency distribution of dive durations from Hodgson’s visual observations and the TDR data from five tracked dugongs presented similar distribution patterns (Fig. 3.4), supporting the choice of these two parameters. I could not draw parallel comparisons between the frequency distributions of the minimum dive depth between the visual observations and the TDR data because the depth records from the visual observations were unavailable.

3.4.2 Error in depth records

The small dive threshold implies that the sources of error (wave action, location of TDRs on animals’ body and animal behaviour relative to sampling interval) had minimum influence on dive records from the five dugongs tagged in Hervey Bay. These dugongs mostly occurred in shallow areas or sheltered embayments. The range of error was initially expected to be at least 2 m since I consider the maximum length between the head and the trail stock was estimated as 2 m.

Although the sampling interval influences results obtained from data loggers (Boyd 1994; Myers *et al.* 2006; Hays *et al.* 2007), the frequent sampling interval (2 s) of the TDRs deployed to these dugongs appeared to adequately capture the dugong's surfacing events despite these existing sources of errors. In future, it is possible to test systematically whether these parameter values vary with environmental conditions. For example, smaller parameter values might be used when interpreting dives from an animal that occurs in sheltered bays and larger values used with an animal moving through exposed open seas.

3.4.3 Future studies

The category "Implausible dive" could be expanded to include dives identified by the software that extend well beyond the known diving capacity of the study animal. The *diveMove* software identified several dives ≥700 s. Upon visual inspection of the dive profiles, however, many of these longer dives showed two or more obvious surfacing movements. As a result, my analysis would be improved by further independent estimates of maximum dive duration to set an upper as well as lower "time threshold".

When submergence time from visual observations is not available, as is often the case for free-ranging animals, the minimum as well as maximum time threshold could be estimated from a visual inspection of the dive records to identify the shortest and longest "well-formed" dive profiles. Such an approach however requires careful examination of numerous dives, preferably with a quantitative basis, as surprisingly long dives can be real (*e.g*. Hochscheid *et al.* 2005). Implementation of the methodology presented in this chapter relied on the availability of an estimate of minimum dive duration for a "time threshold", because dive depths alone did not provide a robust basis for discriminating a dive from artefacts. The time threshold was obtained from an independent visual behavioural study of dugong diving by Hodgson (2004).

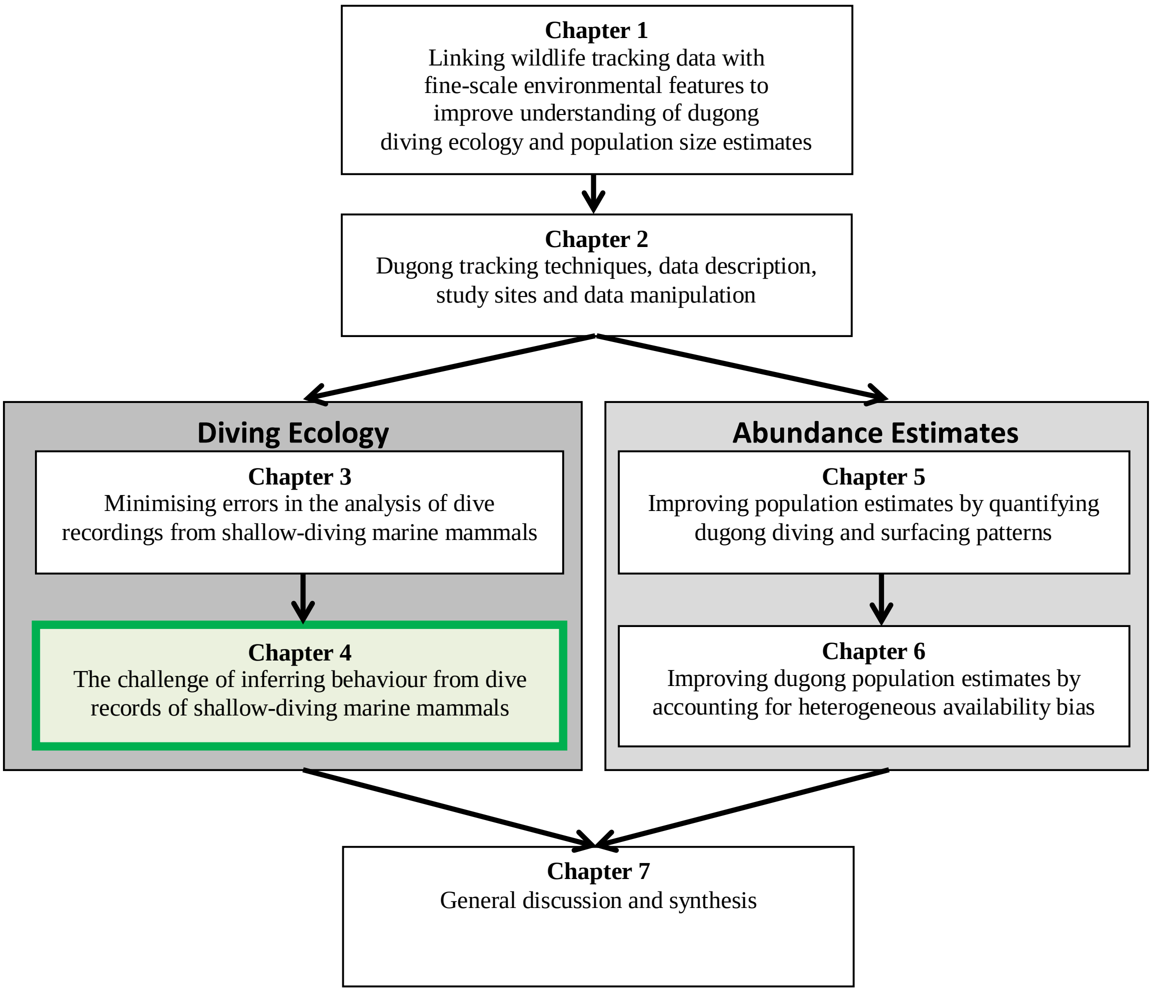
3.4.4 Challenges

The inherent issues associated with the correct identification of a dive from depth data are common to all diving animals. Deep-diving animals make shallow dives in particular locations (*e.g.*, breeding area), in different life stages or between deep dives (Nolet *et al.* 1993; Hays *et al.* 2001; Elliiott and Gaston 2009). The correct identification is however more critical to studies of shallow-diving animals as these animals spend most or all the time in shallow areas (Croll *et al*. 1992; Hays *et al.* 2007; Hodgson 2004). The approach presented here has potential application to a wide range of studies of aquatic species, and should be particularly useful for studies of shallow-diving animals, such as sirenians, dolphins and turtles.

3.5 Chapter summary

- The large volume of data acquired from TDRs can be analysed using dive analysis software, but the application of such software has received relatively little attention.
- The empirical procedure presented in this chapter selected optimum values for the two parameters that are critical for obtaining reliable results: the zero-offset correction (ZOC) and the dive threshold.
- Dive data from shallow-diving coastal dugongs and visual observations from an independent focal sampling study were used to develop and test a procedure that minimises errors in dive identification.
- Depth records were initially cleaned of drift in zero-reading and spikes using custom software.
- Dives were classified into Unrecognised dives (ZOC or DT) by using different values of ZOC and DT. The Unrecognised dives were further classified into Plausible and Implausible dives based on the time threshold, established from the independent visual observational study.
- Comparison of these dive types indicated that a ZOC of 1 m and dive threshold of 0.9 m gave the largest number of Plausible dives and smaller numbers of other dive types, and were the optimum values for the dugong data examined.
- Selection of these two parameter values was supported by frequency distribution patterns of dive durations from TDRs and the visual observations.
- The present procedure has application to other shallow-diving animals such as coastal dolphins and turtles.

Chapter 4: The challenge of inferring behaviour from dive records of shallow-diving marine mammals[2]



Classifying the dives of shallow-diving marine mammals such as the dugong is challenging. Classification depends on reliable dive phases (*e.g.*, descent, bottom, ascent phases) and resultant parameters (*e.g.*, descent/ascent time, bottom time, maximum dive depth), however, it is often difficult to identify different dive phases in shallow dives, and standard classification approaches did not yield interpretable results. In this chapter, I describe an alternative approach. I use logistic regression models based on dive records linked to fine-scale location data and fine-scale environmental attributes to estimate probabilities of: (1) a dive having or not having access to the seafloor; and (2) a dive having access to the seafloor in a location where seagrass is present or absent. I describe dives meeting these criteria to draw insights into dugong diving behaviour.

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[2] I plan to submit a version of this chapter to Marine Ecology Progress Series as Hagihara, R., H. Marsh, C. Roefsema, R. E. Jones. The challenge of inferring behaviour from dive records of shallow-diving marine mammals.

Chapter 4: The challenge of inferring behaviour from dive records of shallow-diving marine mammals

4.1 Introduction

The behaviour of animals is best described and understood in the context of their local environment (Jessopp *et al.* 2013). Several studies have deduced patterns of habitat use and foraging behaviour by linking behavioural data (horizontal and vertical movements) and oceanographic features (*e.g.*, Lea and Dubroca 2003; Bailleul *et al.* 2007; Howell *et al.* 2010). These studies provide valuable insights into the feeding ecology and habitat use of marine mammals, especially in remote, data-scarce areas (*e.g.*, Polar Regions).

Environmental conditions, habitat types, and location of food patches are typically heterogeneous in space and time. Combining behavioural data with habitat descriptions where both are recorded at fine spatio-temporal scales would enable informed inferences about fine-scale diving behaviour, such as a single dive. As high resolution habitat information is often unavailable or difficult to obtain, few studies (*e.g.*, Sheppard *et al.* 2009; Jessopp *et al.* 2013) have attempted such an approach.

In the absence of environmental data, earlier studies of marine mammal diving behaviour classified two-dimensional data (time and depth) into dive types (*e.g.*, Square, U, V, and skewed), and the behaviour of the study animal was inferred from the classified dive types. This practice considerably expanded insights into underwater animal behaviour. Dives were classified using manual approaches based on visual inspection (*e.g.*, Le Boeuf *et al.* 1988; Wilson and Block 2009) and statistical methods (*e.g.*, a combination of principal component analysis and a variant of cluster analysis, factor analysis, and discriminant functions: Boyd *et al.* 1994; Schreer and Testa 1995; Wilson *et al.* 2014). These approaches have been used singly or in combination (Hindell *et al.* 1991; Schreer and Testa 1996; Malcolm and Duffus 2000; Baechler *et al.* 2002; Beck *et al.* 2003; Thums *et al.* 2008).

A statistical approach provides objective and efficient classification of voluminous data and is often preferred over a manual technique. Nonetheless, Malcolm and Duffus (2000) claim manual classification allows more subtle variations in the geometry of a dive profile to be identified; such variations may be indicative of behavioural differences. The choice of classification methodology typically depends on the volume of data to be classified, as well as on prior knowledge of behaviour or ecology of the study animal. Regardless of the classification techniques, validation of the putative behaviours associated with dive types is generally challenging.

Recent studies have collected a range of information on free-ranging animals and their environment using multiple sensing units. The complementary information has been combined with dive records to yield greater insights into diving behaviour (*e.g.*, Hochscheid *et al.* 1999; Lesage *et al.* 1999; Davis *et al.* 2003; Seminoff *et al.* 2006; Goldbogen *et al.* 2008; Thomson et al. 2011; Viviant *et al.* 2014), improved dive classification, and sometimes provided a measure of validation. Several studies have pointed out that more than one behaviour has been assigned to a single dive type (Lesage *et al.* 1999; Davis *et al.* 2003; Thomson *et al.* 2011). Nonetheless, these studies illustrate the advantages of using data additional to dive records for enhancing the capacity of interpretation.

For studies of dugongs, Chilvers *et al.* (2004) classified dives from satellite-tracked dugongs equipped with TDRs. Square- and U-shaped dives (67%) were interpreted as feeding dives, V-shaped dives (8%) as exploratory dives, and shallow dives as either travelling (22%) or resting (3%). Chilvers e*t al.* (2004) did not have accurate information on the animal location, and the putative functions that Chilvers *et al.* (2004) ascribed to the dives have not been validated.

The classification of dive records from shallow-diving animals such as dugongs is particularly challenging as it is often extremely difficult to identify distinct phases in a shallow a dive (*e.g.*, descent, bottom, and ascent phases). Thus dive parameters calculated from these dive phases are difficult to interpret. I used conventional classification techniques (principal component analysis/k-means cluster analysis, factor analysis, classification tree) on dugong dive data. Although the resultant clusters were numerically distinct, they did not visually differentiate dive types or as dives whose location made feeding possible (over seagrass meadows) versus impossible (in areas where seagrass is absent).

In this chapter, I present an alternative approach. Instead of classifying dives into discrete dive types, I use logistic regression models based on dive metrics (*e.g.*, descent rate, bottom time, vertical displacement, maximum depth, ascent time, ascent rate, asymmetry and ascent rate divided by descent rate) obtained from simple two-dimensional data (time and depth). The logistic regression models estimate the probability that a dive will meet each of the following criteria: a) mid-water dives that did not provide the dugong with access to the seafloor and dives that did; and b) dives that enabled the dugong to access the seafloor in areas where seagrass is present and absent (Fig. 4.1). The dives that had various likelihoods of achieving these criteria were examined further in order to draw insights into the dugong diving behaviour.

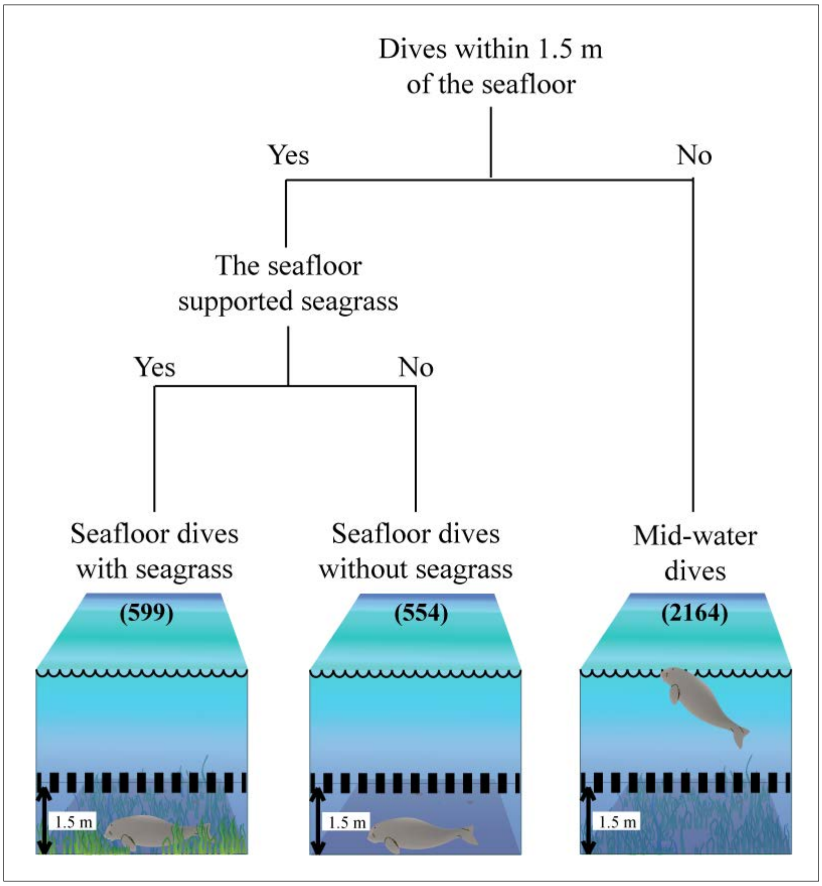


Figure 4.1 Schematic diagram illustrating dives that achieve 3 criteria. Numbers of dives examined are represented in brackets.

4.2 Materials and methods

4.2.1 Study animals, sites, and tracking units

Dugongs are strict bottom-feeders, as opposed to manatees which feed on submerged, floating, and emergent plants, and other food items found in any position of the water column (Hartman 1979; Powell 1996; Lefebvre *et al.* 2000; Colares and Colares 2002; Courbis and Worthy 2003; Guterres-Pazin *et al.* 2012). Although dugongs sometimes consume benthic fauna associated with seagrass communities such as ascidians (Preen 1995a), seagrass is their primary food and they are regarded as seagrass community specialists (Heinsohn *et al.* 1977; Marsh *et al.* 1982; Preen 1992; Masini *et al.* 2001; André *et al.* 2005; De Iongh *et al.* 2007; Marsh *et al.* 2011b).

In this chapter, I examined four dugongs fitted with GPS satellite tracking units and TDRs in Moreton Bay 2011 with the aim of developing the technique that can be subsequently used on a larger data set. Seagrass occurs extensively over shallow banks in inshore waters of Moreton Bay. I used the seagrass model generated for these shallow banks (refer to assumptions of the seagrass model in Section 4.2.7). In contrast, no or little seagrass is found offshore, the east side of Moreton Bay (Fig. 2.2) (Stevens and Connolly 2005; Phinn *et al.* 2008).

The number of days for which both satellite locations and dive records were available ranged from 16 to 78 days per animal as explained in Chapter 2. Specification of the tracking units and description of the study site are detailed in Table 2.1.

4.2.2 Definitions

Dives were divided into two groups according to the following criteria (Fig. 4.1):

1. Dives that did not enable the tracked animal to have access to the seafloor (mid-water dives); and
2. Dives that enabled the tracked animals to access to the seafloor (seafloor dives).

The second group was further divided into two subgroups, depending on whether or not the seafloor supported seagrass, determined by using the seagrass model.

A dugong was assumed to have access to the seafloor when the maximum dive depth reached within 1.5 m of the seafloor. This assumption was necessary due to errors in the depth records resulting from: 1) the depth resolution of the TDR (± 0.5 m); 2) the dugong's body angle and movements; 3) location data (spatial resolution of <75 m); 4) bathymetry model (spatial resolution of 100 m; Beaman 2010); and 5) water depths estimated using the bathymetry model and tidal records (Maritime Safety Queensland, Department of Transport and Main Roads 2011) (see details in Chapter 3).

4.2.3 Data set

Dives were profiled in *diveMove* (ver. 0.9.7, Luque 2007) in R (ver. 2.15.3, R Development Core Team), with 0.5 m zero-offset correction and 1 m dive threshold. These thresholds were quantitatively determined using the methodology described in Chapter 3 which optimised dive recognition from shallow-diving dugongs.

The initial data manipulation of location data and dive records is described in Section 2.4. The dives generated in *diveMove* were then associated with environmental variables (water depth and seagrass presence/absence). Dives that occurred within 5 min of satellite location fixes (10 min in total) were sub-sampled (Fig. 2.3B), assuming the associated environmental variables remained constant for the 10-min period. Although a dive was defined as departure ≥1 m from the surface, dives that had a maximum dive depth exceeding the estimated water depth were removed. Such errors probably originated from errors in bathymetry models, tidal adjustments and depth measurements from TDRs. Furthermore, dives with a maximum dive depth of <3 m were excluded to avoid the problems associated with dive phase recognition in very shallow dives.

4.2.4 Dive parameters

The 16 dive parameters initially examined were either produced in *diveMove* or calculated from the output parameters, following Schreer and Testa (1995, 1996) and Lesage *et al.* (1999) (Table 4.1). As multicollinearity increases, regression parameters become unreliable and lead to incorrect coefficients (errors in magnitude and sign), or with huge standard errors (Slinker and Glantz 1985; Zuur *et al.* 2013). Several alternative thresholds of Variance Inflation Factor (VIF) have been suggested; Zuur *et al.* (2007) recommends <3 whereas Montgomery *et al.* (1992) recommend <5 to 10. Thus if two dive parameters had a correlation coefficient of >0.7 or had a VIF of >5, which is a relatively relaxed threshold, only one of the two parameters was retained in the model. Bottom distance was divided by bottom time to provide a measure of the vertical displacement relative to the time spent on the bottom phase of the dive (ID 5; Table 4.1).

Table 4.1 The dive parameters used in the logistic regression models and their descriptions.

ID	Dive parameters	Descriptions
1	Descent time (s)*	Time spent during a descent phase
2	Descent distance (m)	Vertical distance travelled during a descent phase
3	Descent rate (m/s)*	Rate of descent
4	Bottom time (s)*	Time spent during a bottom phase
5	Vertical displacement (m)*	Vertical distance travelled during a bottom phase divided by the time spent during the bottom phase
6	Max. dive depth (m)*	Maximum dive depth reached during a dive
7	Ascent time (s)*	Time spent during an ascent phase
8	Ascent distance (m)	Vertical distance travelled during an ascent phase
9	Ascent rate (m/s)*	Rate of ascent
10	Dive time (s)	Time spent during all phases
11	Asymmetry*	Ascent distance divided by descent distance
12	Post dive duration (s)	Time spent at the surface
13	Bottom time/ descent rate	Bottom time divided by descent rate
14	Ascent rate / descent rate*	Ascent rate divided by descent rate
15	Descent time proportion	Descent time divided by dive time
16	Ascent time proportion	Ascent time divided by dive time

*Parameters retained for further analyses

4.2.5 Relevant dive parameters

I performed two Generalized Linear Models (GLMs) with binomial distribution (logistic regression) to identify the dive parameters that were highly associated with each of the two binary response variables: 1) mid-water versus seafloor dives; and 2) seafloor dives over areas where seagrass is present and absent. The remaining number of explanatory variables (n = 9) as indicated by asterisk in Table 4.1 was still large and some of these variables might have been irrelevant to describing the binary response variables described above. Thus relevant variables were determined on the basis of their relative importance using automated model selection approach. The relative importance of a variable is obtained from the sum of Akaike weights across all models included in the confidence set. Akaike weights indicate a relative likelihood of a model being the best model, given the models examined. Variables with a relative importance of >0.5 were retained for further examination. When the two packages produced different results, only parameters that were identified by both as having a relative importance of >0.5 were retained. A High Power Computer (HPC) was employed for the iterations.

The models were compared based on the Akaike Information Criterion, corrected (AICc). For this automated model selection and relative importance estimation, I used two R packages *MuMIn* (ver. 1.10.0, Bartoń 2014) and *glmulti* (ver. 1.0.7, Calcagno 2013) in R 3.0.3 (R Development Core Team, 2014), as each employed a slightly different algorithm; *glmulti* is faster, uses less memory, and can handle larger data sets (Calcagno and de Mazancourt 2010). The number of models required to estimate the relative importance of the parameters was determined based on the 95% confidence set. The codes are provided in Appendix 4.1.

These nine numerical dive parameters were used as explanatory variables for each logistic regression on two datasets (1 and 2 above). All variables were treated as main effects. Dataset 1 included all dives in water >3 m deep. Dataset 2 included only dives in water 3–<5 m deep. The georeferenced seagrass map was limited to depths less than 10 m, and even within this range, seagrass at the study site was restricted mainly to shallower waters (refer details in Section 4.2.7). Since many of the dive attributes were affected by the maximum dive depth, the logistic regression for bottom dives dugongs made in areas where seagrass is present and absent needed to be controlled for the biased depth distribution of seagrass.

I attempted to include the individual animal as a random factor, but the resulting model failed to converge. This means that data are pseudoreplicated and larger data are needed to confirm the random effect from individual animals.

This process resulted in eight of the nine dive parameters marked with asterisks in Table 4.2 achieved high relative importance using both *MuMIn* and *glmulti* (see Appendix 4.1 for details), and were used in each of the two logistic regressions. I used R package *lm.beta* (Behrendt 2014) to obtain standardized coefficients.

Table 4.2 Relative importance of nine dive parameters identified in predicting a likelihood of attaining: A) mid-water versus seafloor dives, and B) seafloor dives over areas where seagrass was present versus absent. The numbers in brackets represent the number of models in the confidence set (95%) used to obtain relative importance.

		A)		**B)**	
ID	**Dive parameters**	***MuMIn* *(3)***	***glmulti* *(2)***	***MuMIn* *(8)***	***glmulti* *(3)***
1	Descent time	0.4	0.4	1.0	1.0
2	Descent rate*	1.0	1.0	1.0	1.0
3	Bottom time*	1.0	1.0	1.0	1.0
4	Vertical displacement*	1.0	1.0	0.3	0.3
5	Maximum depth*	1.0	1.0	1.0	1.0
6	Ascent time*	1.0	1.0	1.0	1.0
7	Ascent rate*	1.0	1.0	0.8	1.0
8	Asymmetry*	1.0	1.0	1.0	1.0
9	Ascent rate divided by descent rate*	0.3	1.0	0.5	0.7

*Parameters retained

4.2.6 Dive characterisation

The eight relevant dive parameters identified above were transformed into categorical variables for ease of interpretation and to test for overdispersion. Use of categorical variables also allowed a visual comparison of observed and predicted responses. Each explanatory variable was divided into three groups (at percentiles of 33 and 66) or four groups (at percentiles of 25, 50, and 75) depending on their distributions. The response variables were the two binary variables described in Section 4.2.5. Over-dispersion was examined using dispersion statistics based on Pearson's residuals (Zuur *et al.* 2013). Standardised coefficients were obtained in *lm.beta* (ver. 1.5-1; Behrendt 2014).

The results of these analyses allow, for any given dive, an estimate of the probability that the dive reached the seafloor, and if it did, the probability that it was over seagrass. I then compared numerical dive characteristics of the three dive groups: mid-water dives, seafloor dives in areas where seagrass was present and absent. The thresholds of high and low likelihoods of achieving the above categories were determined based on predicted values generated by the logistic regressions and the frequency distributions of each dive groups. All dive statistics are reported with means ($\bar{x}$) and standard errors (±).

4.2.7 Assumptions

Assumptions made in fitting these models, together with possible problems, are:

1. The seagrass model provides an accurate reflection of seagrass distribution at the time of dugong satellite tracking.
    - Seagrass abundance and distribution vary seasonally, and the seagrass map used is for 27 July 2011. As seagrass abundance and distribution decreases towards the Austral winter (July-August) (Preen 1995), earlier dugong tracking months (May to June) would have larger seagrass biomass and spatial extent. Thus some dugong locations from GPS transmitters identified as outside of the seagrass map might actually carry seagrass.
    - Accurate generation of the seagrass map generation has a depth limit as it relies largely on water clarity and the depth to which light penetrates through the water column. Although the satellite images were taken during

low tides (to provide maximum exposure of the substratum), the vertical spatial coverage of the model is <10 m. Deeper seagrass is not captured in the model.

- The seagrass model was generated from field sampling of seagrass whose colour bands are identified on satellite imageries and then extrapolating the seagrass values to the entire seagrass model over shallow banks of Moreton and Amity banks (Roeflsema *et al.* 2009, 2014): the extrapolation is subject to error. In addition, low biomass seagrass may not be captured by satellite images.

Despite the potential for underestimation, 70 to 82% of satellite points from the four dugongs within Moreton Bay were over the seagrass model. The magnitude of uncertainty in the generation technique of the seagrass model is unknown.

2. The water depth represents the actual water depths experienced by tracked dugongs.

   - The water depth I used to determine whether a particular dive had access to the seafloor was estimated from a bathymetry model (spatial accuracy of ± 100 m) and tidal height information from available locations (Amity Point and South Passage), and therefore is subject to error. Shallow areas are subject to additional errors due to constant movements of sand (pers.comm Beaman). The tidal adjustments were done by associating each satellite fixes to the closest tidal reference locations available, and are also subject to errors.

   Although I used the best information available, depth estimates are therefore necessarily approximate.

3. Depth records collected from TDRs reflect the actual depths that dugongs were located in the water column at the time of recording.

   - The depth records are subject to errors from depth resolution of TDRs, wave action, shift in barometric pressure over time, and dugong's body angle (refer Chapter 3 for detail). For this reason, I defined the access to the seafloor as achieved when the maximum dive depth reached within 1.5 m of the seafloor.

   Within the range determined by TDR resolution, this assumption is reasonable, given the methodology described in Chapter 3. The methodology is designed to minimise potential errors.

4. Dugongs mostly feed over seagrass meadows.

- As described under Section 4.1, previous studies have found that seagrass dominated dugong stomach contents (*e.g.*, Marsh *et al.* 1982), however dugongs also consume thin-shelled burrowing mussels (Anderson 1989), polychaete, and colonial ascidians (Preen 1995a). Especially in winter when the biomass of seagrass is reduced. In winter dugongs become nitrogen-limited, and they may make significant use of these alternate food sources (Preen 1992).

While it is likely that most dugong feeding occurs over seagrass, tracking encompassed the winter season so some feeding dives may have occurred elsewhere. Dugongs also perform other behaviours such as resting and socialising over seagrass meadows (Hodgson 2004). Thus identification of particular dives as "feeding dives" because they reached the bottom over seagrass is unlikely always to be correct. For these reasons, it is not feasible to assign particular dive types to particular behaviours

4.3 Results

4.3.1 General

In total 150,714 dives ($\bar{x}$ = 620.2 ± 17.6 dives per day per animal) were recorded from all four dugongs. After sub-sampling around GPS/QFP fixes and $\geq$3 m of maximum dive depth, the dataset was reduced to 3,317 dives. The mean maximum dive depth from this subset of data was 4.58 ± 0.04 m (median 3.5 m), and mean dive duration was 2.5 ± 0.03 min (median 2.2 min). The maximum dive depth was recorded from a dugong MB 3 and was 31.5 m. All dugongs dived to depths exceeding20 m.

4.3.2 Predictive models

The fit of the two categorical logistic regressions was adequate with dispersion statistics of 1.0 for the model predicting mid-water and seafloor dives and 1.1 for the model predicting seafloor dives in areas where seagrass is present and absent. Predicted and observed proportions of dives achieving different criteria had linear relationships regardless of the number of dives, also indicating the model adequacy (Fig. 4.2).

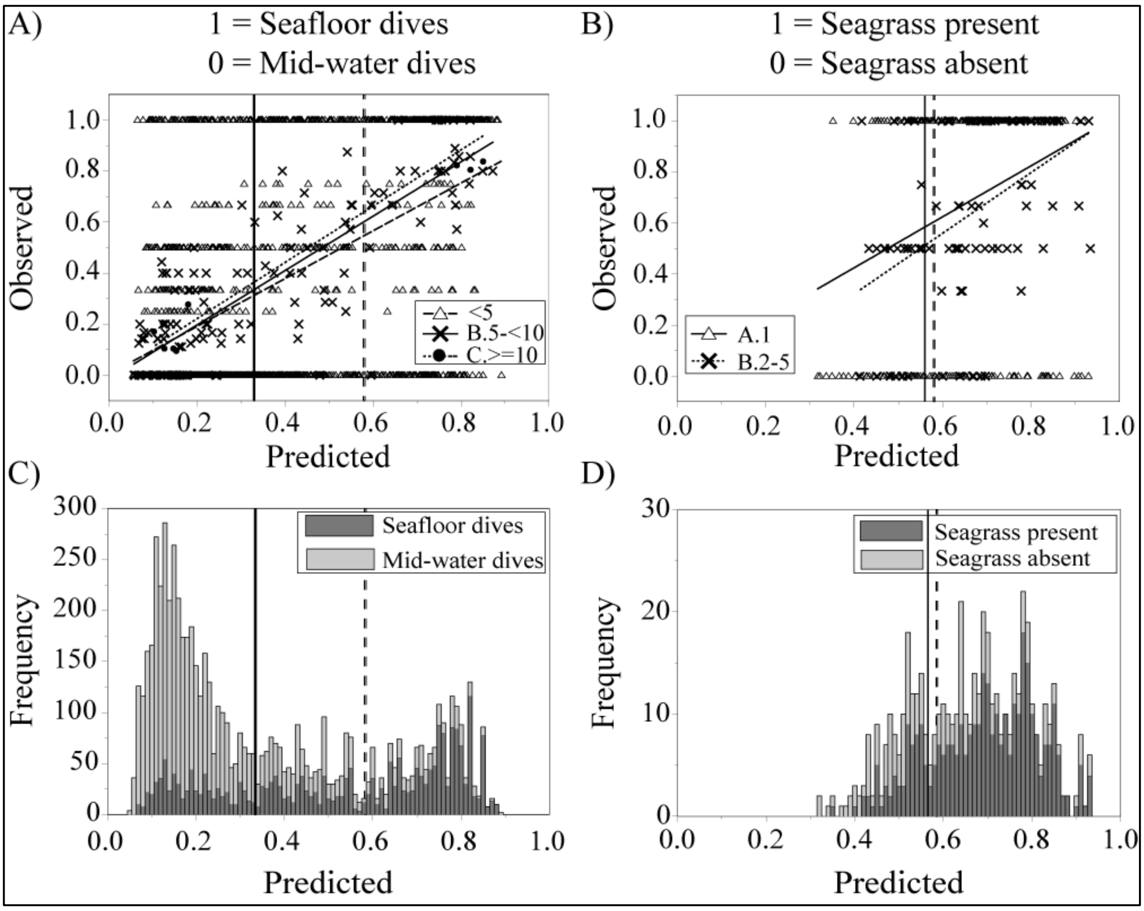


Figure 4.2 Given a set of predictor variables, predicted against observed likelihoods of attaining: A) seafloor and mid-water dives and B) seafloor dives in areas with seagrass presence and absence, coded with the number of dives. Graphs C) and D) show frequency distribution of each dive whose likelihood was predicted by logistic models. Vertical lines represent thresholds of high (dotted) and low (straight) likelihoods of accessing the seafloor (C) and accessing the seafloor in areas supporting seagrass (D).

Mid-water and seafloor dives were highly associated with all eight variables, particularly ascent rate, bottom time, and vertical displacement in decreasing order of explanatory power (Table 4.3A). For instance, compared to a dive with an ascent rate of less than 0.06 m/s, the odds of a dive with an ascent rate of 0.06 to 0.16 m/s allowing the dugong to access the seafloor were 1.9 times higher than for a dive that had an ascent rate of <0.06 m/s, and 5 times higher for a dive with 0.16 to <0.27 m/s, and 15 times higher for a dive with >0.27 m/s.

All variables except ascent rate divided by descent rate, maximum dive depth, and bottom time were significant in differentiating between the seafloor dives over areas with and without seagrass. Dives over an area with or without seagrass varied with respect to ascent rate, descent time, ascent time, and ascent rate divided by descent rate (in decreasing order of explanatory power; Table 4.3B). For instance, the odds that a dive with an ascent rate of 0.3 to 0.4 m/s was over seagrass were 2.9 times higher than for a dive that had ascent rate <0.2 m/s The corresponding odds ratios for a dive with an ascent rate of 0.2 to 0.3 m/s was 1.6 times; 1.8 times for >0.4 m/s. The analysis of deviance table is given in Appendix 4.2.

Table 4.3 Coefficients (original and standardised) of the logistic regressions for: A) mid-water and seafloor dives and B) seafloor dives over the areas where seagrass is present and absent. The parameters were categorised into two or three groups depending on the distribution of the data.

A) Mid-water and seafloor dives		**Coefficients**	**Std. coefficients**	**Std. Error**	**t value**
(Intercept)		-1.544	0.000	0.274	-5.645
Descent rate:	0.08 to <0.14 m/s	-0.146	-0.148	0.099	-1.470
	0.14 to <0.23 m/s	-0.108	0.111	0.121	-0.895
	≥0.23 m/s	0.369	0.381	0.149	2.476
Bottom time:	25 to <55 s	0.176	0.180	0.090	1.968
	55 to <107 s	0.360	0.366	0.091	3.974
	≥107 s	0.563	0.577	0.098	5.736
Vertical displacement:	0.28 to <0.35	-0.236	-0.266	0.071	-3.318
	≥0.35	-0.491	-0.549	0.081	-6.073
Max. dive depth:	3.5 m	-0.231	-0.213	0.092	-2.515
	3.5 to <5 m	-0.412	-0.427	0.089	-4.625
	≥5 m	-0.342	-0.364	0.131	-2.622
Ascent time:	15 to <25 s	-0.250	-0.254	0.107	-2.324
	25 to <44 s	-0.437	-0.452	0.142	-3.077
	≥44 s	-0.047	-0.047	0.194	-0.240

Ascent rate:	0.06 to <0.16 m/s	0.643	0.733	0.145	4.425
	0.16 to <0.27 m/s	1.606	1.667	0.196	8.184
	≥0.27 m/s	2.735	2.777	0.228	11.980
Asymmetry:	1	-0.152	-0.173	0.102	-1.487
	>1	-0.204	-0.164	0.142	-1.437
Ascent rate/descent rate:	0.62 to <1	-0.012	-0.012	0.103	-0.113
	1 to <2	-0.051	-0.050	0.129	-0.394
	≥2	0.106	0.110	0.17	0.606

B) Seafloor dives over areas where seagrass is present and absent		**Coefficients**	**Std. coefficients**	**Std. Error**	**t value**
(Intercept)		-0.767	0.000	1.027	-0.747
Descent time:	10 to <16 s	-0.386	-0.385	0.391	-0.988
	16 to <28 s	-0.468	-0.454	0.567	-0.825
	≥28 s	-0.806	-0.796	0.741	-1.087
Descent rate:	0.1 to <0.2 m/s	0.207	0.207	0.442	0.469
	0.2 to <0.3 m/s	0.004	0.004	0.628	0.006
	≥0.3 m/s	0.508	0.505	0.782	0.649
Bottom time:	30 to <70 s	-0.153	-0.154	0.266	-0.577
	70 to <95 s	0.316	0.298	0.310	1.018
	≥95 s	0.010	0.010	0.291	0.035
Max. depth:	3.5 m	0.158	0.151	0.280	0.563
	4 to 4.5 m	-0.281	-0.230	0.313	-0.897
	5 m	-0.005	-0.003	0.495	-0.010
Ascent time:	8 to <11 s	0.870	0.806	0.413	2.108
	11 to <18 s	0.736	0.708	0.535	1.375
	≥18 s	0.739	0.733	0.745	0.993
Ascent rate:	0.2 to <0.3 m/s	0.471	0.448	0.440	1.071
	0.3 to <0.4 m/s	1.075	0.977	0.587	1.831
	≥0.4 m/s	0.564	0.583	0.679	0.831
Asymmetry:	1	0.495	0.470	0.410	1.205
	>1	0.581	0.465	0.507	1.148
Ascent rate/descent rate:	0.9 to <1.4	-0.056	-0.055	0.317	-0.178
	1.4 to <2.6	0.423	0.419	0.367	1.154
	≥2.6	0.703	0.677	0.538	1.306

4.3.3 Dive characteristics

Dives that had a low likelihood of accessing the seafloor (mid-water dives), which are found in the left of solid line in Figure 4.2C, had shorter average bottom times (59.75 ± 1.26 s) and larger vertical displacements (0.35 ± 0.002) than dives that had a likelihood of accessing the seafloor both over seagrass (bottom time = 69.91 ± 2.51 s; vertical displacement = 0.30 ± 0.005; Fig. 4.3) or in areas without seagrass (bottom time = 64.86 ± 4.16 s; vertical displacement = 0.33 ± 0.01). These mid-water dives also had slower ascent rates (0.10 ± 0.001 m/s) than the other two dive types (seagrass: $\bar{x}$ = 0.36 ± 0.01 m/s; no seagrass: $\bar{x}$ = 0.25 ± 0.10 m/s).

The seafloor dives that had high likelihoods of accessing the seafloor in locations where seagrass occurs (the right of dotted lines in Figure 4.2D) were characterised by short descent (23.14 ± 1.44 s) and ascent times (11.07 ± 0.48 s) as well as relatively fast descent (0.24 ± 0.01 m/s) and ascent rates (0.36 ± 0.01 m/s). These dives had an asymmetry of 1 (1.00 ± 0.01). In contrast, seafloor dives that had low likelihood of having seagrass on the seafloor (the left of solid lines in Figure 4.2D) had longer descent and ascent times (descent time = 29.13 ± 1.63 s; ascent time = 27.58 ± 1.94 s) and slower decent and ascent rates (descent rate = 0.15 ± 0.01 m/s; ascent rate = 0.25 ± 0.03 m/s; asymmetry = 0.94 ± 0.02). Dive profiles of each dive group are illustrated in Figure 4.3; their summary statistics are in Appendix 4.3.

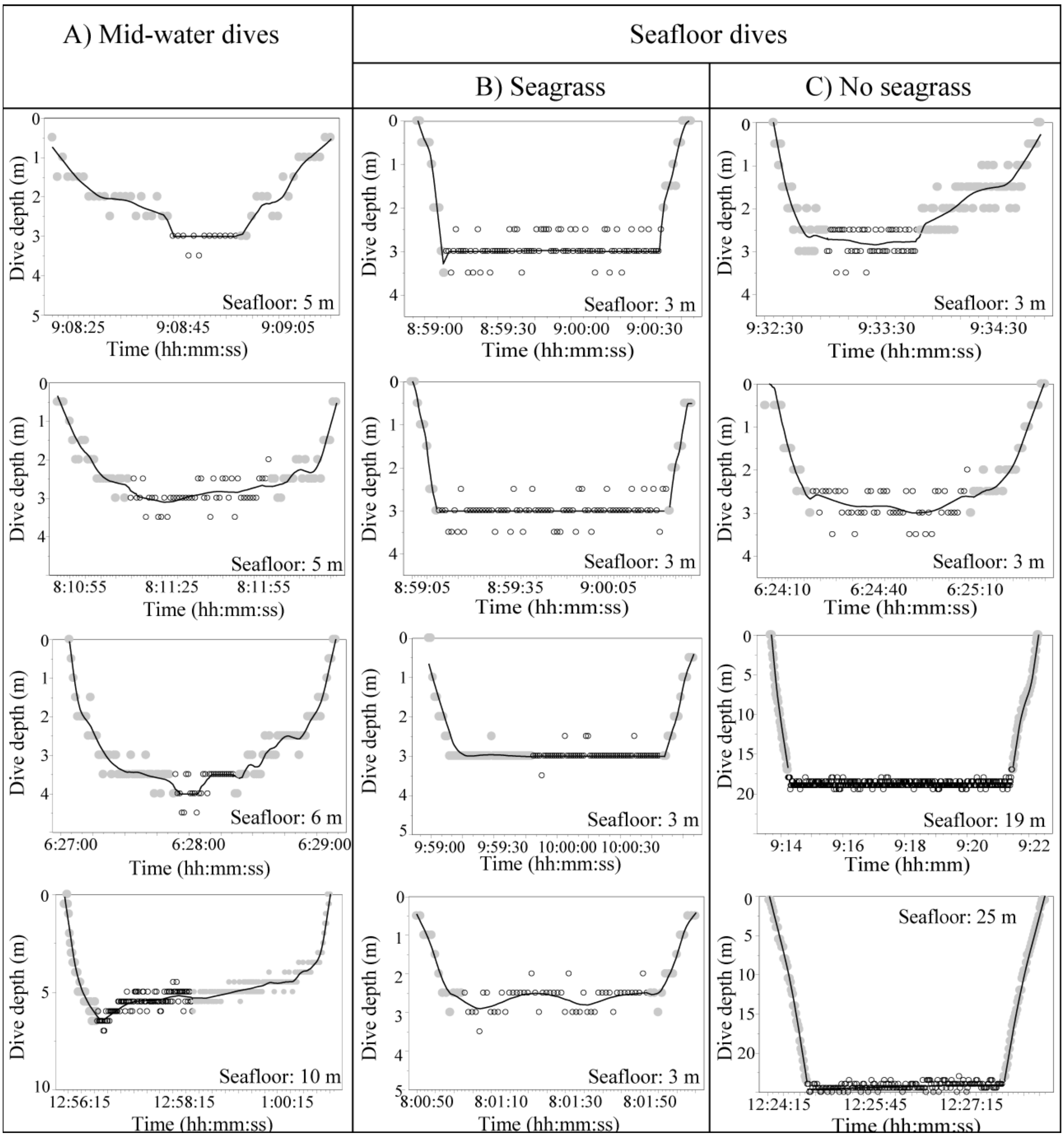


Figure 4.3 Examples of A) mid-water and seafloor dives in locations where seagrass is B) present and C) absent. The descent and ascent phases are represented by closed dots, and the bottom phase by open dots.

4.4 Discussion

4.4.1 Dive classification

Studying behaviour of shallow-diving animals such as dugongs has the potential to reveal important insights into their feeding ecology. However, the classification of their dive parameters is extremely challenging because they feed on aquatic plants predominantly found in shallow waters (Marsh *et al.* 2011b) and the majority of their dives are shallow. Thus reliable delineation of dive phases are extremely difficult, especially using software developed for deeper diving animals.

I used logistic regression models to associate dive attributes with (a) the probability of a dive accessing or not accessing the seafloor and (b) the probability that a dive accessing the seafloor in locations where seagrass is present or absent. Although my analysis used relatively simple two-dimensional data as opposed to more detailed movement information (*e.g.*, information that might be provided by 3D sensors or accelerometers), dive attributes that led to high likelihoods of attaining these criteria allowed some inferences about dugong diving behaviour. This inference was made possible by linking animal tracking data with fine-scale environmental information.

I did not attempt to assign behavioural type to each of the three dive groups. As Section 4.2.7 states, it is possible for multiple behaviours to occur over seagrass meadows. Although dugongs primarily forage seagrass, they also consume animal matters in areas outside of seagrass meadows. The overlap of dive shapes in different locations also confirmed the difficulty of extrapolating behaviour from the data I examined.

Another key attribute of my modelling approach was the use of dives that were identified using three quantitatively determined thresholds of time, ZOC (zero-offset correction), and maximum dive depth (refer details in Chapter 3). This process maximised the correct identification of dives while minimising errors associated with depth records resulting from resolution of the TDR, wave action, and orientation of the animal’s body.

Sub-sampling of dives ensured reliable association with spatially and temporally heterogeneous environmental attributes (*e.g.*, Phinn *et al.* 2008; Knudby and Nordlund 2011). This process also reduced the potential for autocorrelation effects. However, the subset of dives (instead of the whole dataset) that were made close to the time of GPS/QFP uplinks represented only 4% of all dives recorded for these dugongs.

The logistic regression models predicted the likelihood of accessing the seafloor ranging between 0.05 and 0.89 for different categorical combinations of dive parameters (Fig 4.2). Differentiation between a seafloor dive in environments where seagrass is present and absent was less successful with likelihoods ranging from 0.32 to 0.93. Nonetheless, dive characteristics such as descent and ascent rates clearly differed between these dive groups.

These dives used to produce the logistic regression models could be considered as a training set (*e.g.*, Schreer and Testa 1996). Independent data sets would be required to determine whether these models have sufficient predictive power for different environments or times of year. Increase in sample size in terms of duration and animals would also improve the model performance.

4.4.2 Dive characteristics

The bottom times of seafloor dives in areas where seagrass is present ($\bar{x}$ = 69.91 ± 2.51 s) and absent ($\bar{x}$ = 64.86 ± 4.16 s) seagrass were both significantly longer than that of the mid-water dives ($\bar{x}$ = 59.75 ± 1.26 s). The long bottom duration was probably because the seafloor provides the dugong with the environment for two important functions, feeding and resting. Dugongs are benthic feeders, primarily feeding on seagrass (Heinsohn *et al.* 1977; Marsh *et al.* 1982; Preen 1992; Masini *et al.* 2001; André *et al.* 2005; De Iongh *et al.* 2007) but also algae (Anderson 1989) and benthic invertebrates such as ascidians (Preen 1995a), thin-shelled burrowing mussels, and possibly sea pens (Anderson 1989). Their highly deflected rostrum and mandibular symphysis (~70°) make dugongs obligatory bottom-feeders (Domning 1978a), whereas the lesser rostral deflection of the Amazonian manatees (25–41°) and West Indian manatees (15–40°) allows manatees to feed throughout the water column (Domning 1978b).

Dugongs and manatees also use the substratum for resting. Using a blimp-cam, Hodgson (2004) observed dugongs resting on the seafloor as well as at the surface and in mid water, although seafloor resting was least frequent (approx. 25% of all resting times). This percentage may be biased due to how the resting behaviour was defined and Hodgson’s (2004) observations that were mainly over shallow seagrass beds in daylight when animals are mostly feeding. Anderson (1982) also observed dugongs resting just below the water surface but was unable to observe underwater behaviours due to high turbidity at his study site. In contrast, the West Indian manatees may be predominantly bottom-resters. Hartman (1979) observed Florida manatees resting over limestone shelves, oyster bars, and seagrass and considered surface resting to be largely a transitory behaviour between surfacing and diving. Antillean manatees rest in depressions on the substratum called “manatee resting holes”, favouring quiet sheltered locations (Bacchus *et al.* 2009).

The longer bottom time found in seafloor dives in areas where seagrass is present may be because dugongs are maximising their feeding time. These dives had significantly shorter and faster descent and ascent times and rates than the seafloor dives in environments where seagrass was absent. Bottom time as a percentage of dive duration was highest in seafloor dives over seagrass (0.67), followed by seafloor dives in environments without seagrass (0.53), and mid-water dives (0.40). This behavioural tactic aligns with the optimum diving theory of Kramer (1988), which states that diving is a cost to air breathing vertebrates thus diving animals maximise the time spent at depths where the resource return (*e.g.*, food, predator avoidance, or mating opportunity) is the greatest.

To my surprise, mid-water dives ($\bar{x}$ = 149.01 ± 1.76 s) had longer average durations than seafloor dives ($\bar{x}$: seagrass = 104.11 ± 2.91 s; no seagrass = 121.57 ± 4.94 s). Nonetheless, the bottom phase of mid-water dives was significantly shorter than for seafloor dives and the descent and ascent rates were slower; ascent rates were much slower. Taken together, these results suggest that dugongs may spend less energy (or oxygen) per second for these dives to extend submergence time. The energy conservation tactics require additional information on travel speed or change in body angle.

The smaller vertical displacement observed during the bottom phase of seafloor dives irrespective of the presence of seagrass compared to the mid-water dives is consistent with independent behavioural and physical observations. Dugongs frequently feed on seagrass with their bodies horizontal to the substratum by slowly moving forward supported by their forelimbs. Marsh *et al.* (1978) observed calluses on the anterior ventral part of the forelimbs in all dugong carcasses examined (number not specified) and hypothesised that the calluses were related to feeding. Dugongs typically employ two feeding modes: excavating and cropping (*sensu* Wirsing *et al.* 2007a): excavating refers to dugongs furrowing the sediment to consume both above- and below-ground seagrass; cropping refers to animals eating above-ground plant parts only. The two feeding modes probably produce similar horizontal body movements and dive profiles with minimum tail movements. Feeding dugongs initiate an ascent to the surface by pushing off the seafloor with their flippers rather than an active thrust with their tails (Marsh *et al.* 2011b). Hartman (1979) also observed Florida manatees using flippers to walk on the substratum barely touching their bodies on the substratum and pushing their bodies off the seafloor with their forelimbs after resting without using their tail.

Vertical displacement during the bottom phase of mid-water dives ($\bar{x} = 0.35 \pm 0.002$) was larger than in seafloor dives in the absence of seagrass ($\bar{x} = 0.33 \pm 0.01$)) and in seafloor dives in seagrass communities ($\bar{x} = 0.30 \pm 0.005$). This result was probably due to dugongs using their tails in active propulsion during mid-water dives (TDRs attached near the tailstock), and also because their location adjacent to the bottom during seafloor dives constrains vertical movement.

4.4.3 Dive shapes

Mid-water dives had several geometries (U- and V-shaped), probably reflecting a range of behaviours. In other aquatic species, V-shaped dives are often interpreted as exploratory or travelling dives (*e.g.*, Williams and Kooyman 1985; Schreer and Testa

1996; Crocker *et al.* 1997). These dives often occur just before U-shaped dives (feeding) (Schreer and Testa 1996). The function of skewed dives (a variant of V-shaped dives) has been attributed to resting, gliding, or food digestion (*e.g.*, Hindell *et al.* 1991; Crocker *et al.* 1994).

The profiles of seafloor dives in locations where seagrass is present were mainly Square shaped with some U-shaped dives, whereas seafloor dives in environments where seagrass is absent were mainly U-shaped but had some Square profiles. U-shaped mid-water dives were less common but were also observed (Fig. 4.3). Chilvers *et al.* (2004) had speculated that both Square- and U-shaped dives from satellite tracked dugongs could represent both feeding and resting, and also described an "Erratic" dive type, which was not observed in my study. Square or U-shaped dives of several marine mammals have been interpreted as foraging dives (*e.g.*, Le Boeuf *et al.* 1988; Hindell *et al.* 1991; Bengtson and Stewart 1992). This interpretation is supported by diel differences in diving patterns, which are believed to reflect vertical movement of their prey. Wiggles (vertical displacement) in the bottom phase of these dives have been interpreted as animals locating and ingesting preys within aggregated food patches (*e.g.*, Scheer and Testa 1996; Lesage *et al.* 1999; Baechler *et al.* 2002). The functions of Square and U-shaped dives are however not limited to foraging and resting. Even though Square dives (Type 1) in green and the loggerhead turtles are highly associated with benthic resting and foraging (Hochscheid *et al.* 1999), video cameras attached to the turtles revealed that turtles also performed travelling during square dives (Seminoff *et al.* 2006; Thomson *et al.* 2011).

4.4.4 Dive statistics

Most dugong dives were relatively shallow with a mean maximum dive depth of 4.6 ± 0.04 m, even in the $\geq$3 m subset of data. The result was similar to that (4.8 ± 0.4 m) reported by Chilvers *et al.* (2004) who restricted their analysis to dives with maximum dive depth of $\geq$1.5 m. The maximum dive depth observed in this study was 31.5 m, slightly shallower than the value (36.5 m) presented in Sheppard *et al.* (2006) but deeper than the maximum (20.5 m) reported by Chilvers *et al.* (2004). All four dugongs I studied made dives exceeding 20 m deep, which is more than twice the reported maximum dive depth of manatees (9 m; Reynolds 1981). Edwards *et al.* (2007) found that Florida manatees fitted with TDRs spent 19% of time in water <1 m deep in the winter aggregation site near power plant discharges, where a cow and a calf pair spent 81.8% of time. Similarly the West Indian manatees (*Trichechus manatus manatus*) tracked with GPS transmitters in Mexico were in water <6 m deep and spent a large proportion of time (51.6%) in water <2 m deep (Castelblanco-Martínez *et al.* 2014).

The mean dive duration from my study was 2.5 ± 0.03 min, which was again similar to that reported by Chilvers *et al.* (2004) ($\bar{x}$ = 2.7 ± 0.17 min). Other studies based on visual observations of dugongs in shallow waters (<6 m) have reported variable mean dive durations, ranging from 0.9 min (Anderson 1982), 1.2 min (Anderson and Birtles 1978), 1.3 min (Hodgson 2004) to 6 min (Whiting 2002). Apart from Chilvers' and Hodgson's estimates, which included various behaviours, all other submergence times are from foraging dugongs. Whiting's (2002) submergence time is an outlier, considerably longer than other studies. The discrepancy may be due to Whiting's dugongs feeding on algae over a rocky reef, whereas other studies observed dugongs feeding on seagrass over sandy substratum. As algae are not the major food for dugongs (Marsh *et al.* 1982; Preen 1992; De Iongh *et al.* 2007), these dugongs might have also been engaged more in other activity such as resting.

I did not estimate maximum dive duration, as visual inspection of the longest dives (few exceeded 10 min) revealed some of these dives consisted of >1 dives. The result highlights the need to establish a maximum time threshold, as well as the minimum threshold (16 s), that was used for dive identification in Chapter 3.

The longest recorded submergence times for dugongs are 8.4 min from a captive dugong (Kenny 1967) and 11 min (658 s) for wild dugongs observed from a bridge (Whiting 2002) and 12.4 min based on dive records collected from TDRs (Chilvers *et al.* 2014). All of these times are much shorter than the maximum dive duration of 24 min recorded for wild Florida manatees (Reynolds 1981a). Gallivan *et al.* (1986) estimated that the aerobic dive limit of Amazonian manatees was 19 min (small animal) to 22 (large animal) min based on 1) oxygen concentration in the lungs of the two Amazonian manatees, 2) their lung volume, and 3) the volume of gas exchanged through expiration and inspiration from another Amazonian manatee (Gallivan and Best 1980), 4) blood volume of Florida manatees (Scholander and Irving 1941), and 5) oxygen affinity of Florida manatee blood (White *et al.* 1976). Gallivan *et al.* (1986) considered that this approach probably underestimate the aerobic dive limit, as they did not account for oxygen stored in the tissue. Similar physiological studies do not exist for dugongs. Nonetheless, Gallivan *et al.* (1986)'s calculations suggest that the longest submergence times listed here for both wild dugongs and manatees should be within their aerobic dive limits.

4.4.5 Deep benthic dives

The maximum depth of seafloor dives over seagrass was 7 m in this study. This figure is probably truncated by the restriction of seagrass to relatively shallow waters of Moreton Bay and the depth limit of the seagrass model (<10 m; Roeflsema *et al.* 2009). In offshore waters of Moreton Bay, 40% of seafloor dives (44 dives) exceeded 10 m with a maximum of 25 m. These deep bottom dives in offshore waters are unlikely to be feeding dives, as there is little or no seagrass is found in that area (Stevens and Connolly 2005; Phinn *et al.* 2008).

Deep benthic dives may assist dugongs to orient and navigate. Dugong MB 2 dived consecutively to the seafloor at depth of 10 m up to 25 m on 15 separate days, mostly along the 20 m isobath. This dugong rarely ventured into waters exceeding 30 m deep. Thus 20 m may have been the depth limit of her activity space (home range), and she might have used deep dives to orient herself. Dugong MB 1 and 3 dived to the seafloor of *ca*. 16 m at the mouth of South Passage, which connects the inshore and offshore waters of Moreton Bay. Again, these six dives may have been used for navigation. Although they were all recorded on different days or time of day, the associated satellite fixes were within 3 to 200 m. The two dugongs were travelling from offshore waters into inshore waters on four occasions; in the other two occasions the dugongs were heading to inshore but when they reached the mouth of South Passage, a narrow passage between Moreton Island and North Stradbroke Islands, they turned offshore again.

Sheppard *et al.* (2006) speculated that the 5-min deep consecutive dives (to >21 m) that they recorded from a satellite tracked dugong assisted the dugong to navigate during a long distance travel (290 km) from Burrum Heads to Keppel Island, Queensland (Australia). It is unknown whether this dugong was diving to the seafloor, but the flat bottom profiles suggest that it was. The authors speculated that dugongs use a combination of visual and tactile modalities for navigation. Sirenians have sensitive hairs distributed all over their body and their hairs function as a highly developed sensory organ (Kamiya and Yamasaki 1981; Reep *et al.* 1998; Marshall *et al.* 2003).

Sheppard *et al.* (2006) also suggested that deep seafloor diving in dugongs may function as an anti-predator tactic (Sheppard *et al.* 2006). In Shark Bay, Western Australia, Wirsing *et al.* (2007a) described dugongs switching feeding modes between excavating and cropping in response to the density of tiger sharks. In warm months (February to May) when shark abundance was highest, dugongs limited the time spent foraging using excavation. This feeding mode generates sediment plumes which may reduce the dugong’s capacity for surveillance. Whether the dugongs spent more time using cropping during these months was not mentioned. Wirsing *et al.* (2007a,b) stated, even though seagrass density was higher at the core of seagrass patches, dugongs in Shark Bay selected peripherals of seagrass meadows during the time of high shark density. Although the use of this microhabitat increased the likelihood of dugongs encountering predatory sharks, it facilitated dugongs escaping into deep waters if a shark attacked.

Although a similar study of dugong and shark microhabitat use has not been conducted in eastern Australia, dugong predation risk from large sharks in Moreton Bay is likely to be much lower than in Shark Bay, as a result of the long term Shark Control Program for bather protection along the eastern Queensland coast (Dudley 1997; Gribble *et al.* 1998). Nonetheless, dugong remains have been found in the stomach of tiger sharks in Shark Bay in Western Australia as well as waters off Townsville, eastern Australia (Simpfendorfer 1992; Heithaus 2001; Simpfendorfer *et al.* 2001). It is unknown how much of these remains resulted from scavenging rather than active predation.

4.4.6 Future studies

Software improvements

More reliable recognition of dives from shallow-diving dugongs may require algorithms that differ from the functions *descent.crit.q* and *ascent.crit.q* available in *diveMove*. For instance, the software-identified descent phase of some dugong dives actually extended into the bottom phase (Fig. 4.5). Modification of software thresholds above did not change how the phases of these shallow dives were identified. The *diveMove* package may be more suited to animals such as seals and sea lions that make much deeper foraging dives (*e.g.*, elephant seals, fur seals, gray whales).

Analysis of bouts

The dives that had a high probability of achieving particular criteria could be used as a starting point to identify bouts of different types to better understand animal behaviour, feeding frequency, activity patterns, and energetics. Bouts are a series of dives that have similar function (Boyd *et al.* 1994; Beck *et al.* 2003; Austin *et al.* 2006; Wilson *et al.* 2014). As food patches sought by carnivorous marine mammals occur in 3-dimentional planes in varying distributions and densities (Mori 1998), these animals often perform bouts of dives (Le Boeuf *et al.* 2000). Bouts often vary with shape, duration, and maximum depth, and different bout types may represent different foraging tactics and behaviour (Boyd *et al.* 1994; Beck *et al.* 2003; Austin *et al.* 2006; Wilson *et al.* 2014).

Bottom-feeders like gray whales and walrus (Nelson *et al.* 1987; Bornhold *et al.* 2005) also make consecutive feeding dives, leaving visible feeding trails on the seafloor. Both dugongs (Hodgson 2004) and Florida manatees (Hartman 1979) perform bouts when travelling or resting; manatees were observed to rest continuously for up to 2 to 6 h (Hartman 1979). Excavating dugongs leave feeding trails *ca.* 2 to 8 m long and 10 to 40 cm wide (Anderson and Birtles 1978; Preen 1992). Each feeding trail has been interpreted as a record of feeding performed during a single dive.

Use of additional sensors

Complementary data from additional sensing units rather than using stand-alone two-dimensional dive data (Thomson *et al.* 2011) have the potential to expand understanding of dugong diving behaviour and may enable classification of dives using conventional multivariate classification approach. Such study is valuable for understanding dugongs in turbid water which precludes visual studies. Potentially useful devices for dugongs include accelerometers, 3-D motion sensors (Hochscheid *et al.* 1999), hydrophones (Tsutsumi *et al.* 2006; Hodgson 2007; Kukuchi *et al.* 2014), and (video) cameras. The first three devices are more suited to the turbid coastal habitats frequented by dugongs. This point is discussed in more detail in Section 7.3.1.

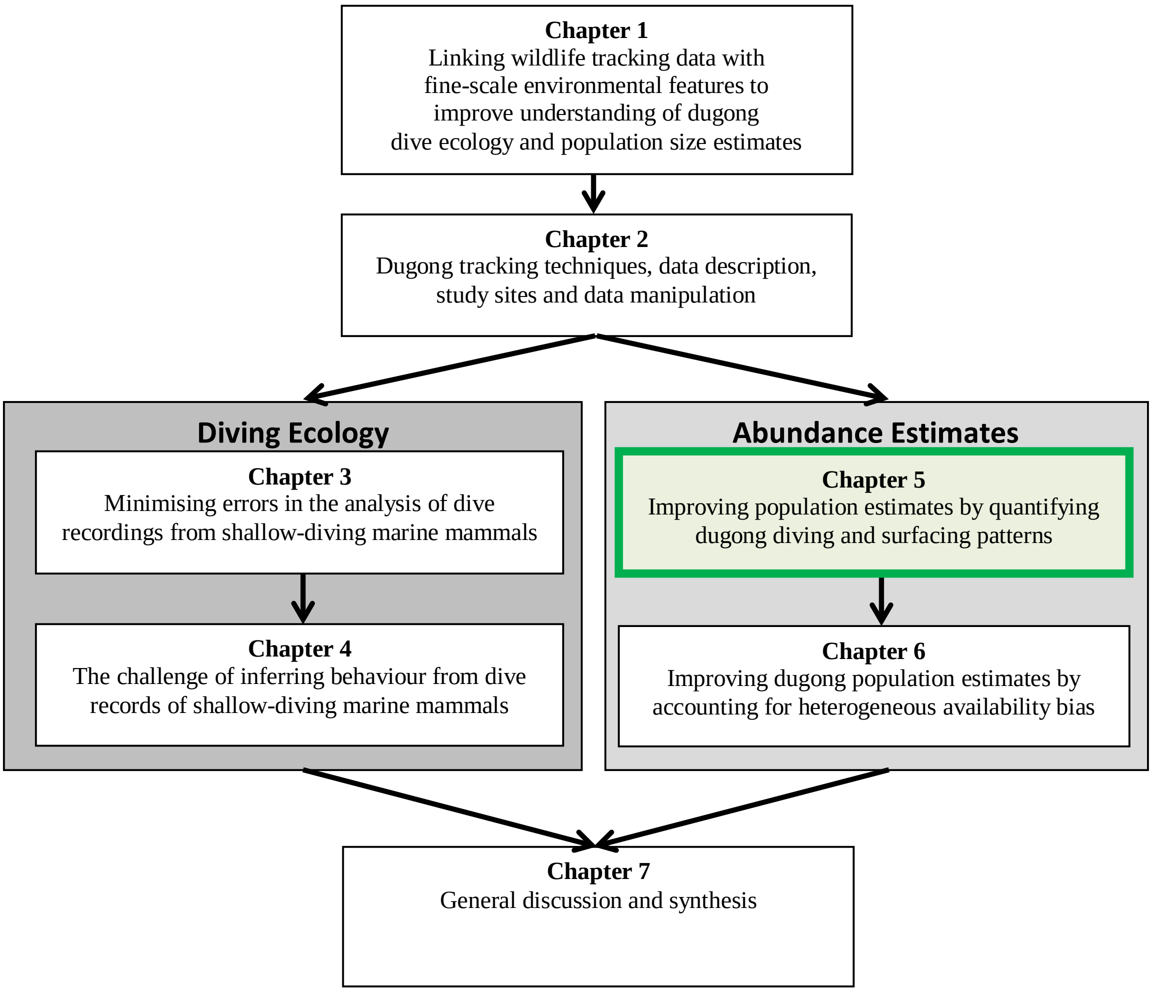
4.4.7 Concluding remarks

Animal behaviour tends to be highly heterogeneous because animals are responding to environmental conditions, habitat types, and food patches that also vary spatially and temporally. Thus linking fine-scale behavioural data with fine-scale habitat descriptions provided insights into dugong diving behaviours at single dive basis. The predictive models allowed me to draw insights into dugong diving behaviour. This approach may be applicable to other shallow diving aquatic vertebrates (*e.g*., manatees, dolphins, turtles, sharks), especially to benthic feeders such as walrus and gray whales, which also leave visible feeding furrows on substratum (Nelson *et al.* 1987; Bornhold *et al.* 2005).

4.5 Chapter summary

- Fine-scale wildlife tracking data (depth records and GPS data) were linked with fine-scale habitat features to obtain insights into dugong diving behaviour in the context of their environment.
- Data from four dugongs tagged in Moreton Bay 2011 using TDRs, GPS satellite transmitters, and relevant environmental attributes were used to develop logistic regression models to predict probability of performing 1) mid-water dives versus seafloor dives, and 2) seafloor dives in locations where seagrass is present or absent.
- The mean maximum dive depth was 4.6 ± 0.04 m, and mean dive duration was 2.5 ± 0.03 min. All four dugongs dived to >20 m; the deepest dive recorded was 31.5 m. These records were similar to earlier studies.
- Mid-water dives were generally deeper than the two types of seafloor dives and had slower ascent rates and larger vertical displacement on the bottom phase indicating more activity. Dive profiles ranged from U- and V-shaped.
- Seafloor dives in seagrass communities had shorter and faster descent and ascent times and rates, longer bottom time, and small vertical displacement during the bottom phase, and a flat bottom profile (Square shaped) than seafloor dives in environments without seagrass.
- Seafloor dives in areas without seagrass had also similarly long bottom time and small vertical displacement during the bottom phase, but descent and ascent rates were slower than for dives in seagrass communities. The dives were predominantly U-shaped.
- Dugongs may make deep benthic dives for orientation and navigation.

Chapter 5: Improving population estimates by quantifying dugong diving and surfacing patterns[3]



Diving animals are available for detection from above-water observers when environmental conditions are favourable and the animals are near the surface. The number of animals that are unavailable for detection needs to be estimated to obtain unbiased population estimates. The current availability detection probabilities used in dugong population estimation methodology allow for variation in environmental conditions but use the average time dugongs spend near the surface (constant availability correction). To improve availability detection probabilities, I examine GPS location and dive data from nine dugongs tracked in eastern Australia. In this chapter, I examine the effects of water depth, tidal conditions, and habitat types on dugong surfacing time and estimate availability detection probabilities.

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[3] A version of Chapter 5 has been published as Hagihara, R., R.E. Jones, A. Grech, J.M. Lanyon, J.K. Sheppard & H. Marsh. 2014. Improving population estimates by quantifying diving and surfacing patterns: A dugong example. *Marine Mammal Science* 30:348-366.

Chapter 5: Improving population estimates by quantifying dugong diving and surfacing patterns

5.1 Introduction

Reliable population estimates are pivotal to the design of successful management and conservation actions for threatened marine wildlife (*e.g.*, Anderson 2001). Abundance can be estimated using a variety of sampling techniques and from a range of platforms (*e.g.*, aerial or boat-based), but some individuals of the target species are generally missed (Buckland *et al.* 2004), even when the population is closed and the survey methodology rigidly standardized. Population estimates are therefore often negatively biased (Buckland and Turnock 1992; Laake *et al.* 1997).

Aquatic wildlife may be undetected when environmental conditions are unfavourable (*e.g.*, turbid water, glare, glitter on the surface) and target species exhibit characteristics that diminish their probability of detection (*e.g.*, inconspicuous colour, small body and pod size, diving behaviour; Anderson 2001, Edwards *et al.* 2007, Langtimm *et al.* 2011). Marsh and Sinclair (1989b) classified the causes of missed animals as availability bias and perception bias (not always mutually exclusive). Availability bias occurs when animals are unavailable for detection due to, for instance, high turbidity and rough sea states. Perception bias arises when observers are unable to detect all the individuals that are available, due to observer's eye sight, search pattern, experience, and fatigue, *etc*. Both types of bias can vary over small temporal and spatial scales within a survey (Buckland *et al.* 2004) and need to be quantified to obtain unbiased population estimates.

Diving and surfacing patterns have been used to account for animals that are not in the detection zone (water column near the surface in which animals are available for detection by above-water observers; Fig. 5.1) and to estimate an important component of availability bias. Diving data have been collected by VHF receivers (*e.g.*, Schweder *et al.* 1991*a*, *b*), visual observations (*e.g.*, Barlow *et al*. 1988; Laake *et al*. 1997; Slooten *et al*. 2004), or TDRs (*e.g.*, Pollock *et al.* 2006; Edwards *et al.* 2007;

Fonnesbeck *et al.* 2009). These availability bias estimates are however generally based on average surfacing durations (*e.g.*, Barlow *et al.* 1988; Laake *et al.* 1997; Skaug *et al.* 2004).

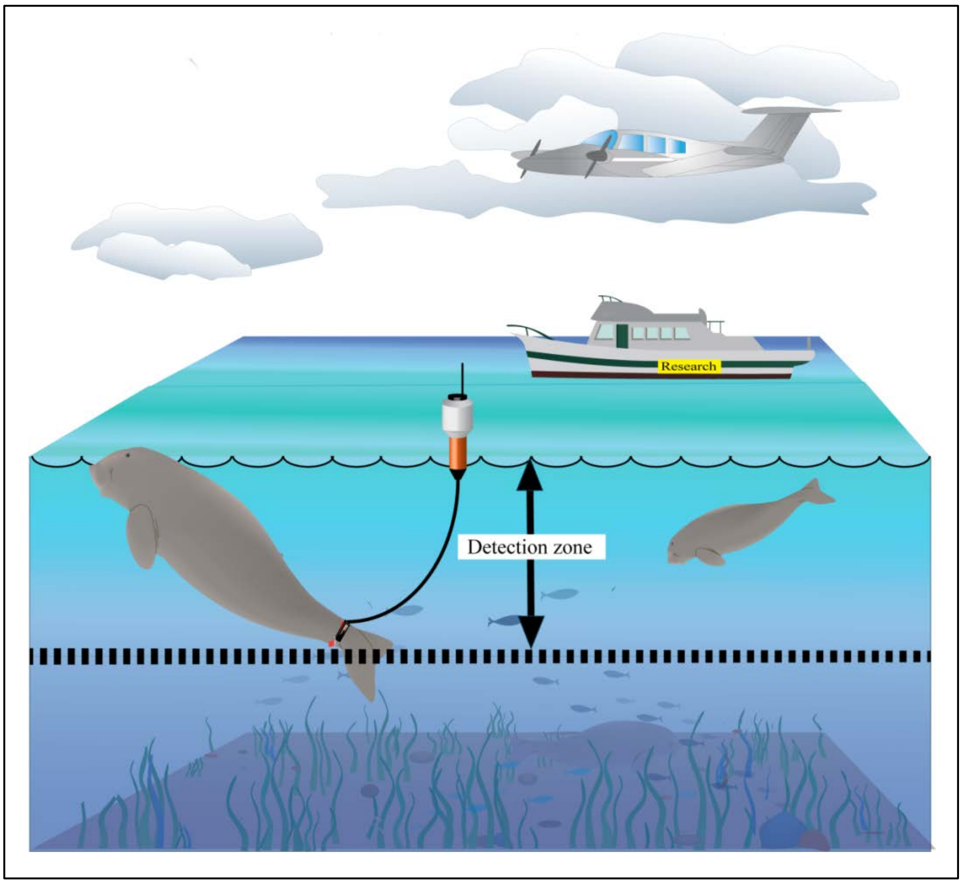


Figure 5.1 Diagram of detection zone in which dugongs are available for detection from above-water observers during population surveys.

The assumption that these averages are representative across all survey conditions is likely to be violated as surfacing times or availability for detection of aquatic wildlife are found to vary with habitat type (Florida manatees: Langtimm *et al*. 2011), season (minke whales *Balaenoptera acutorostrata*: Stockin *et al*. 2001), season and dive depth (green turtles, and loggerhead turtles *Caretta caretta*: Thomson *et al.* 2012), and location (leatherback turtles: James *et al.* 2006; basking sharks *Cetorhinus maximus*: Southall *et al.* 2005).

The standard aerial survey methodology for the dugong employs a variant of distance sampling technique and quantifies availability and perception bias separately (Marsh and Sinclair 1989b; Pollock *et al.* 2006). Perception bias is estimated using two pairs of observers and mark-recapture models. My focus in this chapter and Chapter 6 is on availability bias, which Pollock *et al.* (2006) estimate using two sets of information:

1. Survey-specific information on turbidity and sea state to account for the depth of the detection zone, which varies within and among survey areas; and
2. Estimates of the average time dugongs spend in those variable depths of detection zones.

Pollock *et al.* (2006) quantified detection zones by using dugong replicas deployed in a fashion similar to secchi disks (Preisendorfer 1986). The replicas were fitted with TDRs, submerged in various levels of turbidity and sea state, and raised from the ocean floor until visible to aerial observers. Pollock *et al*. (2006) determined the depth of detection zones (Fig. 5.1) under various combinations of environmental conditions. The average times dugongs spend in these detection zones were estimated using data collected from TDRs fitted to wild dugongs. The probabilities of dugongs being in the detection zones were then estimated, allowing availability of a dugong under specific environmental conditions to be estimated.

The methodology developed by Pollock *et al.* (2006) assumes that the proportion of time a dugong spends within a specified detection zone is unaffected by environmental variables. This simplistic assumption was unavoidable due to insufficient number of GPS location data obtained from earlier generations of GPS transmitters, and therefore insufficient to characterise the variability in surfacing patterns at fine spatial scale.

I used data collected from TDRs and GPS transmitters fitted to nine dugongs and examined the effects of water depth, tidal conditions, and habitat types on the availability for detection, specifically, on the proportion of time that dugongs spent in detection zones using generalized linear mixed models (GLMMs).

I then estimated and compared the corrected number of dugongs using: 1) the depth-specific availability detection probabilities and 2) constant availability detection probabilities across water depth from Pollock *et al.* (2006). This approach enabled me to examine the effects of environmental conditions on dugongs' surfacing patterns at a fine scale and determine whether heterogeneous availability estimates improve dugong population estimates. As this chapter provides exploratory assessment, I have examined the proportions of time dugongs spent at the surface and estimated availability bias for only two detection zones (0–1.5 m for turbid water and Beaufort sea state 3 and 0–2.5 m for clear water and sea state <2). In Chapter 6, I estimate availability detection probabilities for all classes of environmental conditions.

5.2 Materials and methods

5.2.1 Study animals, sites, and tagging units

In this chapter, I used data collected from five dugongs tracked in Hervey Bay 2003/2004 and four dugongs tracked in Moreton Bay 2011. General descriptions of these two sites are detailed in Section 2.3. The five dugongs in Hervey Bay were each fitted with a GPS/Argos systems unit (Telonics Inc., Mesa, Arizona, USA) from July to August in 2003/2004. The four dugongs in Moreton Bay, were each fitted with GEN4 GPS/Argos systems unit (Telonics Inc., Mesa, Arizona, USA) from May to August in 2011. Further details on animals and specification of GPS units and TDRs are given in Table 2.1.

5.2.2 Data preparation

As described in Section 2.4, the tracking data were pre-processed using custom software, which identified the level of the water surface (zero-offset) and removed dugong spikes – biologically implausible rapid changes in depth (Fig. 2.3, Hagihara *et al.* 2011). Depth records subsampled around GPS/QFP fixes were used in the following section to ensure reasonably accurate association of environmental condition experienced by tagged dugongs at the time of each location fix (Fig. 2.3C).

Bathymetric models and tidal records (Maritime Safety Queensland, Department of Transport and Main Roads) were used to estimate the water depth at the time and geographic location for each fix. The bathymetric models of 100 m spatial resolution were generated by Sheppard (2008) in Hervey Bay and by Beaman (2010) in Moreton Bay. The depth at the location of each fix was identified by importing the bathymetric models and location fixes into ArcGIS 9.3.1. Tidal heights (LAT) were added to the depth on the bathymetric charts (MSL) to calculate the water depth experienced by the dugong at the time of each fix. I assumed that estimated water depths remained constant for the 10 min around each fix (Fig. 2.3).

Previous experiments using dugong replicas found that the availability of dugongs varies with levels of turbidity and sea state (Pollock *et al.* 2006). Following Pollock *et al.* (2006), I examine the proportion of time dugongs spent in two detection zones: 0–1.5 m of the surface for turbid water and Beaufort sea state 3 (rougher conditions with very few whitecaps); and 0–2.5 m of the surface for clear water and sea state ≤ 2 (calm conditions with no whitecaps).

I assigned “1” when a depth measurement was recorded within each of the detection zones and “0” when a depth measurement was recorded outside of the detection zone (Fig. 5.1). The proportion of time dugongs spent in each detection zone was calculated by the sum of these numbers divided by the number of depth records. Dive records were excluded when dive depths exceeded the depth of water as occasionally happened in shallow waters (*e.g.*, <2 m), probably because of discrepancies between the bathymetric models and the GPS/QFP location fixes.

5.2.3 Representativeness of subsets

The subsampled data I examined might be biased if some habitats (*e.g.*, shallow) or behaviours (*e.g.*, resting) had higher fix rates than others (*e.g.*, deep water or travelling fast). Short surfacing times (>30 s for a GPS fix and ~5 s for a QFP fix) fail to generate a location fix, because the GPS radio frequency is attenuated by salt water and the GPS units turn off to save battery life whenever the saltwater sensor on the unit is submerged, such as when the dugong is diving (>3 m) or swimming rapidly, causing the unit to be dragged underwater (Marsh and Rathbun 1990).

I compared the distributions of the dive depths from the subsets associated with location fixes and those not associated with fixes using contingency tests to determine how representative the fix-associated subsets of dive data were of the entire dive data set. The subsets of dive measurements were collected around the time GPS/QFP fixes. A location was fixed every 30 min or 1 h at most. In contrast, the TDRs continued to collect dive measurements every 1 or 2 s over the deployment periods.

I used all available dive data associated with fixes. For the non-fix associated depth data, four sets of one-day dive data were randomly selected from each of the nine dugongs (four × one-day dive data × nine animals). Statistical tests were performed separately for Moreton and Hervey Bays. Depth records were categorized into five bins: 0 to <5 m, 5 to <10 m, 10 to <15 m, 15 to <20 m, and ≥20 m. For the Hervey Bay data, the last two categories were combined due to small sample sizes. This was because in Hervey Bay, previous GPS transmitters deployed to dugongs provided GPS fixes only (no QFP fixes), therefore fewer location fixes were obtained from these units in deeper waters where surfacing opportunities of GPS units are less compared to shallow waters, or at day time when the tagged dugongs were presumed to be active, causing the transmitter to be dragged underwater (refer to Section 2.2).

5.2.4 Estimating availability bias

I examined the effects of the following three categorical variables on the proportions of time the tracked dugongs spent in the two detection zones 0–1.5 m and 0–2.5 m:

1. Water depth – 2 to <5 m, 5 to <10 m, 10 to <15 m, 15 to <20 m, 20 to <25 m, and ≥25 m;
2. Tidal conditions – flow and ebb tides; and
3. Habitat types – inshore and offshore waters.

For analysis of the detection zone 0–1.5 m, I excluded data from water depth ≤1.5 m because a dugong in this depth range is fully available for detection by definition even if it was on the seafloor (Pollock *et al.* 2006). The next shallowest water depth I examined was 2 m because the TDR resolution was 0.5 m. The shallowest category for the detection zone 0–2.5 m was 3 to <5 m for the same reason.

In water >5 m deep, water depths were binned with intervals of 5 m up to 25 m. The 5 m interval ensured that all animals were sufficiently represented in each bin. For the offshore waters, 35 m was my data limit with all animals represented, however the limit from the inshore dataset was 30 m. The statistical model required all water depth categories to be represented in each combination of tide and habitat categories. I therefore used >25 m as the final water depth category. Water depth was treated as a categorical variable rather than a continuous variable for three reasons: 1) even though the bathymetry model I used provided the best spatial accuracy (± 100 m) available, this spatial resolution was not fine enough to using it as a continuous variable; 2) water depth was estimated from the bathymetric model and tidal information and subject to error; and at lesser significance than (1 and 2), 3) water depth and the proportion of time dugongs spent at the surface showed a non-linear relationship, which is unsuited to linear models. Due to problems (1) and (2), I have used wider depth category (*e.g.*, 5 to <25 m and >25 m) in Chapter 6. Alternative approach was to use General Additive Model (GAM). However, GAM applies smoothers to data and does not provide equations, thus unsuitable for estimating availability detection probabilities used in dugong aerial survey estimation methodology.

Flow tides indicated tidal condition before high tides and ebb tides after high tides. The Moreton Bay dugongs made frequent excursions between two very different habitats: inshore waters where seagrass meadows extend and deeper offshore waters, east of Moreton and North Stradbroke Islands (Fig. 2.2; Phinn *et al.* 2008; Lyons *et al.* 2012). I expected diving patterns in these habitats to be different, because dugongs over seagrass meadows would primarily be feeding, and feeding individuals may spend more time submerged to excavate or crop seagrasses than when offshore where no or little seagrass is found, therefore not feeding (Marsh *et al*. 2011b). I therefore compared the dugong’s availability for detection in each of these habitat types for the Moreton Bay dugongs only. This approach was subsequently justified by my research on dugong diving behaviour described in Chapter 4. Location (bays) was not used as an additional predictor variable. Although the number of dugongs was similar in both bays (5 dugongs in Hervey Bay and 4 dugongs in Moreton Bay), the Hervey Bay tracking study provided a smaller amount of data than the Moreton Bay tracking study. This is because the Hervey Bay tracking study used previous model of GPS transmitters and did not provide QFP fixes. In contrast, the Moreton Bay study, which used later technology, provided both GPS and QFP fixes. The increase in location fixes also increased the amount of depth records that could be used in this chapter. The later transmitters used in Moreton Bay and Shoalwater Bay dugong tracking also enabled me to use individual dugong as random factor in Chapter 6.

Logistic regression via generalized linear mixed models (GLMMs) was employed, as the response variable was binary and this statistical method can accommodate random components from individual dugongs (Breslow and Clayton 1993). I used Gaussian Hermit Quadrature estimation with *lme4* (ver. lme_4 0.999999-2, Bates *et al.* 2012). Model specification is found in Appendix 5.1. Akaike Information Criterion (AIC) and Chi-square tests were used to compare models. Diagnostic plots were used to check the performance of individual models.

Dive data comprised a time-series of depth records separated by 1 or 2 s and were strongly autocorrelated. Visual inspection of dive profiles indicated that successive dives tended to be similar. To ensure independent samples, I treated 10 min as a sampling unit (the subsampled period around a GPS/QFP fix; Fig. 2.3). The 10 min interval ensured that at least one complete dive was included in a sample. Longer intervals were not appropriate because the location of the dugong could change and the estimated water depth needed to remain constant during a sampling unit.

A saturated model was first examined using individual dugong as a random factor and water depth, tidal condition, and habitat types as categorical fixed factors. The model was reduced by removing the tidal variable because some water depth and tide combinations had few observations, and because no tidal effects were identified during exploratory data analysis.

I estimated the probabilities of dugongs being in the detection zones using GLMM linear predictor estimates. The 95% confidence intervals for the predicted values were also calculated based on fixed factors. Data manipulations and statistical analyses were executed using S Plus version 8.0 (TIBCO Software 2007) and R 2.15.1 (R Development Core Team).

5.2.5 Case study: Estimating corrected number of dugongs

Based on previous aerial survey data collected in Hervey Bay conducted in 2001, 2005, and 2011 (Lawler 2002; Marsh and Lawler 2006b; Sobtzick *et al.* 2012), I estimated corrected numbers of dugongs using: 1) depth-specific availability detection probabilities estimated in this chapter; and 2) constant availability detection probabilities across water depth from Pollock *et al.* (2006). The constant probabilities were 0.47 for the detection zone 0–1.5 m and 0.65 for the zone 0–2.5 m. The dugong sightings were classified according to water depth categories, <2 m (or <3 m), 2 to <5 m (or 3 to <5 m), 5 to <10 m, 10 to <15 m, 15 to <20 m, 20 to <25 m, and ≥25 m. The number of dugongs was estimated as the number counted during a survey divided by the probability of dugongs being in one of the detection zones (*e.g.*, 53 dugongs / 0.65 ≈ 82 animals). All surveys were conducted in November.

5.2.6 Aerial survey methodology

Aerial survey methodology for dugongs followed a variant of distance sampling technique. Two pairs of observers on either side of an aircraft surveyed a transect 200 m wide on the water surface. The 200 m transect was delineated by fiberglass rods attached to artificial wing struts on the aircraft. Distance categories (50, 100, and 150 m) within the strip were marked by colour bands on the artificial wing struts. When a group of dugongs was detected, an observer recorded a number of animals sighted, position (distance) of the animals indicated by the colour bands and other information such as environmental condition. Because dugongs surface cryptically only for 1-2 s (Anderson and Birtles 1978), a large amount of measurement error was found in the assignment of dugong sightings to distance classes within the transect strip (Pollock *et al.* 2006). However, Pollock *et al.* (2006) found there was no decline in detection with distance across the 200 m survey strip. Detailed survey methodology is provided in Marsh and Sinclair (1989b) and Pollock *et al.* (2006).

5.3 Results

5.3.1 Representativeness of subsets

For each of the four Hervey Bay dugongs which used the previous model of GPS transmitters, the range of maximum dive depths associated with location fixes was biased towards shallow areas (max. dive depth 2–7 m). Randomly selected data showed a wider range (max. dive depth 9–17 m). There was a significant difference between the distributions of the fix-associated and random subsets of dive depths ($\chi^2 = 11.20$, df = 3, $P = 0.01$). In contrast, the distributions of fix-associated (8–19 m) and the random (10–15 m) maximum dive depths from Moreton Bay dugongs were not significantly different ($\chi^2 = 0.27$, df = 4, $P = 0.99$). I therefore performed the following statistical analyses on data from Moreton Bay dugongs only. Appendix 5.2 shows the raw proportions of time dugongs spent in the two detection zones for both the Moreton and Hervey Bay dugongs.

5.3.2 Model selection

Detection zone 0–1.5 m: the best model included the fixed factor of water depth only (Model 3, Table 5.1A). Although Models 1 and 2 did not differ significantly from Model 3 (Model 1 and 3: $\chi^2 = 11.19$, df = 6, $P = 0.08$; Model 2 and 3: $\chi^2 = 1.29$, df = 1, $P = 0.26$), I chose the most parsimonious model (Model 3), which also had the smallest AIC value. Model 4, with the single factor of habitat had a significantly poorer fit ($\chi^2 = 50$, df = 4, $P < 0.0001$). Once the fixed factors were determined, I examined the number of quadrature points for the Gaussian Hermit Quadrature approximation based on AIC values and Chi-square tests. I chose 100 quadrature points as the fit was significantly better than models with a smaller number of quadrature points (Table 5.1B).

Detection zone 0–2.5 m: the fixed factors of water depth and habitat and the interaction of the two produced the best model (Model 1, Table 5.2A), which provided a significantly better fit than all other alternative models (Model 1 and 2: $\chi^2 = 11.4$, df =

5, *P* <0.05; Model 1 and 3: $\chi^2 = 12.87$, df = 6, *P* <0.05; Model 1 and 4: $\chi^2 = 46.6$, df = 10, *P* <0.0001). Again, 100 quadrature points gave the best fit (Table 5.2B). Model outputs from the two analyses are provided in Table 5.3.

5.3.3 Estimating availability bias

Detection zone 0–1.5 m: the availability detection probability was high (0.61) for water depths of 2 m to <5 m (Fig. 5.2A). The probability declined as water depth increased, reaching its minimum (0.29) in water 10 to <15 m deep and remained relatively low in water up to 25 m deep. In water depths ≥25 m, the dugongs spent almost as much time in the detection zone (0.57) as they did in water depths 2 to <5 m. Between water depths of 5 and 25 m, these probabilities were lower than the average probability of availability (0.47; dotted line in Fig. 5.2A) across water of all depths.

Detection zone 0–2.5 m: when the detection zone was deeper, the availability detection probability was higher in most depth categories (Fig. 5.2B). Although habitat affected detection probabilities, the difference between inshore and offshore habitats was only substantial in the two shallowest depth categories (that is, water depths up to 10 m). In deeper water, the confidence intervals for the inshore habitat included the mean of the offshore habitat. The depth-specific probabilities were lower than the constant probability (0.67; dotted line in Fig. 5.2B) in water depths 3 to <5 m for offshore waters and between 5 and 15 m for both habitats.

Table 5.1 Comparison of models A) using various fixed factors and their associated indicator values for assessing the model fit and B) using different number of quadrature points used in the approximation and their associated indicator values. The response variable was the proportion of time dugongs spent in the detection zone 0–1.5 m.

A)	**Model**	**Fixed factors**	**Random factor**	**Variance (SE) of random effects**	**AIC**	**BIC**	**LogLik**	**deviance**
	1	water depth, habitat, water depth × habitat	animal	0.48 (0.69)	115.0	153.1	-44.5	89.0
	2	water depth, habitat	animal	0.45 (0.67)	114.9	138.3	-49.5	98.9
	3^	water depth	animal	0.41 (0.64)	114.2	134.7	-50.1	100.2
	4*	habitat	animal	0.26 (0.51)	157.3	166.1	-75.6	151.3
B)	**Model**	**Fixed factors**	**Random factor**	**nAGQ**	**AIC**	**BIC**	**LogLik**	**deviance**
	1*	water depth	animal	2[1]	114.2	134.7	-50.11	100.2
	2*	water depth	animal	5	114.2	134.7	-50.11	100.2
	3*	water depth	animal	10	114.2	134.7	-50.11	100.2
	4^	water depth	animal	100	110.0	130.5	-48.0	96.0

^models selected, *models significantly different from the model selected, [1]integer >1 leads to Gaussian Hermit Quadrature approximation

Table 5.2 Comparison of models A) using various fixed factors and their associated indicator values for assessing the model fit and B) using different number of quadrature points used in the approximation and their associated indicator values. The response variable was the proportion of time dugongs spent in the detection zone 0–2.5 m.

A)	**Model**	**Fixed factors**	**Random factor**	**Variance (SE) of random effects**	**AIC**	**BIC**	**LogLik**	**deviance**
	1^	water depth, habitat, water depth × habitat	animal	0.18 (0.43)	90.8	128.5	-32.4	64.8
	2*	water depth, habitat	animal	0.14 (0.40)	92.2	115.4	-38.1	76.2
	3*	water depth	animal	0.12 (0.35)	91.7	111.9	-38.8	77.6
	4*	Habitat	animal	0.11 (0.34)	117.4	126.1	-55.71	111.4
B)	**Model**	**Fixed factors**	**Random factor**	**nAGQ**	**AIC**	**BIC**	**LogLik**	**deviance**
	1*	water depth, habitat, water depth × habitat	animal	2[1]	90.8	128.5	-32.4	64.8
	2*	water depth, habitat, water depth × habitat	animal	5	90.8	128.5	-32.4	64.8
	3*	water depth, habitat, water depth × habitat	animal	10	90.8	128.5	-32.4	64.8
	4^	water depth, habitat, water depth × habitat	animal	100	86.6	124.3	-30.3	60.6

^models selected, *models significantly different from the model selected, [1]integer >1 leads to Gaussian Hermit Quadrature approximation

Table 5.3 Outputs of generalized linear mixed models (GLMMs) using Gaussian Hermite Quadrature estimation. Linear predictors (Estimate) are used to estimate probabilities of dugong being in the detection zones 0–1.5 m or 0–2.5 m.

	Term	**Estimate**	**Std Error**	**z value**	**Pr(>|z|)**
Detection zone 0–1.5 m	Intercept	0.4447	0.3370	1.319	
	water depth 5 to <10 m	-1.2608	0.1959	-6.437	***
	water depth 10 to <15 m	-1.3312	0.1783	-7.465	***
	water depth 15 to <20 m	-1.0965	0.2028	-5.407	***
	water depth 20 to <25 m	-1.0907	0.2343	-4.656	***
	water depth ≥25 m	-0.1709	0.3258	-0.525	
Detection zone 0–2.5 m	Intercept	-0.7159	0.8780	-0.815	
	water depth 5 to <10 m	1.3114	0.8733	1.502	
	water depth 10 to <15 m	0.9858	0.8600	1.146	
	water depth 15 to <20 m	1.3955	0.8680	1.608	
	water depth 20 to <25 m	2.0610	0.9125	2.259	*
	water depth ≥25 m	2.7761	0.9636	2.881	**
	habitat (inshore)	2.0142	0.8737	2.305	*
	water depth 5 to <10 m: habitat (inshore)	-2.7738	0.9369	-2.961	**
	water depth 10 to <15 m: habitat (inshore)	-1.9153	1.1665	-1.642	
	water depth 15 to <20 m: habitat (inshore)	-1.9717	1.1319	-1.742	.
	water depth 20 to <25 m: habitat (inshore)	-2.7353	1.0180	-2.687	**
	water depth ≥25 m: habitat (inshore)	12.9231	3844.3640	0.003	

significance codes: <0.001 =***; 0.001-<0.01 =**; 0.01-≤0.05 =*

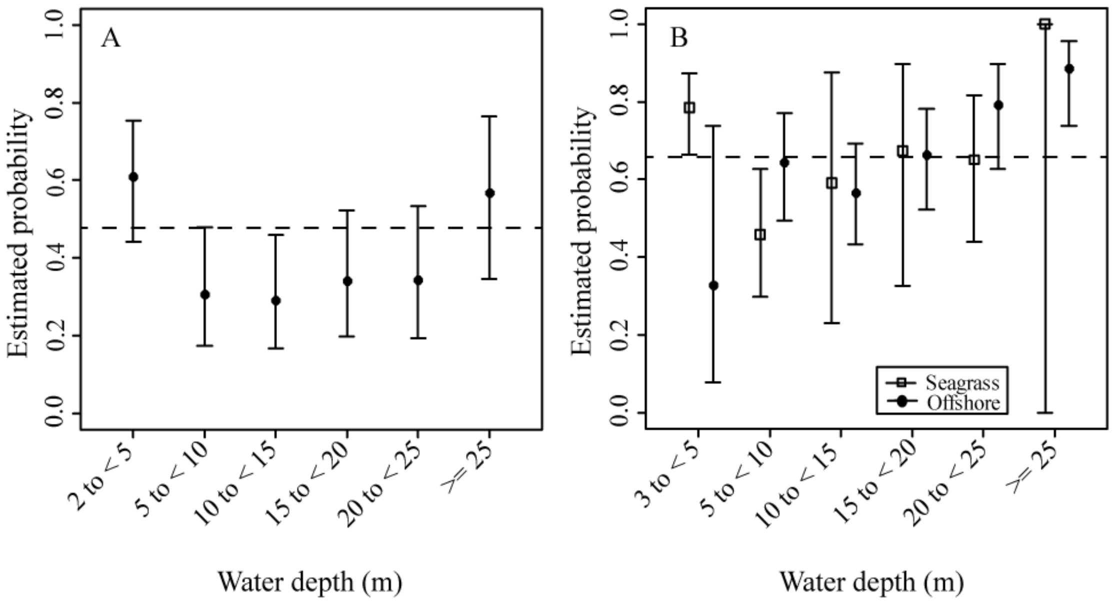


Figure 5.2 Estimated probabilities of dugongs being in the detection zones A) 0–1.5 m and B) 0–2.5 m. The error bars represent 95% confidence intervals. The dotted lines show the constant probabilities from Pollock *et al.* (2006) for each of the combination of water turbidity and sea state (*i.e.*, detection zone).

5.3.4 Case study: Estimating corrected number of dugongs

Most dugongs were sighted in water depths of 2 to <15 m in the 2001 (80%), 2005 (90%), and 2011 (70%) aerial surveys of Hervey Bay (details in Sobtzick *et al.* 2012). For the detection zone 0–2.5 m, similarly large numbers of dugongs were sighted from water 3 to <15 m: 58% in 2001, 70% in 2005, and 57% in 2011.

In most water depth ranges except 2 to <5 m (or 3 to <5 m) and ≥25 m, depth-specific availability corrections resulted in higher dugong numbers being estimated than the constant corrections (Fig. 5.3). The differences in the estimated numbers based on the depth-specific and constant corrections were larger when the detection zone was 0–1.5 m than 0–2.5 m. The total numbers of dugongs estimated across the water depth range were also higher when finer corrections at each water depth bin were applied than those using constant corrections.

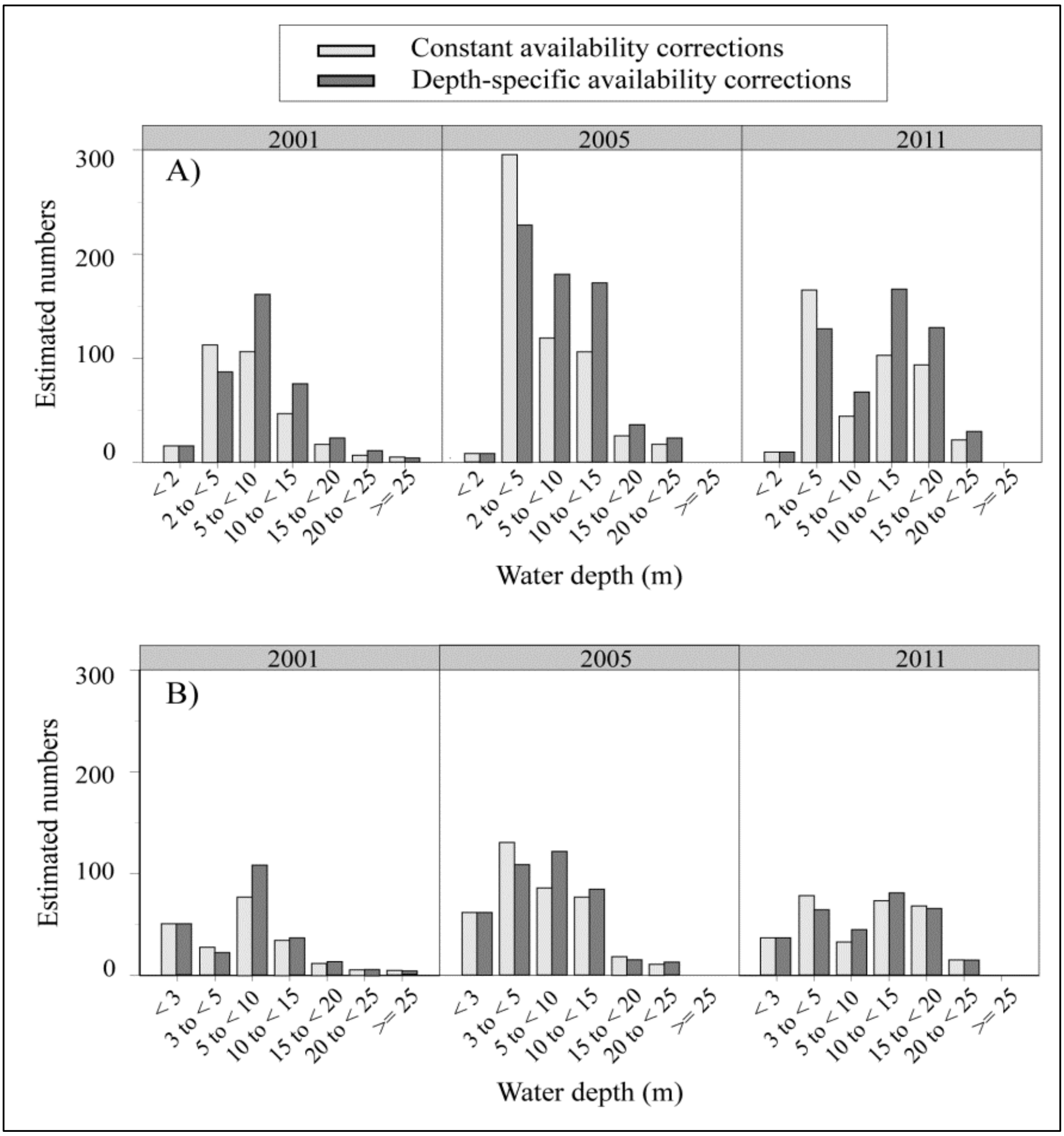


Figure 5.3 Number of dugongs estimated using constant detection probabilities for A) turbid water and sea state 3 (0–1.5 m) and B) clear water and sea state ≤2 (0–2.5 m) from Pollock *et al.* (2006) and depth-specific probabilities obtained in this study. The estimated numbers were extrapolated from uncorrected dugong counts collected during aerial surveys conducted in 2001, 2005, and 2011 in Hervey Bay (Lawler 2002; Marsh and Lawler 2006; Sobtzick *et al.* 2012).

5.4 Discussion

5.4.1 Availability bias

The availability of dugongs for detection by aerial observers varied with water depth. Where the detection zone was narrow (0–1.5 m), the availability detection probability reached 50% only in very shallow water (2 to <5 m) and very deep water (≥25 m). When the detection zone was wider (0–2.5 m), the availability detection probability was larger but showed some evidence of variation between habitats. The habitat effect was largely confined to shallow water depths. The dugongs were expected to be less available for detection over inshore waters than in offshore waters because they would be spending more time on the seafloor feeding on seagrass in inshore waters (see Chapter 4). This pattern was observed in water 5–10 m deep, but for water depths below 5 m the pattern was reversed, with very low estimated availability in the offshore habitat and high availability over inshore waters. However, there were relatively few data points from this shallowest water depth category in offshore waters; more data are needed to confirm or refute this puzzling result. Where water was ≥10 m deep, the availability of dugongs was similar regardless of habitat type.

The number of dugongs estimated using depth-specific availability detection probabilities was lower in waters 2 to <5 m and 3 to <5 m than those estimated using constant corrections because in shallow waters, depth-specific availability estimates were positively biased compared to the constant estimates. In contrast, in waters 5–25 m deep, the estimated number of dugongs was higher using depth-specific rather than constant availability estimates, because the former availability estimates were smaller than the latter ones. In water <2 m and <3 m deep, there was no difference in the estimated numbers of dugongs as all dugongs in these water depths were assumed to be available for detection, and no correction was applied to these sightings.

All these estimates are underestimates; not all combination of turbidity levels and sea states are incorporated in correcting each dugong count, and I did not account for perception bias and sampling fraction in the calculation. Abundance is re-estimated in Chapter 6. Nonetheless, the fact that a large proportion of dugongs were sighted in water $\geq$5 m (46–58%), where the depth-specific availability bias were smaller than the constant availability in most depth categories, suggests that overall, the use of heterogeneous detection probabilities would have produced larger population estimates for the three surveys examined here.

The scale of these effects on the final population estimates will depend on turbidity and sea state at each dugong sighting and survey location. Differences in the number of dugongs estimated using the depth-specific and constant probabilities were larger when the detection zone was 0–1.5 m. Thus if water in the survey area is turbid and Beaufort sea state 3 (occasional whitecaps), lower availability bias estimates will be used, leading to larger population estimates. If the water is less turbid and Beaufort sea state $\leq$2 (no whitecaps), population estimates will be less than under marginal survey conditions.

The distribution of dugongs across the bathymetric range will also affect the final population estimates (refer Chapter 6). If a large proportion of dugongs is sighted in waters 5–25 m deep where depth-specific availability is low, the lower availability estimates will produce larger abundance estimates. The opposite situation will apply if many dugongs were sighted in shallow areas.

The fluctuations in dugong population estimates observed in repeat surveys of the same area have been largely attributed to temporary migration into or out of the survey area (*e.g.*, Marsh *et al.* 1997). However, the work presented here suggests that a more parsimonious reason for some of these differences in the population abundance estimates is inter-survey differences in the depth distribution of dugongs within a survey area. For example, the between-survey differences in the number of dugongs sighted in Hervey Bay (Lawler 2002; Marsh and Lawler 2006; Sobtzick *et al.* 2012; see Fig. 5.3) can be plausibly explained by inter-survey differences in the dugong distribution within the survey region.

5.4.2 Comparison with previous studies

Differences between my data and those collected in other studies make meaningful comparisons difficult, as I examined dugong diving patterns in relation to their fine-scale geographic locations (and hence water depths). Interpretation of such data has not been described before in literature on dugongs. Nonetheless, across the depth range, the proportions of time dugongs spent in the detection zones found in my study were generally slightly lower than those presented in Chilvers *et al*. (2004). Based on dive data collected from dugongs in western, northern and northeastern Australia, these authors found that the dugongs spent 53% (SE = 3%) of their daily activities within 1.5 m of the surface. In my study, Moreton Bay dugongs spent 44% (SE = 4%) in this depth zone over inshore; 38% (SE = 2%) offshore.

Several studies have report that tidal patterns regulate the horizontal movements of dugongs between inshore and offshore waters. For example, based on visual observations using aircraft and boats, Anderson and Birtles (1978) described dugongs moving to inshore feeding grounds during flooding tides and leaving these areas as the tide receded. No dugongs were found feeding in offshore shoal areas in high tide. Similarly, GPS satellite tracking show dugongs moved closer to the shore during high tides than during low tides (Sheppard *et al.* 2009). All of these studies indicate that dugongs move horizontally with diel tidal fluctuations to exploit shallow intertidal seagrass pastures.

However, I did not identify tidal effects on the surfacing times of dugongs. It is possible that such an effect may exist in very shallow areas or areas with pronounced tidal ranges. I did not examine shallow dives in water $\leq$1.5 m, because the availability of dugongs to aerial observers was assumed to be 1 by definition (Pollock *et al*. 2006). The tidal range in Moreton Bay is relatively small (<2 m) and water depth and tidal factors were confounded because I used tidal records to estimate the actual water depth at the time of satellite location fixes. My data suggest that tidal fluctuations have less effect on the vertical positions of dugongs in the water column than on their horizontal movements.

5.4.3 Future directions

Results from this chapter are preliminary in terms of estimating availability bias for dugong population estimates from aerial surveys. I sampled only nine dugongs, and the time spent in the detection zones differed slightly among individuals. Chapter 6 examines additional data collected in Moreton Bay (N = 9 dugongs) and Shoalwater Bay (N = 3 dugongs). Nonetheless, the consistency of the depth effects observed across habitat types indicates that in general, availability correction factors should vary with water depth. Algorithms need to be developed to include information on the dugong's depth-specific surfacing patterns as well as the information on water turbidity and sea state that is presently collected.

The generic application of the results described here to dugong population estimation required the development of a technique to incorporate the standard errors associated with the probability of a dugong being in the detection zone under various survey conditions into the standard error of the population estimates. This technique followed Pollock *et al.* (2006) and is described in Chapter 6. The spatial population models based on the aerial survey data that have been developed for systematic conservation planning (Grech and Marsh 2007; Grech *et al*. 2008; Grech *et al*. 2011) will also be improved by incorporating the depth-specific availabilities into the dugong density models.

Additional data from a range of inshore and offshore habitats are also required for better estimates of dugong availability correction factors, even though the range of water depths examined here covered a large proportion of area surveyed during aerial surveys of the north-eastern Australian coast. For example, most of the areas surveyed in Moreton Bay (70%) and Hervey Bay (90%) are within the range of water depths I examined (Lawler 2002; Marsh and Lawler 2006; Sobtzick *et al.* 2012). In other areas such as the Great Barrier Reef World Heritage Area, the proportion is lower (~59%) (Sobtzick *et al.* 2014).

I examined data collected in winter, however aerial surveys are generally conducted in summer. At the higher latitude limits of their range in summer, dugongs are most frequently sighted over shallow seagrass meadows, but in winter they are also sighted in deeper waters where sea temperatures are warmer (Preen 1992; Lanyon 2003; Sheppard *et al.* 2006; Holley *et al.* 2006; Marsh *et al.* 2011a). If an aerial survey is conducted in winter, the depth distribution of dugongs may be different, an explanation suggested by Lanyon (2003) for the seasonal differences in dugong population abundance estimates she observed in Moreton Bay. Water temperature may affect a dugong's diving patterns through behavioural or physiological responses and hence its availability to aerial observers. Thus availability estimates from this study can be applied to winter surveys in the Moreton Bay region, and wider application will require more data from other locations and seasons. Additional factors that may affect availability bias such as glare, glitter on the water surface, and social associations (*e.g.*, solitary, herding or a cow with a calf) also warrant examination.

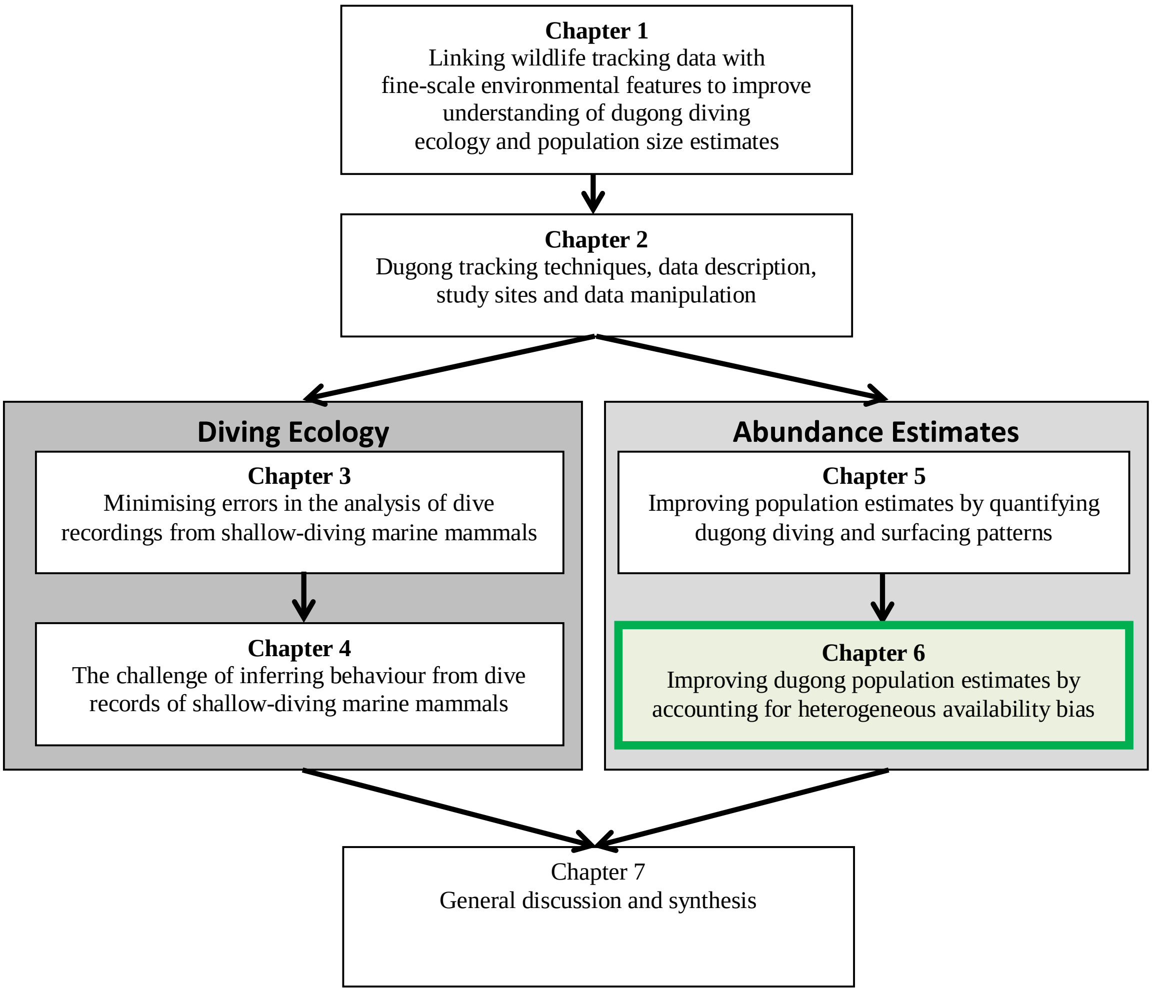
5.4.4 Applicability to other diving species

Techniques such as those developed in this study could be used to incorporate heterogeneous availabilities into survey methodologies from aerial and vessel-based surveys of other aquatic wildlife to improve the accuracy of population estimates. Heterogeneous availability has been found in other taxa including marine mammals. Stockin *et al.* (2001) reported that the surfacing intervals of minke whales were shorter in June and July, and longer in May and August. Florida manatees are less available for detection when the surface temperatures drop in winter because they stayed submerged longer (Langtimm *et al.* 2011). Thomson *et al.* (2012) find that green turtles also remain submerged longer in winter; their oxygen consumption slows down in lower water temperatures (Hochscheid *et al.* 2005). Location is another source of variation in diving and surfacing times. Thomson *et al.* (2012) describe the diving patterns of green turtles differing with dive depth; the deeper the dive depth, the shorter the surface interval. Leatherback turtles spend more time at the surface when migrating through pelagic waters than in feeding grounds (James *et al.* 2006). Southall *et al.* (2005) show that sharks frequently feed and cruise at the surface during summer, and the surfacing patterns vary with location.

5.5 Chapter summary

- Diving animals are available for detection from above the water when environmental conditions are favourable and the animals are near the surface. The number of animals that are unavailable for detection needs to be estimated to obtain unbiased population estimates.
- The current availability correction factors used in aerial surveys for the dugong allow for variation in environmental conditions but use the average time dugongs spend near the surface (*i.e.*, constant availability detection probability).
- To improve estimates of availability detection probabilities, I examined effects of water depth, tidal conditions, and habitat types on dugong surfacing time using generalized linear mixed models (GLMMs).
- Availability for detection differed with water depth, and estimates of depth-specific availability detection probabilities were often lower than the constant estimates from Pollock *et al.* (2006). The habitat effect was less influential, and I did not detect a significant tidal effect.
- The numbers of dugongs estimated using depth-specific availability detection probabilities were higher than those obtained using constant detection probabilities across water depth.
- Dugong population estimates are affected by survey conditions but also distribution of animals across water depths within survey areas.
- The methodology may be applicable to other aquatic wildlife using aerial and vessel-based surveys.

Chapter 6: Improving dugong population estimates by accounting for heterogeneous availability bias[4]



In this chapter I improve the accuracy of dugong population estimates by incorporating me asurements of heterogeneous diving behaviour into estimates of the availability detection probability (availability bias). Estimates of detection zones are revised based on further experiments using dugong replicas (Dugong Secchi Disks) and more accurate TDRs. I then estimate depth-specific availability detection probability using data from 16 dugongs each fitted with a GPS unit and a TDR in Moreton and Shoalwater Bays on the eastern Queensland coast. Aerial survey data previously collected in Moreton Bay, Hervey Bay, and Torres Strait are used to re-estimate dugong population sizes based on the heterogeneous depth-specific availability detection probabilities.

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[4] I plan to submit a modified version of this chapter to *Marine Mammal Science* as Hagihara, R., S. Sobtzick, R.E. Jones, L. M. Marsh & H. Marsh. Improving population estimates by accounting for dugong's heterogeneous availability bias.

Chapter 6: Improving dugong population estimates by accounting for heterogeneous availability bias

6.1 Introduction

Robust estimates of population size are central to determining the status of species (IUCN 2015) and designing scientifically based management responses. There are two important attributes of robust estimates of population size: accuracy (closeness of the estimate to its actual value) and precision (repeatability of the estimate) (*e.g.*, Caughley 1974). Both attributes need to be considered when designing aerial surveys of both terrestrial and aquatic wildlife.

Uncertainties in the estimates of mammal abundance arise from inappropriate sampling design, observer error, and heterogeneity in the environmental conditions (*e.g.*, Caughley 1974; Forney 2000; Seavy *et al.* 2007), and the appearance or behaviour of the target species (*e.g.*, Anderson 2001; Edwards *et al.* 2007; Langtimm *et al.* 2011). Precision can be minimized through appropriate sampling design; observer error can be reduced by training. However, it is more challenging to compensate for heterogeneity in the environment and animal traits.

Improving the precision of a population estimate increases the likelihood of detecting a trend when it is actually occurring (Gerrodette 1987). Many studies have focussed on increasing precision (reducing the coefficient of variation), assuming that environmental variability and animal traits are constant through time and space. Relative measures of abundance are then used as indices to detect trends, a process that may be assisted by power analysis (*e.g.*, Gerrodette 1987; Taylor and Gerrodette 1993; Zielinski and Stauffer 1996). Yet a major challenge associated with relative abundance is that the index does not always reliably reflect changes in abundance (Link and Nichols 1994a; Conroy 1996; Gibbs *et al.* 1998; Larsen *et al.* 2001; Wilson *et al.* 2011).

Both environmental conditions and animal traits are typically heterogeneous in space and time (Pollock *et al.* 2004). This heterogeneity may reduce the statistical power to detect trends and introduces uncertainty as to whether apparent trends represent true changes in population size (Forney 2000). Thus the problems associated with fluctuating biases also need to be addressed to improve estimates of population abundance.

Three kinds of biases have been considered in population abundance studies: absence bias (*sensu* Lefebvre 1995), availability bias and perception bias (*sensu* Marsh and Sinclair 1989b). Absence bias is caused by the absence of animals from a fixed survey area due to spatial or temporal shifts in their distribution (Myer and Bowen 1989; Lefebvre *et al.* 1995; Forney 2000; Rowat *et al.* 2009). For instance, the distribution of small cetaceans in the North Pacific Ocean changes over time, and a fixed survey area targets different proportions of the populations from one survey year to another (Forney 2000). Availability bias refers to animals that are missed due to unfavourable environmental conditions (*e.g.*, water turbidity, sea state, cloud cover, glitter at the surface) and animal traits (*e.g.*, group size, body colour, body size, diving patterns; Marsh and Saalfeld 1990; Marsh and Sinclair 1989b; Mullin and Fulling 2004; Edwards *et al.* 2007; Kessel *et al.* 2013; Robbins *et al.* 2014). Perception bias arises from observers missing animals that are available for detection.

Marsh and Sinclair (1989b), Pollock *et al.* (2006), and Edwards *et al.* (2007) have developed techniques to estimate the different components of the detection probabilities for aerial surveys of sirenians (dugongs and manatees). Many surveys have covered very large areas (tens of thousands of square kilometres in the case of dugongs in Australia) to counter absence bias. For dugongs, availability bias is accounted for by estimating the proportion of animals that are missed due to water turbidity, sea state, and average dugong diving and surfacing behaviours (Pollock *et al.* 2006). Two pairs of observers and Mark-Recapture models are used to estimate perception bias (Pollock *et al.* 2006).

In Chapter 5, I demonstrated that the heterogeneity of the dugong's diving and surfacing patterns across the depth gradient, an environmental variable not considered by Pollock *et al.* (2006) causes changes in the probability of detecting dugongs during aerial surveys. Based on the proportion of time dugongs spent in the detection zones that were estimated by Pollock *et al.* (2006), I found that the dugong's availability detection probability varied with water depth and was higher in shallow waters (< 5 m) and lower in deeper waters 5 to 25 m deep.

In this chapter, I extend the work described in Chapter 5. I estimate depth-specific availability detection probabilities by: 1) repeating the Pollock *et al.*'s (2006) experiment using dugong replicas (Dugong Secchi Disks) to improve the estimates of detection zones (*sensu* Pollock *et al.* 2006) with higher resolution TDRs; and 2) incorporating measurements of heterogeneous diving behaviour with respect to water depth into the estimates of availability detection probability based on the improved detection zones. The improved availability detection probability was used to re-estimate dugong abundance size from aerial survey data collected in Moreton Bay, Hervey Bay, and Torres Strait (Marsh *et al.* 2011a; Sobtzick *et al.* 2012). For (2), I used depth measurements collected from 16 dugongs tracked in Moreton Bay and Shoalwater Bay, two important dugong habitats on the eastern coast of Queensland (Marsh *et al.* 2011a).

6.2 Methods

6.2.1 Study animals, sites, and tagging units

Table 2.1 summarises the specification of the GPS tracking units and TDRs and the biological details of 16 dugongs tracked in Moreton Bay and Shoalwater Bay (Moreton Bay: four dugongs from 2011 and nine dugongs from 2012; Shoalwater Bay: three dugongs from 2012; Fig. 2.3).

6.2.2 Re-evaluation of detection zones using Dugong Secchi Disks

Estimating availability bias requires independent measurements external to an aerial survey of: 1) the depth of the detection zones (Fig. 5.1); and 2) the proportion of time the target species spend in the detection zones.

Following Pollock *et al.* (2006), Dugong Secchi Disks – two-dimensional dugong replicas that mimicked the silhouette of a dugong as seen from an aerial survey aircraft – were used in experiments at six combinations of three turbidity classes 2, 3, 4 and two

Beaufort sea state levels ($\leq$2 and 3; Table 6.1). Turbidity class 1 occurs when the water is shallow and the seafloor clearly visible. By definition when turbidity class equals 1, a dugong is available for detection and the availability bias must be 1 (full detection), which does not need to be experimentally determined.

Table 6.1 The four turbidity classes and description of each class encountered during dugong aerial surveys (*sensu* Pollock *et al.* 2006).

Turbidity class	Turbidity	Depth range	Visibility of seafloor
1*	Clear	Shallow	Clearly visible
2	Variable	Variable	Visible but unclear
3	Clear	Deep	Not visible
4	Turbid	Variable	Not visible

*Experiment for turbidity 1 was not conducted as availability detection probability is 1 by definition.

Dugong Secchi Disk

Two Dugong Secchi Disks were fabricated from marine plywood and fibreglass: one measured 2 m long representing a juvenile dugong; the second a 2.4 m long adult. The dorsal surface of each Dugong Secchi Disk was painted a brown colour to resemble wild dugongs as seen by aerial observers. A TDR with a finer depth resolution (0.08 m, DST milli-F manufactured by Star-Oddi, Gardabaer, Iceland) was set to record depth at every second and mounted on each Dugong Secchi Disks. All TDRs were synchronised to the time of the GPS units carried by aerial observers. The buoyancy of the Dugong Secchi Disks was experimentally adjusted by attaching scuba weights, enabling them to be raised slowly from the sea floor. Each disk was attached to a separate pulley system.

Experimental design

Before each experimental trial, both Dugong Secchi Disks were lowered to depths where they could not be seen by the two highly experienced aerial observers situated in a R44 helicopter hovering *ca*. 500 feet (normal dugong aerial survey height) above sea level. On receipt of radioed instructions from the lead observer, a vessel-based operator began raising the two disks in staggered random order. Each observer independently recorded the GPS time and disk type (juvenile or adult) when the Dugong Secchi Disk was sighted. The two observers were acoustically isolated during the experiment and did not communicate. The trial was repeated at least four times for each of the six combinations of water turbidity and Beaufort sea state.

Estimating detection zones

The experiment was carried out between April 2013 and April 2014 on an opportunistic basis. Environmental conditions (water turbidity, sea state, cloud cover, cloud shadow, glitter at the water surface, and angle of sun) were confounded and were impossible to be isolated experimentally under natural conditions. Thus we used a composite index, Environmental Conditions Class (ECC), which refers all environmental conditions that affect availability bias. The results from the small and large Dugong Secchi Disks were combined because during an aerial survey an observer is unable to reliably differentiate a dugong 2 m long from a dugong 2.4 m long.

6.2.3 Estimating availability detection probability

Availability detection probabilities were estimated based on the revised detection zones using dive data from 16 dugongs for Environmental Conditions Classes 2, 3 and 4. Depth records (Fig. 2.3C) from dugongs tracked in Moreton and Shoalwater Bays were not separated by location because of the small sample numbers from Shoalwater Bay (three dugongs) compared with Moreton Bay (13 dugongs). Data preparation and statistical analyses are as outlined in Chapters 2 and 5.

Generalized linear mixed models (GLMMs) based on binomial distributions were used to predict the proportion of time the dugongs spent in each detection zone. The response variable was binary: presence and absence of dugongs in a specific detection zone. Water depth was the single explanatory categorical variable with three levels (1.5 to <5 m, 5 to <25 m, and $\geq$25 m) because the uncertainty associated with the bathymetric model, water depth estimation using tidal heights precluded the use of continuous depth data (refer to Section 5.2.4 for detailed reasoning). Water depth was tidally adjusted using bathymetry models (Moreton and Shoalwater Bays: Beaman 2010) and tidal records (Maritime Safety Queensland, Department of Transport and Main Roads 2011; National Tidal Centre, Australian Bureau of Meteorology 2011). Data collected from inshore waters between 0800 and 1600 h were used to estimate availability bias, as aerial surveys are conducted in coastal waters during daylight hours. Animals were treated as a random variable in these analyses.

Although exploratory analysis indicated that the proportion of time dugongs spent in the detection zones varied with habitat with seagrass presence and absence, the effect of habitat was not examined here. Dugongs mostly occur in habitats where the seagrass biomass is low and ephemeral (Marsh *et al.* 2011b). Fine-scale seagrass information was only available from Moreton Bay, as reliable seagrass model was not available for the other areas where the water is turbid. Thus the presence/absence of seagrass cannot be verified by observers during a dugong survey. Thus even if I had estimated availability detection probabilities for dugongs had been developed for each habitat type in Moreton Bay (as done in Langtimm *et al.* 2011), the information would be inapplicable to most other aerial survey regions.

In contrast with Chapter 5, the effect of tidal state *per se* was not examined in this chapter, as there was a limit to the variables that could be accommodated in the simulation model for estimating the standard errors of population abundance (Pollock *et al.* 2006). The simulations tended not to converge if a large number of variables were used. Combining tidal conditions also increased the sample size used to estimate availability bias for each water depth category.

Standard errors of the availability bias were estimated on the raw scale using the delta method to determine a multiplier for the standard error on the link scale. GLMMs were performed using lme4 package (lme_4 0.999999-2, Bates *et al.* 2012) in R 2.15.1

(R Development Core Team 2011). All other data manipulation and statistical analyses were executed in S Plus version 8 (TIBCO Software 2007).

6.2.4 Estimating population abundance

Dugong population abundance was estimated by correcting for survey fraction and availability and perception biases following Marsh and Sinclair (1989b) as extended by Pollock *et al.* (2006). Aerial survey data collected in 2011 for Moreton and Hervey Bays (both in November; Sobtzick *et al.* 2012) and Torres Strait (March; Marsh *et al.* 2011a) were used to re-estimate dugong population abundance . Abundance was estimated separately for each survey block in each survey region with $\geq$5 dugong sightings as for previous studies (*e.g.*, Marsh *et al.* 2011b; Sobtzick *et al.* 2011, 2014; Fig. 6.1). Dugong sightings were tidally adjusted using bathymetry models from Beaman (2010) for Moreton Bay and Hervey Bay and Lewis (2001) for Torres Strait.

Standard errors of the estimated population abundance were generated in Python using a Monte Carlo simulation method with 10,000 iterations and the method of estimating variance and standard error are described in Pollock *et al.* (2006). The simulated standard error for availability bias incorporated uncertainty (standard errors) from the availability detection probabilities which were estimated from: 1) estimates of detection zone; and 2) the proportion of time dugongs spent at each detection zone. In all three areas, it was assumed that all animals were sighted if they were in herds of more >10 animals because the animals in these herds were counted in circling rather than in passing mode in an attempt to obtain a complete count. Thus the bias corrections did not apply to these sightings.

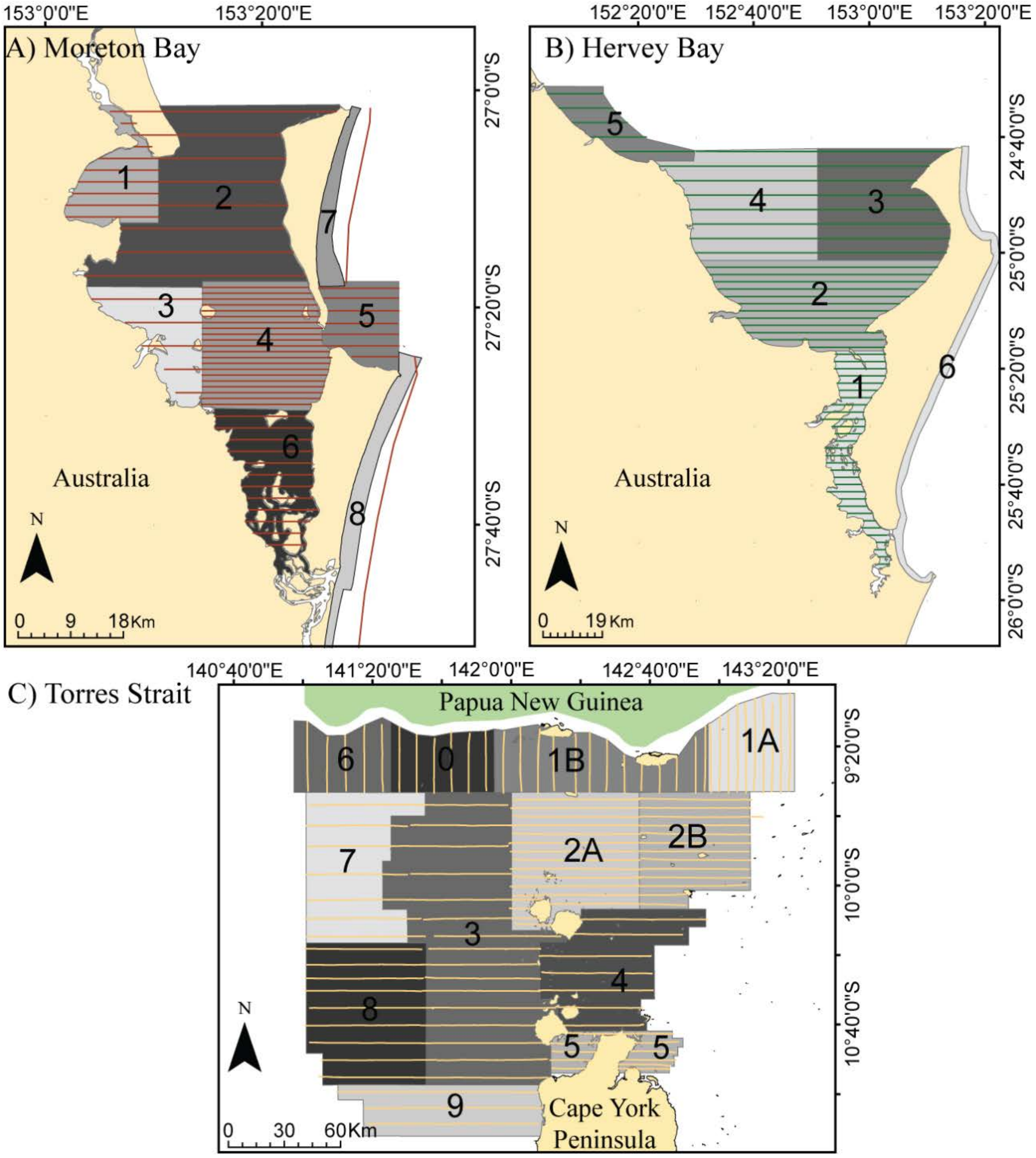


Figure 6.1 Survey blocks and transect lines of the dugong aerial surveys conducted in 2011 over A) Moreton Bay, B) Hervey Bay, and C) Torres Strait.

6.3 Results

6.3.1 Estimating the detection zone

The mean depths at which Dugong Secchi Disks were spotted for each Environmental Conditions Class (ECC) are given in Table 6.2. Detection zones for ECC 2 were 0–2.0 m, 0–3.5 m for ECC 3, and 0–1.5 m for ECC 4. These values are somewhat different from those assumed in Chapter 5 based on the earlier work of Pollock *et al.* (2006), presumably largely because of the increased resolution of the TDRs used, compared with those used in the earlier study.

Table 6.2 Mean depths at which Dugong Secchi Disks were spotted for Environmental Conditions Classes (ECCs) 2, 3, and 4 and their detection zones.

Environmental Conditions Class	Mean depth (m) (stdev)	Detection zones (m)
1	n/a*	all
2	2.07 (0.50)	0-2.0
3	3.45 (0.59)	0-3.5
4	1.59 (0.70)	0-1.5

*Experiment for ECC 1 was not conducted as availability detection probability is 1 by definition.

6.3.2 Estimating availability detection probability

Estimated availability detection probabilities were the lowest for ECC 4 (detection zone 0–1.5 m), ranging between 0.338 and 0.598 depending on water depth, followed by ECC 2 (detection zone 0–2.0 m) with 0.442 to 0.780 and ECC 3 (detection zone 0–3.5 m) with 0.693 to 0.872 (Fig. 6.2).

For ECC 2 and 4, estimates of depth-specific availability detection probabilities in the shallowest (2 to <5 m or 1.5 to <5 m) and deepest (>25 m) depth categories were higher than or the same as the constant probabilities (Fig. 6.2A,C). The heterogeneous detection probabilities were lower in water 5 to <25 m deep than the constant ones for both water visibilities 2 and 4. For ECC 3, depth-specific detection probabilities in all depth categories were higher than constant probabilities (Fig. 6.2B). Table 6.3 summarises availability detection probabilities for all 13 sightability classes, including ECC 1 (no correction). Again these values are somewhat different from those assumed in Chapter 5 based on the earlier work of Pollock *et al.* (2006).

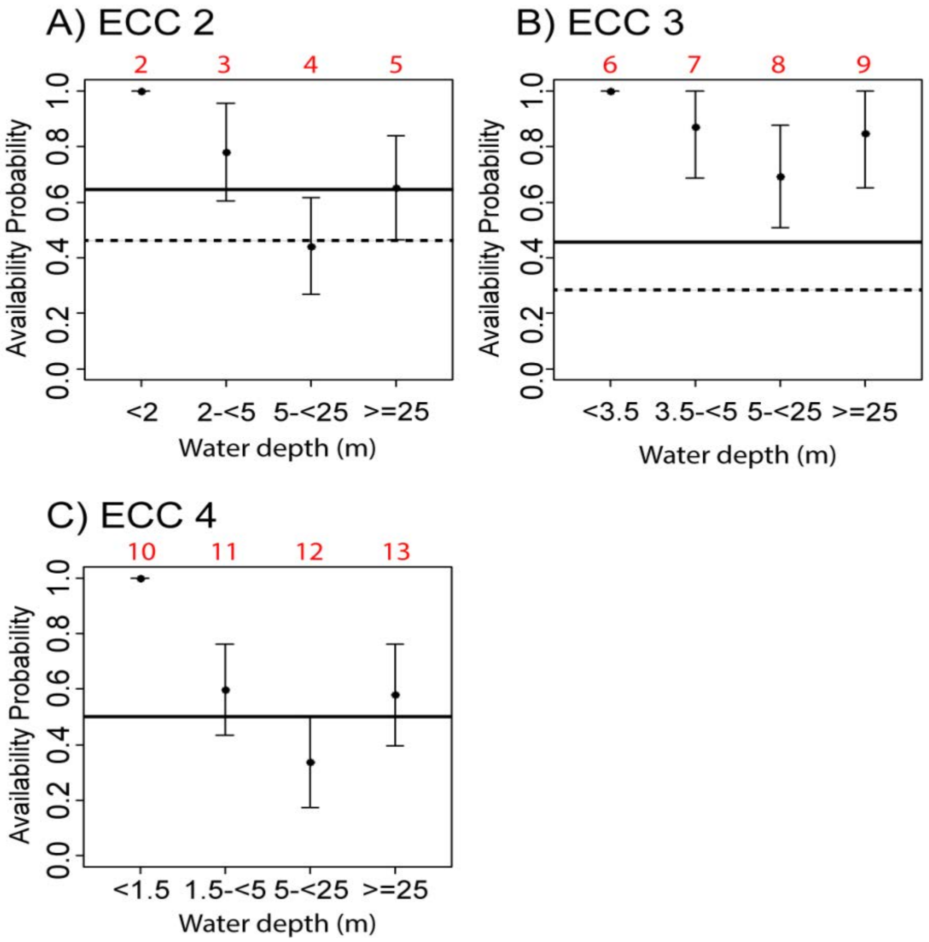


Figure 6.2 Estimated availability detection probabilities for A) Environmental Conditions Class (ECC) 2 (detection zone 0–2 m), B) 3 (detection zone 0–3.5 m), and C) 4 (detection zone 0–1.5 m). Vertical lines represent standard errors. Horizontal lines represent constant availability detection probabilities for sea state <2 (straight) and 3 (dotted). For ECC 4, a dotted line is not visible as the lines generated from both sea states overlap. Red numbers indicate sightability class.

Table 6.3 Estimated availability detection probabilities (Availability *pr*) for for Environmental Conditions Classes (ECCs) (including ECC 1), which resulted in 13 sightability classes. Note the differences between these values and those assumed in Chapter 5 based on the earlier work of Pollock *et al.* (2006).

Environmental Conditions Class	**Detection zone (m)**	**Depth of water**	**Estimated availability *pr* (se)**	**Sightability Class**
1	all	all	1.000	1
2	0–2.0	<2	1.000	2
		2 to <5	0.780 (0.175)	3
		5 to <25	0.442 (0.175)	4
		>25	0.652 (0.188)	5
3	0–3.5	<3.5	1.000	6
		3.5 to <5	0.872 (0.186)	7
		5 to <25	0.693 (0.185)	8
		>25	0.848 (0.197)	9
4	0–1.5	<1.5	1.000	10
		1.5 to <5	0.598 (0.165)	11
		5 to <25	0.338 (0.166)	12
		>25	0.580 (0.183)	13

6.3.3 Corrected dugong numbers

Moreton Bay

The total number of dugongs in Moreton Bay was estimated to be 687 ± 104 dugongs using heterogeneous availability corrections. The number was very close to the 700 ± 109 dugongs estimated using constant corrections (Fig. 6.3A). A large proportion (69%) of the dugongs in Moreton Bay was sighted in large herds in shallow clear water for which no correction was applied (Fig. 6.4A). In five sightability classes out of 13 encountered during the survey, the estimated dugong numbers were 2 to 19 dugongs less depending on ECCs using depth-specific corrections (Fig. 6.4B). The other two classes had slightly higher estimates using depth-specific corrections (6 dugongs more for ECC 2 and depth 5 to <25 m; and 27 dugongs more for ECC 4 and depth 5 to <25 m).

Hervey Bay

In contrast to the results reported in Chapter 5 in Hervey Bay, the estimated number was 1409 ± 442 dugongs using the depth-specific availability detection probabilities, and was 620 dugongs less (31% decrease) than the estimates using constant availability detection probabilities (2029 ± 573 dugongs; Fig. 6.3B). The largest difference was found in Block 2, where 887 ± 407 dugongs were estimated using heterogeneous corrections and 1363 ± 533 dugongs using constant corrections. Deep clear water (ECC 3 and depth 5 to <25 m) was the most prevalent environmental condition encountered (57% of dugong sighting) during the transect flights (Fig. 6.4C), where 813 dugongs (60% decrease) of dugongs were estimated using depth-specific corrections (1357 dugongs from constant corrections). The difference between these results and those reported in Chapter 5 is due to the improved availability correction factors for deep clear water obtained from the additional Dugong Secchi Disk experiments.

Torres Strait

In Torres Strait, using depth-specific availability detection probabilities resulted in a 28% increase in the population estimate (16,157 ± 2370 dugongs compared with 12,604 ± 2170 dugongs using the method assuming that availability bias was independent of depth; Fig. 6.3C). The depth-specific availability estimates resulted in increased estimates of the number of dugongs in all blocks. The largest difference was found in Block 2A (33% increase) and Block 3 (36% increase). Most of the survey were flown over deep turbid waters (5 to <25 m and ECC 4) and 72% of dugong sightings were sighted in such conditions (Fig. 6.4E). Depth-specific availability detection probabilities for this combination of ECC 4 and water depth were lower than constant detection probabilities (Fig. 6.2). These heterogeneous availability detection probabilities only resulted in examples of 38% more dugongs (13,467 dugongs) than examples using constant detection probabilities (9,777 dugongs). Population estimates for each survey block in Moreton Bay, Hervey Bay, and Torres Strait are tabulated in Appendix 6.1.

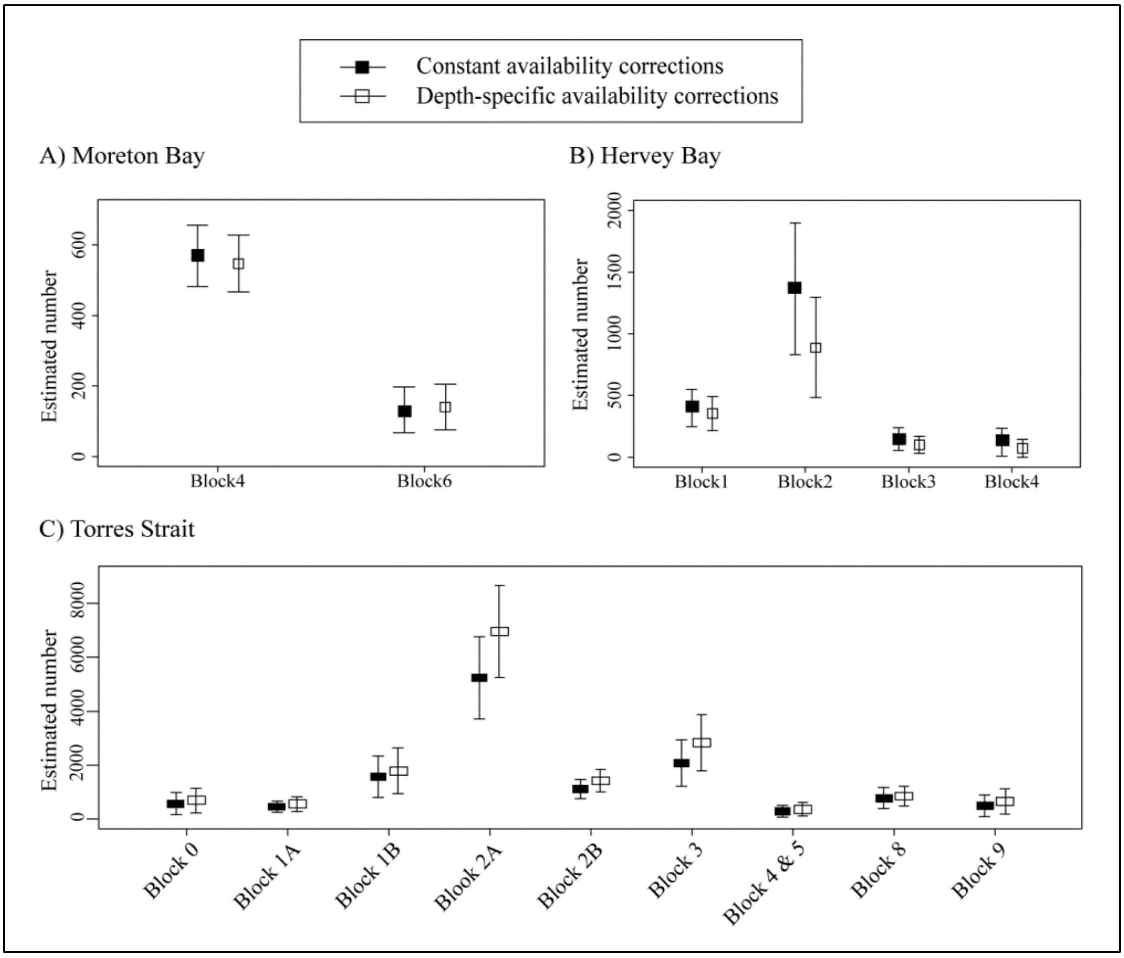


Figure 6.3 Estimates of dugong population size in A) Moreton Bay, B) Hervey Bay, and C) Torres Strait using constant (closed squares, Pollock *et al.* 2006) and depth-specific availability (open squares) detection probabilities. Error bars represent standard errors.

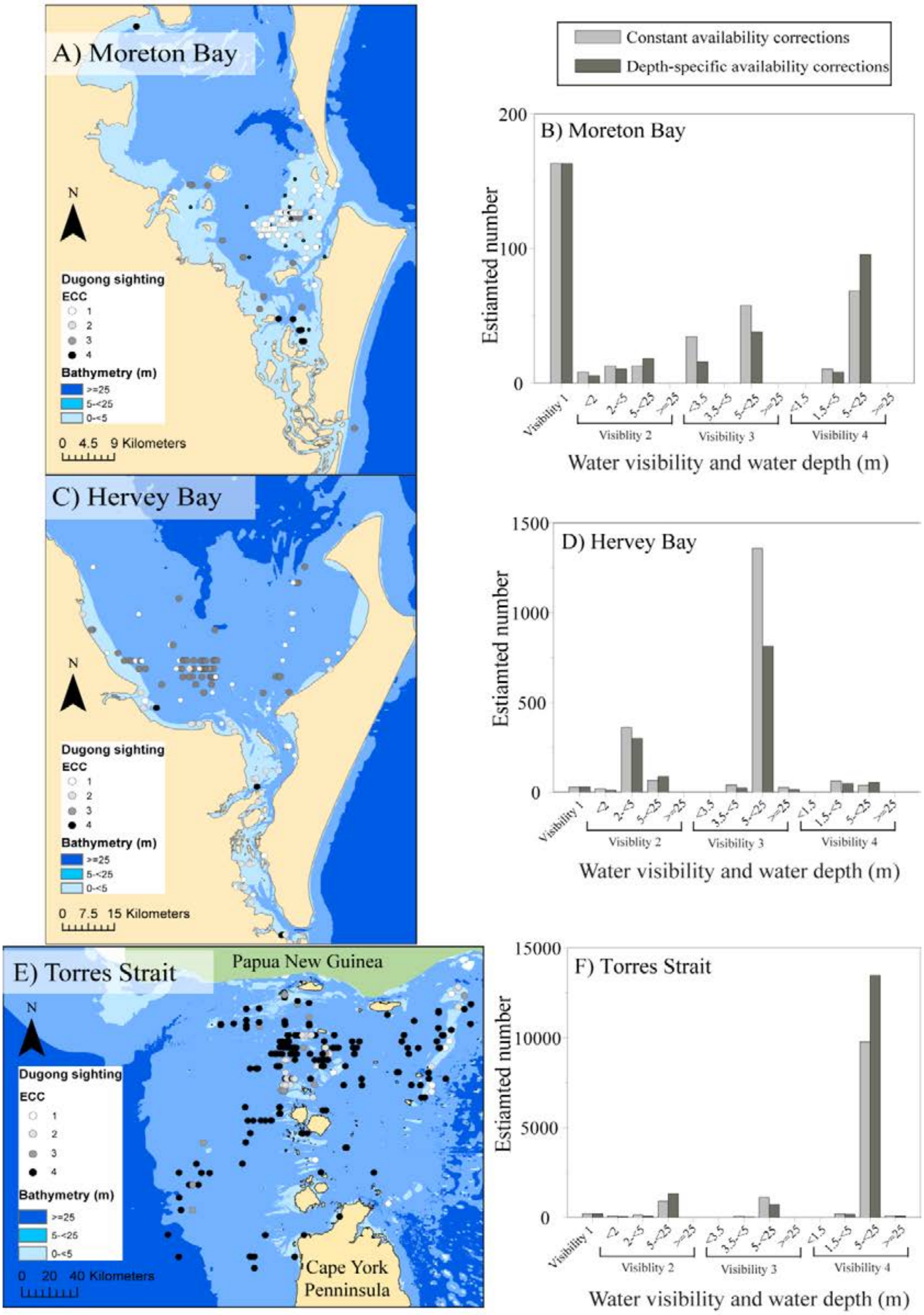


Figure 6.4 ECC 1, 2, 3, and 4 observed at the time of each dugong sighting during aerial surveys in A) Moreton Bay, C) Hervey Bay, and E) Torres Strait. Each dot represents a sighting of a dugong group. The number of dugongs estimated using constant availability detection probabilities (light gray; Pollock *et al.* 2006) and depth-specific availability detection probabilities (dark gray) for B) Moreton Bay, D) Hervey Bay, and F) Torres Strait.

6.4 Discussion

6.4.1 Improving abundance estimates

Environmental conditions and animal behaviour are inevitably heterogeneous across wildlife surveys and accounting for these factors should improve survey methodologies and thus population estimates. Few studies account for heterogeneity in animal traits, especially diving behaviour (*e.g.*, Schweder *et al.* 1991a,b; Innes *et al.* 1996; Laake *et al.* 1997; Okamura *et al.* 2006; Pollock *et al.* 2006; Barlow and Forney 2007; Edwards *et al.* 2007), and fewer studies have examined the effect of both heterogeneous environmental and diving behaviour on availability bias (Thomson *et al.* 2012; Hagihara *et al.* 2014). To my knowledge, this is the first study to incorporate the effect of environmental conditions and water depth on diving behaviour into estimates of availability bias for estimating abundance of marine wildlife even though several studies have followed Pollock *et al.* (2006) and used Secchi Disk techniques to estimate the detection zone (*e.g.*, sharks: Kessel *et al.* 2013; Robbins *et al.* 2014; marine turtles: Fuentes *et al.* 2015).

Population abundance estimated from depth-specific availability detection probabilities had standard error estimates similar to (or sometimes smaller than) the standard errors of abundance estimates from constant detection probabilities (Fig. 6.3). These results indicate precision has not been reduced by increasing the number of sightability classes from 9 to 13 (Table 6.3). Accuracy is improved by correcting for each dugong sightings at specific sighting condition and water depth. Nonetheless the population sizes estimated in this study are still likely to be an underestimate because the number of dugongs present in the areas in which they were not sighted during survey was not estimated (Martin *et al.* 2014).

I examined the proportion of time dugongs spent at the surface in two habitat types (areas with and without seagrass). However fine-scale seagrass information is unavailable in most dugong habitats, due to extensive areas surveys need to cover (>25,000-40,000 km^2) and most of these areas are deep and satellite imageries cannot depict conditions on substratum. Thus detection probabilities estimated for each habitat type will not be applicable for abundance estimation. Langtimm *et al.* (2011) estimated availability detection probabilities for each habitat type (*e.g.*, offshore, near-shore bays), but their spatial extent is much smaller (~<1%) than the area for dugongs aerial surveys.

Using spatially heterogeneous corrections for availability bias should assist in correcting for shifts in the spatial distribution of a target species within survey areas between surveys (Marsh 1995). For coastal species such as dugongs, the depth of water can vary by a large percentage even within a single transect, particularly if the transect is across a depth gradient as is usual for many coastal surveys to increase the precision of the population estimate. Previous aerial surveys have demonstrated changes in dugong distribution between surveys (*e.g.*, Marsh *et al.* 2011b; Sobtzick *et al.* 2012). If a large proportion of a population is distributed over deeper waters due to reasons such as inshore seagrass dieback, fewer animals will be spotted. Under such circumstances constant corrections for availability bias will result in lower abundance estimates even if the population size is unchanged.

6.4.2 Survey protocol

Distinguishing animals that are not detected due to environmental conditions such as water turbidity and animals that are absent in the survey area due to environmental changes (*e.g.*, resource depletion) is extremely difficult. However, some of these biases can be addressed by two different approaches: 1) improving availability detection probability using information on water visibility and diving patterns in relation to water depth (availability bias), as done in this study; and 2) survey designs that encompass areas large enough to capture moving animals (absence bias). The first approach attempts to capture animals that are in the survey area but not detected as animals shifted their distribution or environmental conditions due to seagrass dieback and water temperature (Marsh *et al.* 2011b). For (2), survey designs for sirenians need to be carried out at spatial scales that reduce the risk of absence bias. As described above, dugongs and manatees make individualistic long distance movements causing absence bias.

Regardless of the survey designs that attempt to minimise some of major biases, survey methodology requires attention to survey logistics. Adequate observer training is necessary, but even experienced observers can miss animals. Thus estimating perception bias (*sensu* Marsh and Sinclair 1989b) which includes both missing an animal and misidentification of species (*e.g.*, Conn *et al.* 2013) will improve reliability of population size estimates. Calm survey conditions (*e.g.*, $\leq$ 2) is recommended wherever possible, as whitecaps on the water surface and movements of water and other suspended materials in the water column deter observer's attention and capacity to detect animals. Such error is perhaps reduced greatly using unmanned aerial surveys (UAVs) (Koski *et al.* 2009; Sardà-Palomera *et al.* 2012; Hodgson *et al.* 2013).

Considerable evidence indicates that dugongs access inter-tidal seagrass at high tide. Thus they are more likely to be in shallow clear water (ECC 1) and available for detection at high tide (see *e.g.*, Tracey *et al.* (2014) which was based on a dugong satellite tracking study, anecdotal evidences, and my exploratory analysis using the same dataset with four tidal conditions of flow high, ebb high, ebb low, and flow low). The dugong's differential vertical and horizontal spatial distributions across tidal cycles can potentially be addressed by surveying shallow dugong habitats at high tide although this can be logistically challenging during large-scale serial surveys in remote regions.

6.4.3 Optimum number of sightability classes

Complicated bias corrections can make it difficult to calculate the uncertainty around a population estimate. Pollock *et al.* (2006) used Monte Carlo simulations to overcome this problem. A limitation of this approach is that numerous sightability classes can result in the simulation failing to converge. In this chapter, tidal conditions were not examined because the number of sightability classes accounting for ECC and water depth was already relatively large (n = 13).

6.4.4 Representativeness of availability estimates

I used the tracking data collected from 16 dugongs, tagged at two locations on the eastern Australian coast during the Austral winter. The unbalanced number of dugongs tagged in each bay (13 dugongs in Moreton Bay and three dugongs in Shoalwater Bay), limited my capacity to test for regional or seasonal differences in diving behaviour. As described in Chapter 5, the dugong's diving and surfacing behaviour varies slightly among individuals and may vary with season.

Direct application of the availability bias estimates reported here to regions that are bathymetrically and environmentally different (*e.g.*, coral reef dominated waters in New Caledonia) from Moreton Bay should be avoided until empirical data on dugong diving behaviour becomes available from an increased number of dugong habitats. Thus the dugong population abundance estimates presented here for Torres Strait should be interpreted cautiously.

Torres Strait is located in eastern Australia, however the difference in the underwater community structure and distribution of seagrass may result in different dugong diving behaviour. The depth distribution of seagrass in Torres Strait extends to 40 m (Long and Poiner 1997), and ~55,000 km^2 of seagrass (38% in Western and 49% in Central Torres Strait) occur in water >10 m deep (Taylor and Rasheed 2011). Dugongs have been frequently sighted in waters 10 to <25 m deep during aerial surveys since 1987 (Marsh and Saalfeld 1990; Marsh and Lawler 1992; Sobtzick *et al.* 2014). Satellite tracking of six dugongs in Torres Strait also documented their occurrence in waters up to ~15 m deep in Central and Western Torres Strait (Gredzens *et al.* 2014). In contrast, seagrass in Moreton Bay mostly occurs in water <10 m deep over shallow banks (Phinn *et al.* 2008; Lyons *et al.* 2012). The seagrass consumed by dugongs also differs in the two locations as summarised by Marsh *et al.* (2011b). In Torres Strait dugongs mostly feed by cropping *Thallasia* leaves (André *et al.* 2005). In contrast, in Moreton Bay dugongs mostly feed on the above- and below-ground plants of pioneer species such as *Halophila ovalis* (Preen 1992; McMahon 2005). The differences in seagrass distribution and species may result in different dugong feeding behaviour, which may lead to different diving and surfacing patterns.

6.4.5 Effects of tracking units

The effects of the tracking devices on dugong diving behaviour are unknown. Some dugongs fitted with GPS and TDRs travelled hundreds of kilometres in a few days (Sheppard *et al.* 2006) indicating that the devices did not preclude such travel for those individuals. Berga *et al.* (2014) examined the effects of satellite tags and a secondary tag which records diving depth using two groups of harbor porpoises: one group with a satellite tag only (control group); and another group with both units (experimental group). For the 3-10 days of deployment period, the dives of the experimental group were significantly shallower than those of the control group, while no effect was found on their dive duration or surface time. The authors admitted that the effect of the secondary tag may have been minor compared with the effect of the primary tag which could not be measured. Measuring the effects of tracking devices on dugongs will be logistically difficult. Thus it is important to reduce tag size (drag) as much possible and to limit the number of animals tagged to that required to provide a robust answer to the scientific question being asked. This topic is further discussed in Chapter 7.

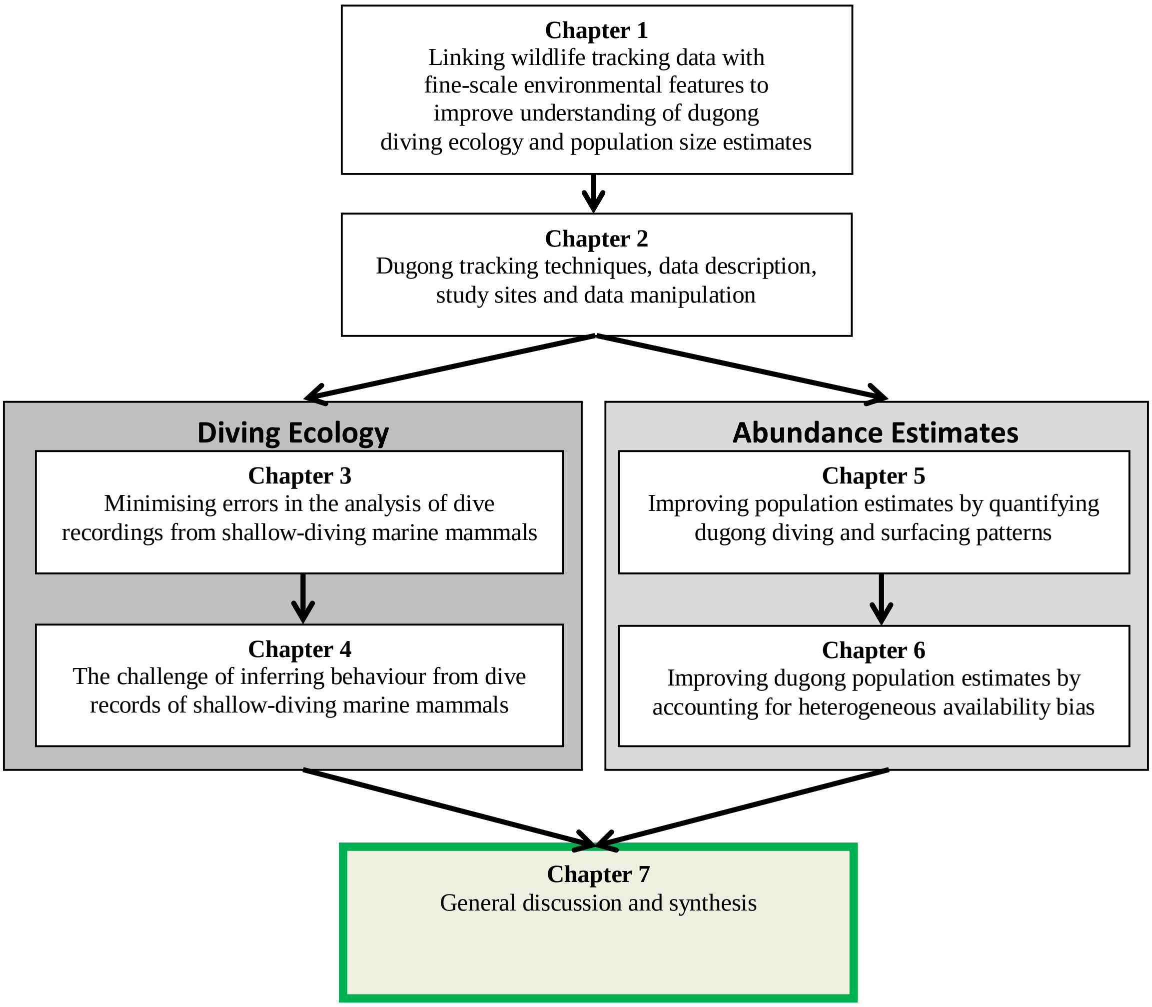
6.4.6 Future directions

The heterogeneity in availability bias may be location-specific (*e.g.*, Mulling and Fullin 2004). Dive records from other regions are required to establish or refute this hypothesis for dugongs. Dugong tag retrieval in remote areas such as Torres Strait has been a logistical challenge due to the high cost of field operations, including recovery of transmitters and TDRs. Comparisons of availability bias from different regions may become possible as pop-up tag technology becomes more accessible (currently each tag costs US $4000) and data retrieval rates improve. The JCU Dugong Group deployed pop-up satellite tags on two Moreton Bay dugongs in early 2014 as a pilot study. Data recovery from the two units was variable (75% and 15%). The Group is planning the location specific studies of dugong diving and surfacing behaviour in Torres Strait. Meanwhile, the approach presented here should be an improvement on the technique of Pollock *et al.* (2006).

6.5 Chapter summary

- Precision and accuracy are two important attributes of robust population abundance estimates for assessing population trends and planning management responses.
- Environmental conditions and animal behaviour are heterogeneous, and the proportion of animals available for detection varies spatially and temporally. This variability reduces the accuracy of population abundance estimates and lowers statistical power to detect trends.
- Using improved estimates of detection zones that account for ECCs, the composite term including water visibility and sea state, and diving records from 16 dugongs, I re-estimated heterogeneous availability detection probabilities in relation to water depth.
- The change in population estimates using the new methodology was variable in each region:
    - The estimated population abundance in Moreton Bay was 687 ± 104 dugongs based on heterogeneous availability detection probabilities, very similar to the estimate of 700 ± 109 dugongs based on constant availability detection probabilities.
    - The estimate of Hervey Bay dugong population was 620 animals (31%) smaller using heterogeneous availability detection probability (1409 ± 442 dugongs) than using the constant ones (2029 ± 573 dugongs).
    - The dugong population of central and western Torres Strait was 16157 ± 2370 dugongs using the new methodology, compared with 12,604 ± 2170 dugongs based on the assumption of availability being constant across water depths, a 28% increase using the heterogeneous availability detection probabilities.
- Heterogeneous availability bias may be location-specific.
- Direct application of availability estimates presented here to other locations with very different environmental and bathymetric features from shallow clear waters of Moreton Bay should be avoided.

Chapter 7: General discussion and synthesis



In this final chapter I consider the key findings of my thesis in the context of its aims and the contribution of my findings to: (a) shallow-diving dugong diving ecology and (b) the methodologies for studying shallow diving animals and estimating wildlife abundance. I conclude with recommendations for future research on dugong ecology using animal tracking technology, and aerial or boat-based surveys for estimating population size more robust in order to inform management of the dugong and other marine wildlife of conservation concern.

Chapter 7: General discussion and synthesis

7.1 Thesis overview

Because the diving behaviour of the dugong, a coastal marine mammal of global conservation concern (IUCN 2015), varies in space and time with environmental conditions, wildlife tracking data linked to fine scale environmental features has the potential to expand understanding of fine scale dugong ecology and to improve the accuracy of the abundance estimates required for population monitoring.

The overall objectives of my thesis were to maximise the outcomes of wildlife tracking by linking fine-scale dive records with spatial data from remotely-sensed animals and fine-scale habitat models to improve: (a) fine-scale knowledge of the diving ecology of coastal wildlife, and (b) methodologies to estimate their abundance.

To achieve these objectives, I identified the following aims:

1. To develop an empirical procedure to identify dives in shallow diving aquatic wildlife such as the dugong; and

by linking fine-scale dive records with spatial data from remotely-sensed dugongs and fine-scale habitat models,

2. To advance insights into the fine-scale diving ecology of dugongs; and
3. To estimate dugong population size that is more robust by accounting for their heterogeneous diving and surfacing behaviours.

7.1.1 Key findings

Aim 1: Develop an empirical procedure to identify dives in shallow diving aquatic wildlife such as the dugong

Shallow dives are generally difficult to interpret (*e.g.*, Lesage *et al.* 1999; Hays *et al.* 2001; Hagihara *et al.* 2011) because they occur at the limits of the resolution of TDRs and the reliability of dive parameters generated from these dives is generally low or unknown. Many studies have used arbitrary dive thresholds to construct dives from two-dimensional depth records (Nolet and Kruuk 1993; Hays *et al.* 2001; Elliott and Gaston 2009), further exacerbating the challenge of interpreting shallow dives. In Chapter 3, I developed an empirical procedure to determine three optimum thresholds for reliable profiling of dives from the shallow-diving dugong: 1) time threshold; 2) zero-offset correction (ZOC); and 3) dive threshold (DT). This quantitative procedure was essential for interpreting the dugong's diving behaviour in Chapter 4.

Aim 2: Advance insights into fine-scale diving ecology of dugongs

In Chapter 4, using dive metrics obtained from the procedure described in Chapter 3, I built logistic regression models to predict dives that achieved two criteria: a) mid-water dives that did not provide the dugong with access to the seafloor and seafloor dives that did provide the dugongs with access to the seafloor; and b) dives that enabled the dugong to access the seafloor in areas were seagrass is present and absent. I obtained insights into dugong diving patterns at single dive basis. This inference was possible by linking fine-scale behavioural data (depth records: depth resolution ± 0.5 m; and GPS location fixes: spatial resolution ± 2 to <75 m) with a bathymetry model (± 100 m spatial resolution) and a seagrass map (± 10 m spatial resolution).

Dives that had a high likelihood of achieving the above criteria (a and b) had distinct behavioural patterns. Dugongs that had high likelihood of undertaking seafloor dives over seagrass transited quickly between the surface and seafloor and maximised the time spent on the substratum, potentially feeding (Fig. 4.4 and 4.5). Dugongs that had a high likelihood of undertaking seafloor dives in areas without seagrass spent a similarly long time on the bottom but moved more slowly in transit. Mid-water dives tended to be longer, had a shorter bottom phase and even slower transit phases.

Aim 3: Estimate dugong population size that is more robust by accounting for their heterogeneous diving and surfacing behaviours

The current dugong aerial survey methodology accounts for animals that are missed by observers during aerial surveys due to water turbidity, sea state, dugong diving and surfacing patterns (availability bias), and observers missing animals that are available for detection (perception bias; *sensu* Marsh and Sinclair 1989b; Pollock *et al.* 2006). In developing correction factors to account for availability bias, dugong diving and surfacing patterns have been assumed to be constant (Pollock *et al.* 2006). To improve estimates of dugong abundance from aerial surveys, I first improved the heterogeneous availability detection probabilities with respect to water depth using tracking data collected from 16 dugongs in Chapters 5 and 6. The depth-specific availability probabilities were estimated by: 1) repeating Pollock *et al.*'s (2006) experiment using Dugong Secchi Disks using TDRs with finer depth resolutions (Fig. 5.1 and Fig. 6.2) and improving the estimates of detection zones; and 2) estimating the proportion of time dugongs spent in the improved detection zones for each Environmental Conditions Class (ECC).

Using the revised availability detection probabilities, I estimated dugong population abundance in three important dugong habitats in Queensland, Moreton Bay, Hervey Bay, and Torres Strait. The resultant abundance estimates differed to varying degrees from the previous estimates derived using the methodology of Pollock *et al.* (2006). My estimates should be more accurate as they correct for dugong heterogeneous diving and surfacing patterns across water depths. The precision of the estimates did not change substantially.

7.2 Implications of my research

7.2.1 Dive analysis for shallow-diving animals

The methodology I developed in Chapter 3 quantitatively determines zero-offset correction (ZOC) and dive threshold (DT). Both thresholds are commonly used by researchers studying aquatic wildlife to reconstruct dives from two-dimensional depth records. Manually inspecting each dive (*e.g.*, Gordos and Franklin 2002; Bodkin *et al.* 2004; Hays *et al.* 2007; Hazel *et al.* 2009; Witt *et al.* 2010) to adjust the surface level (ZOC) is time consuming, and arbitrarily choosing the dive threshold (DT) (*e.g.*, LeBouef *et al.* 1986; Hindell *et al.* 1991; Panigada *et al.* 1999) excludes a large portion of valuable data, limiting potential new insights, especially for shallow-diving species. My methodology enabled shallow dives to be identified while minimising errors that may interfere with subsequent analysis and interpretation. This empirical approach is an efficient, effective, and accurate method of processing large volumes of dive records and should be applicable to other shallow diving animals such as manatees, dolphins, and turtles.

7.2.2 Dugong ecology

Jessopp *et al.* (2013) stated that animal behaviour is best interpreted within the context of their immediate environment. Although I am certain that all ecologists (including me) agree with this statement, it is often difficult to achieve. Free-ranging dugongs can travel large distances over periods of days and months (Marsh and Rathbun 1990; Sheppard *et al.* 2006a; Gredzens *et al.* 2014). Their seagrass environments vary substantially within a few hundred meters (sometimes even a few meters) (Phinn *et al.* 2008; Knudby and Nordlund 2011) and can change dramatically seasonally and over time, especially as a result of extreme weather events (Marsh and Preen 1995; Roelfsema *et al.* 2009). Measuring the state of the environment at an appropriate spatial and temporal scales can be difficult and expensive and is often most cost-effectively done using remote sensing. In order to obtain new insights into the fine-scale behavioural ecology of the dugong, I used existing high resolution bathymetric and seagrass models and linked them with wildlife tracking data collected from fast acquisition GPS transmitters and improved TDRs in Chapter 4. This approach allowed me to understand dugong diving behaviour under different environmental conditions at the scale of each dive.

Although I could not confirm behavioural type for each dive, my approach suggested that dugongs seems to predominantly rest on the bottom in areas without seagrass, behaviour that has not been detected visually in previous studies due to the dugong's turbid environment. This result highlights the importance of non-seagrass areas for dugongs. Visual inspection of deep seafloor dives in relation to movement data collected from GPS transmitters indicated dugongs utilise the seafloor for orientation and navigation.

My approach could also be applied to studying the diving behaviour of other shallow diving animals such as manatees, dolphins and turtles for which behavioural inference is often difficult because their dives are predominantly shallow.

7.2.3 Aerial survey population estimates

Estimating the absolute abundance of dugongs and manatees is challenging. Marsh *et al.* (2011b) point out that sirenians mostly occur in turbid waters, surface cryptically only for short periods, and therefore are unavailable to aerial observers for much of the time. The probability of detecting these animals varies greatly with environmental conditions and the behaviour of animals, and such variability is heterogeneous among and within years and sites. In Chapters 5 and 6 I improved the estimation methodology developed by Marsh and Sinclair (1989b) and late revised by Pollock *et al.* (2006) by accounting for the heterogeneity in dugong diving behavior across water depths. Such estimation methodology is particularly applicable to many boat- and aerial-based surveys of aquatic wildlife.

Accounting for heterogeneous environmental conditions and animal behaviour should increase the statistical power of surveys to detect trends and provided reliable basis for management initiatives for threatened wildlife (Link and Nichols 1994; Conroy 1996; Gibbs *et al.* 1998; Larsen *et al.* 2001; Wilson *et al.* 2011; Pollock *et al.* 2004). Improving precision of population estimates increases the likelihood of detecting a trend (Gerrodette 1987; Taylor and Gerrodette 1993; Zielinski and Stauffer 1996). However the heterogeneity in environmental conditions and animal behaviour also needs to be addressed, as both accuracy and precision are important attributes of survey population estimates. To my knowledge I am the first researcher to have explicitly corrected for the effect of water depth on diving behaviour and hence availability bias in abundance studies of aquatic wildlife.

Experiments with animal Secchi Disks have been conducted to estimate the detection zone of various aquatic species (dugongs; Pollock *et al.* 2006; sharks: Kessel *et al.* 2013; Robbins *et al.* 2014; marine turtles: Fuentes *et al.* 2015), however my study provides an estimation methodology that accounts for both Environmental Conditions Class (a combined term for water visibility and sea state) and diving behaviour in estimating detection zones using animal Secchi Disks. This technique is potentially transferable to other medium-sized aquatic species residing in turbid waters (manatees, dolphins, turtles, and sharks).

7.3 Future research

7.3.1 Diving ecology

Custom software

The development of custom-made software that is specifically designed to reliably identify the phases of shallow dives from shallow-diving dugongs would be extremely valuable. I used a combination of custom software (R. Jones) and open-source dive analysis packages *diveMove* (ver. 0.9.7, Luque) in accordance with my methodology to determine three key thresholds for dive identification in Chapter 3. This process efficiently and reliably identified dugong dives that were used to draw insights into dugong diving behaviour as described in Chapter 4. Nonetheless *diveMove* is more suited to the analysis of the dives of deep-diving animals (*e.g.*, elephant seals, fur seals, gray whales). For instance, the descent phase of some dugong dives was falsely extended to the bottom phase (Fig. 4.5). Two parameters (*descent.crit.q* and *ascent.crit.q*) in the function *calibrateDepth()* available in *diveMove* regulate the cessation of the descent phase and the onset of the ascent phase, but changing these thresholds had little effect on the demarcation of descent and ascent phases from the bottom phase in these shallow dugong dives.

Researchers studying animals making shallow dives thus face an inherent challenge in reliably identifying the phases of each dive. In addition, deep diving animals make shallow dives during certain life stages or between deep dives (Nolet *et al.* 1993; Hays *et al.* 2001). Researchers often exclude shallow dives from their statistical analysis thereby ignoring an important component of behaviour such as feeding ecology (*e.g.*, Lesage *et al.* 1999). A program explicitly designed for shallow dives would have wide application to both shallow- (manatees, dolphins, turtles) and deep-diving animals (seals).

Use of additional sensors

Complementary data from additional sensing units rather than using stand-alone two-dimensional dive data (Thomson *et al.* 2011) has the potential to expand understanding of dugong diving behaviour and may enable classification of dives using conventional multivariate classification approach. Such study is valuable for understanding dugongs in turbid water which precludes visual studies. Potentially useful devices for dugongs include accelerometers, 3-D motion sensors, hydrophones, and (video) cameras. The first three devices are more suited to the turbid coastal habitats frequented by dugongs.

Three-D motion sensors that detect changes in orientation (activity) of animals have been used to differentiate dives with activity and inactivity (*e.g.*, resting) within U-shaped dives from green turtles (Hochscheid *et al.* 1999). This type of sensor would reveal activity patterns and energetics. Hydrophones attached to captive Amazonian manatees recorded mastication sounds at high detection rates (65–79%) while the manatees were chewing on food plants (Kikuchi *et al.* 2014) . Dugongs also make mastication sounds (Tsutsumi *et al.* 2006; Hodgson 2007), and using hydrophones in association with TDRs and GPS tracking should improve understanding of their feeding ecology. Accelerometers, coupled with habitat descriptions, may also indicate feeding events as dugongs frequently feed by excavating (Anderson and Birtles 1978; Preen

1992; Wirsing *et al.* 2007a), leaving feeding trails. This feeding mode involves forward movement in contrast to resting.

Images from video cameras attached to dugongs have provided little insights due to small image size, turbid waters which obscure shot images, and the dugong's limited behavioural repertoire (M.Heithaus pers comm). Short or intermittent images captured using the current technology may limit the number of successful association with dive records. Cameras may only be useful in clear water (*e.g*., Moreton Bay, Shark Bay). Nonetheless, with careful positioning and orientation, a camera has the potential to provide rich information (*e.g*., which species of seagrass or animal items dugongs consume). Images combined with depth records would provide means of: (1) validating presumed behavioural functions and (2) estimating the time budgets of various behaviours.

Although the size of these tags (and cameras) is increasingly reduced, animal welfare issues (*e.g*., effects of tags on animal behaviour, foraging success, or reproductive capacity) need to be considered and carefully monitored. When instruments were attached, tagged animals or animals with artificial weights were observed to increase oxygen consumption (Costa and Gentry 1986), decrease or alter swimming effort (Cornick *et al.* 2006; Aoki *et al.* 2011; van der Hoop *et al.* 2014), and alter swimming speed and angle of dive descent and ascents (Boyd *et al.* 1997).

Animal ethics

The effects of wildlife tracking and biologging units on wild animals (*e.g*. on behaviour, foraging success, and reproduction) need to be minimised and carefully monitored. In ornithological studies, guidelines exist and recommend the tag weight should not exceed 3-5% of bird body mass (E. 2001; Vandenabeele *et al.* 2011) and no more than 1% of cross-sectional area (Ballard *et al.* 2001) to allow adequate lift and thrust for take-off and flight. This guideline is appropriate for animals that are influenced by gravity such as birds. For marine animals, drags rather than buoyancy created by tags and associated objects such as antennae and attachment platforms has an adverse effect on deployed animals (Wilson *et al*. 2004). Jones *et al.* (2013) conducted experiments using marine turtle models in a wind tunnel to determine the drag created by tags with various surface area and shape widely used in aquatic wildlife studies. The authors generated a universal counter plots which can be superimposed on the various frontal areas of tags used in other species to identify the percentage of increase in drag. This counter plots can be used to customise tag design specific to individual species. Nonetheless tags need to be streamlined to reduce drag, and be as small and light as possible so that equipped animals are not required to expend considerable energy for locomotion (Vandenabeele *et al.* 2011).

Studies that examine the effects of tagging and tags on wildlife are relatively rare, probably because such studies are ethically challenging, difficult to design (difficult to measure and determine adverse effects), and expensive to implement. It is also extremely difficult (mostly impossible) to compare the effects of tagged and non-tagged animals in natural environment. Some studies have not observed significant changes in the behaviour of tagged versus untagged animals (*e.g.*, Sherrill-Mix and James 2008), whereas others have observed animals fitted with tags increasing their oxygen consumption (Costa and Gentry 1986), decreasing or altering their swimming effort (Cornick *et al.* 2006; Aoki *et al.* 2011; van der Hoop *et al.* 2014), or altering their swimming speed and angle of dive descent and ascent (Boyd *et al.* 1997). However, due to the often short nature of these studies, linking the observed adverse effects to overall survival and fitness of an individual is difficult.

However Longitudinal studies do exist and document the costs to tagged animals. Flipper bands on penguins inflict damages to flippers, and their swimming costs increase by 24%, and survival decreased by 28% (Jackson and Wilson 2002). A long term study (10 years) found banded penguins produced 39% fewer chicks and 16% lower survival rate than non-banded birds (Saraux *et al.* 2011). Saraux *et al.* (2011) also found the survival of banded penguins increased after 4.5 years. The tag effect works as selection force, and weak penguins were weeded out during the first half of the 10 year study. These studies show the deleterious changes in fact affect the population growth therefore the deployment period also needs to be considered when planning tagging studies

Because the risk of an animal being disadvantaged by being caught, fitted with a tag, and carrying a tag is not zero, researchers are ethically obliged to maximise the information gained from each animal. This could be done by attaching several sensing units (which may increase the risk of harm) and/or by using all relevant environmental information to maximise the insights gained. Researchers need to be cognisant of the benefits to the researcher and additional burden imposed to an animal carrying several sensors, and acknowledge the data are collected from, varying degree of, impaired animals (Wilson 2011).

Consideration on the potential of optimising the number of tagged animals is also necessary. Further work needs to be done to determine the optimum numbers of animals to track given the associated animal welfare concerns discussed above. Optima may be determined when a large number of animals tracked exhibit similar behaviours (*e.g*., Schofield *et al.* 2013) or by more formal power analysis (*e.g*., Cohen 1988). The appropriate sample size is likely to be species specific.

A tracking methodology designed to minimise the adverse effects on tagged animals needs to reflect ever-improving technologies and human innovation, and respect societal norms regarding animal welfare, especially when researchers are studying rare and threatened species. The Three R’s (Replacement, Reduction and Refinement) are fundamental tenets of ethical animal care and use for experimentation in all non-human vertebrates and cephalopods (see for example Australian Code of Practice, National Health and Medical Research Council 2013). The goal of reduction, the second of the 3R's, is to reduce the numbers of animals used to obtain information of a given amount and precision. The Code of Practice provides guidance for scientific conduct and needs to be consulted when planning future studies. Future dugong tracking studies should use the data obtained to date to conduct cost-benefit analyses concerning the trade-offs between information and animal welfare.

Representativeness of the tagged animals

Given these animal welfare issues, obtaining a representative sample of sufficient size to make robust inferences is generally a challenge, especially when results are to be used to inform management decisions (*e.g.*, Shillinger *et al.* 2012). Satellite tracking is expensive in both monetary and human resources. The number of tracked animals is typically restricted by the budget for tag purchase and field work. Logistics (*e.g.*, weather, animal behaviour, experience of capture and handling) also constrain the number of animals tagged. Animals found in particular areas (*e.g.*, shallow waters, seagrass meadows), sex, or size may have higher catchability. Researchers often work with threatened species, and catching and tagging a large number of animals may not be possible (*e.g.*, colonial birds of a small population size) or banned for ethical reasons. There is always uncertainty about the quality and quantity of data that will be collected from tagged individuals (*e.g.*, sampling interval, data accuracy, tag loss and malfunction, battery longevity and failure).

Despite the challenge of obtaining a large enough representative sample, documenting variation within a population is valuable because such information may better enable researchers to anticipate how populations are likely to adapt to future environmental changes and to plan measures to ameliorate negative impacts. Phenotypic variations in appearance and behaviour (Flint 1996) occur in all taxa (Williams 1992). Wildlife telemetry now has the potential to provide a large volume of information from single animals and typically reveals considerable behavioural variations among individuals, sexes, or age groups (*e.g.*, Le Boeuf *et al.* 1993, 2000; Austin *et al.* 2006; Zeno *et al.* 2008). The challenge is, however, to interpret this variability in terms of environmental drivers while making the assumptions explicit.

7.3.2 Population abundance

Application

Spatially explicit models of dugong density based on aerial survey data (Grech and Marsh 2007; Grech *et al.* 2008; Grech *et al.* 2011) have been very important for systematic conservation planning. My work on depth-specific availability bias described in Chapters 5 and 6 suggests that these models underestimate the importance of dugong habitats in the 5-25 m depth range relative to those in shallower and deeper waters. The models have been improved by incorporating the depth-specific availabilities (Sobtzick *et al.* 2015).

New technology

The TDRs I used archived depth measurements and required tag retrieval for data access, limiting data return at the expense of the costs incurred for the purchase of the tracking units and field operations. I conducted a dugong tracking study in Shark Bay, Western Australia in 2012 with the Western Australian Department of Environment and Conservation and volunteers. We fitted GPS transmitters and TDRs to five dugongs but failed to retrieve data from any of the five TDRs. The entire tracking apparatus was prematurely released from one dugong due to weak link failure in a tether (See Section 2.1 for details of attachment). Although two GPS transmitters were recovered, the two TDRs attached to the same dugongs were lost as their tethers were mutilated at mid length for unknown reasons (possibly boat propellers or shark bites). The remaining two GPS units ceased transmitting and their TDRs could not be located.

Satellite-relayed TDRs which do not need to be retrieved for data access have the potential to provide very useful dive data for dugongs, especially in remote areas or other environments where tag retrieval is extremely difficult (*e.g.*, Torres Strait or Shark Bay). On a pre-determined release date, these tags transmit archived data to satellites. The data are then retrieved via the Argos network (*e.g.*, Merrick *et al.* 1994; Myers *et al.* 2006). These tags can be attached to dugongs in a similar fashion to archival TDRs. Commercially available pop-up tags are currently highly priced (*e.g.*, ~US$4,000 for a MiniPAT, Wildlife Computers). MiniPATs were experimentally deployed by the JCU Dugong team on two dugongs in Moreton Bay between in April 2014 and these tags stayed on the animals for two months as programmed. The rates of successful data recovery from the two units varied from 18% to 75% (unpublished data). The reason for these differences in recovery rates is unknown. With technological improvements and subsequent drops in price, this type of unit will become more useful and accessible and will enable more data to be collected on dugong diving behaviour in diverse environments such as Torres Strait, arguably the most important dugong habitat in the world (Marsh 2011b).

Drones, or unmanned aerial vehicles (UAV) may be the future of dugong aerial surveys. Drones are now widely used in marketing (*e.g.*, real estate), hazard detection (*e.g.*, wild fire), crime prevention and detection (*e.g.*, trespassing, illegal logging), agricultural planning (Zhang and Kovacs 2012), and conservation (*e.g.*, Koh and Wich 2012). Drones provide geo-referenced images and are being used in wildlife surveys including dugong surveys (Jones *et al.* 2006; Koski *et al.* 2009; Sardà-Palomera *et al.* 2012; Hodgson *et al.* 2013). Compared to manned aerial surveys, unmanned surveys using drones have considerable advantages: eliminating observer risk and lowering survey costs and ecological footprints (Martin *et al.* 2012; Hodgson *et al.* 2013). Hodgson *et al.* (2013) successfully tested the capacity of drones to assess dugong habitat use and population status. The images taken by Hodgson *et al.* (2013) captured dugongs, as well as whales, dolphins, and turtles. The use of UAV will solve the challenge of perception bias and improve the data on animal sighting location as images are geo-referenced. If abundance is estimated in a similar way to Marsh and Sinclair (1989b) and Pollock *et al.* (2004), sightings will still have to be corrected for availability bias. My research on the environmental factors influencing the availability of dugongs to aerial observations can be extended and modified for drone application.

7.4 Concluding remarks

My research made major methodological contributions to study the diving ecology of shallow diving wildlife and techniques to estimate their abundance. My research on dugong abundance and habitat use has immediate application to dugong conservation and has the potential to be applied to shallow diving aquatic biota more generically.

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List of Appendices

Appendix 2.1 Protocol for capturing and handling dugongs

The following protocol was developed and refined by Marsh and Rathbun (1990), Lanyon *et al.* (2006), Sheppard *et al.* (2006), and others such as Dr. Nick Gales, Dr. Ivan Lawler, and Mr. Dave Holley (unpublished account). Protocol of health assessment during pursuit, capture, handling, and release follows Flint (2013). A veterinarian or a senior biologist needs to be attendant throughout the capturing and handling processes to minimize the risks on and ameliorate or resuscitate affected animals (Flint 2013).

Equipment and personnel

Two vessels are employed: one as a catcher boat (primary), and another as a support boat (secondary). The primary boat needs to be light in weight to facilitate rapid manoeuvrability but needs to have enough motor power to enable the vessel to travel at speeds of up to 20 knots. The minimum number of personnel for the primary and the secondary boats for the rodeo technique is seven people:

Primary boat:

1. A driver
2. A primary catcher
3. Two dugong handlers
4. A monitor

Secondary boat:

1. A driver
2. A data recorder/equipment handler
3. An extra dugong handler

The catcher and two handlers need to be padded with a helmet and vest for protection.

Pursuit, capture, handling, and release

Phase 1: Pursuit

A candidate dugong is assessed based on the following criteria:

- Proximity to shallows – shallow water which provides a secure platform for dugong catchers to anchor down

- Composition – a lone animal or an individual on the edge of a herd without an attendant calf
- Life stage – adult in an apparent good condition. Quick external health assessment include:
    - No apparent skin conditions (*e.g.*, lesions, sloughing, hyperkeratosis)
    - No loss of soft tissue mass (adipose tissue) around the peduncle and neck, without prominent vertebral column
    - No abnormal behaviour (*e.g.*, accelerated respiration rate)

Once a target dugong is selected, the animal is approached at low speed. When a primary boat is within 50–100 m range, a chase is initiated with rapid acceleration. A monitor records the onset of chase time and starts counting frequency of breathing. The support team remains at a distance (*e.g.*, 100 m) on the deep water side of the primary boat.

The driver of the catch boat keeps the dugong just in front of it but slightly off to the side. This positioning allows catchers to dive forward and land on the dugong's tail, and also prevents collision with the target dugong when it comes up for a breath. The dugong's swim speed slows down when it surfaces to breath. Pursuit is terminated after 10 min. If the animal shows quick succession of surfacing, the chase is also abandoned.

Phase 2: Capture

A capture is initiated after a breath is taken by the dugong. The primary catcher first jumps over the dugong's tail, followed by the other two handlers. The primary catcher holds the tail downwards by pressing it against the chest of the catcher. In this way, the dugong's tail is prevented from making propulsive down strokes, which assists in flight and is dangerous to the catcher. The two catchers assist in straining the dugong, and ensure that the animal is kept in proximity of the surface for easy uptakes of air. A monitor keeps track of breathing. The support boat approaches the dugong and drifts in the area. A person from the support boat may enter the water for further assistance of handling.

Phase 3: Handling

When the dugong is securely detained, the catcher boat approaches the dugong and passes a long float (a swimming pool “noodle”, ~ 1.5 m long) to a handler, who wraps the float underneath the dugong’s axillae. The float is securely held by a person from the catcher boat. The float facilitates the dugong’s breathing and stops the animal from spinning during capture.

One of the handlers collects information on the dugong: body length, girth, sex, and presence or absence of an erupted tusk, which were recorded by a monitor. Another handler securely attaches a tracking apparatus onto the peduncle.

Throughout the handling stage, state of a restrained dugong is continuously monitored. The monitoring criteria are shown as below:

- Respiration rates – allowable rates are between 1–15 breaths every two minutes
- Abnormal behaviour – muscle tremor, squealing, frequent rolling, curling up, or a sign of lethargy

The dugong is held for no more than 6 min.

Phase 4: Release

Upon the release, the noodle float is released first and the tail after, enabling the animal to break free under its own speed. A deployed dugong should be monitored whether the animal was swimming normally. If there are signs of compromise, the animal should be followed at a safe distance and recaptured for veterinary care on water or land if further intervention is required. The assessment criteria include:

- Loss of consciousness
- Loss of ability to swim away
- Signs of trauma caused by capture and handling

Appendix 4.1 Specifications of the algorithms used to quantify the relative importance of terms using *MuMIn* and *glmulti*

MuMIn

```
dive.glm <- glm(propBottom ~ dt + dr + dp + bt + bd.dt + md + at +  ar + assym,
                family=binomial(link="logit"), data = dives)
```

Where,

dtCat = descent time, *dr* = descent rate, *dp* = descent time proportion,
bd.dt = bottom distance divided by bottom time, *md* = maximum depth,
at = ascent time, *ar* = ascent rate, *assym* = ascent distance divided by descent distance

```
# compare all possible combination of single terms
dredgeA <- dredge(diveA)
```

```
# get the best models within 95% confidence set
confA <- get.models(dredge, cumsum(weight) <= 0.95)
```

```
# average the best models
avgA <- model.avg(confA)
```

```
# relative variable importance given in the summary outputs
summary(avgA)
```

glmulti

\# compare all possible combination of single terms

dive.glmulti <- glmulti(dive.glm, level = 1, method = “h”, crit = "aicc")

Where,

level = 1 used only main effects, *method* = “*h*” for an exhaustive method, exploring all possible combinations of terms, *crit* specified a type of information criterion.
“*aicc”* represents Akaike Information Criterion, corrected (AICc),

\# *glmulti* function plots the best 100 models (default) and identify models that are similarly good

\# repeat the above glmulti function, but this time specify the confidence set identified above

dive.glmulti2 <- glmulti(dive.glm, level = 1, method = “h”, crit = "aicc", confsetsize = 2)

Where,

confsetsize determines the number of models to be looked for (*i.e*. the size of the returned confidence set).

\# plot relative importance

plot(dive.glmulti2, type = "s")

Appendix 4.2 Analysis of deviance table for: A) mid-water and seafloor dives, and B) seafloor dives in areas where seagrass is present and absent.

A)	Df	Deviance	Residual Df	Residual Dev.	Significance
Null			3289	5587.68	
Ascent rate/descent rate	3	334.76	3286	5252.92	*
Asymmetry	2	37.00	3284	5215.92	*
Ascent rate	3	1311.63	3281	3904.29	*
Ascent time	3	24.02	3278	3880.27	*
Max. dive depth	3	18.59	3275	3861.68	*
Vertical displacement	2	90.85	3273	3770.82	*
Bottom time	3	38.47	3270	3732.35	*
Descent rate	3	33.43	3267	3698.92	*
B)	**Df**	**Deviance**	**Residual Df**	**Residual Dev.**	**Significance**
Null			381	503.19	
Descent rate	3	9.99	378	493.21	*
Ascent rate/descent rate	2	5.73	375	487.48	
Asymmetry	3	6.40	373	481.08	*
Max. dive depth	3	2.31	370	478.77	
Ascent rate	3	9.28	367	469.48	*
Ascent time	3	4.78	364	464.71	*
Bottom time	3	2.37	361	462.34	
Descent time	3	1.46	358	460.88	*

*Significant with at least P<0.01

The deviances of some dive parameter that were not significant (*e.g.*, ascent rate/descent rate) are larger than the ones from dive parameters that are significant (*e.g.*, descent time). As each dive parameter was added sequentially to the model, parameters added later can have smaller deviance and be insignificant. Thus the order of these parameters was changed several times to ensure significant levels of each parameter, and the significance does not necessarily correspond to the deviance shown in the table.

Appendix 4.3 Mean, median, and standard error of: A) seafloor dives with and without seagrass, and B) mid-water dives.

	Mid-water dives			Seafloor dives					
				Seagrass			No seagrass		
	mean	median	se	mean	median	se	mean	median	se
Descent time (s)	41.35	28.50	0.86	23.14	13.50	1.44	29.13	23.50	1.63
Descent rate (m/s)	0.13	0.12	0.002	0.24	0.24	0.01	0.15	0.14	0.01
Bottom time (s)	59.75	42.00	1.26	69.91	70.00	2.51	64.86	52.00	4.16
Bottom distance divided by bottom time	0.35	0.33	0.002	0.30	0.28	0.005	0.33	0.31	0.01
Maximum depth (m)	4.24	3.50	0.04	3.57	3.50	0.03	3.71	3.50	0.06
Ascent time (s)	47.91	37.50	0.77	11.07	9.50	0.48	27.58	22.50	1.94
Ascent rate (m/s)	0.10	0.09	0.001	0.36	0.33	0.01	0.25	0.15	0.03
Asymmetry	1.00	1.00	0.002	1.00	1.00	0.01	0.94	1.00	0.02
Ascent rate divided by descent rate	1.11	0.77	0.03	2.36	1.48	0.12	2.28	1.00	0.28

Appendix 5.1 Specifications of generalized linear mixed models (GLMMs) using Gaussian Hermit Quadrature estimation

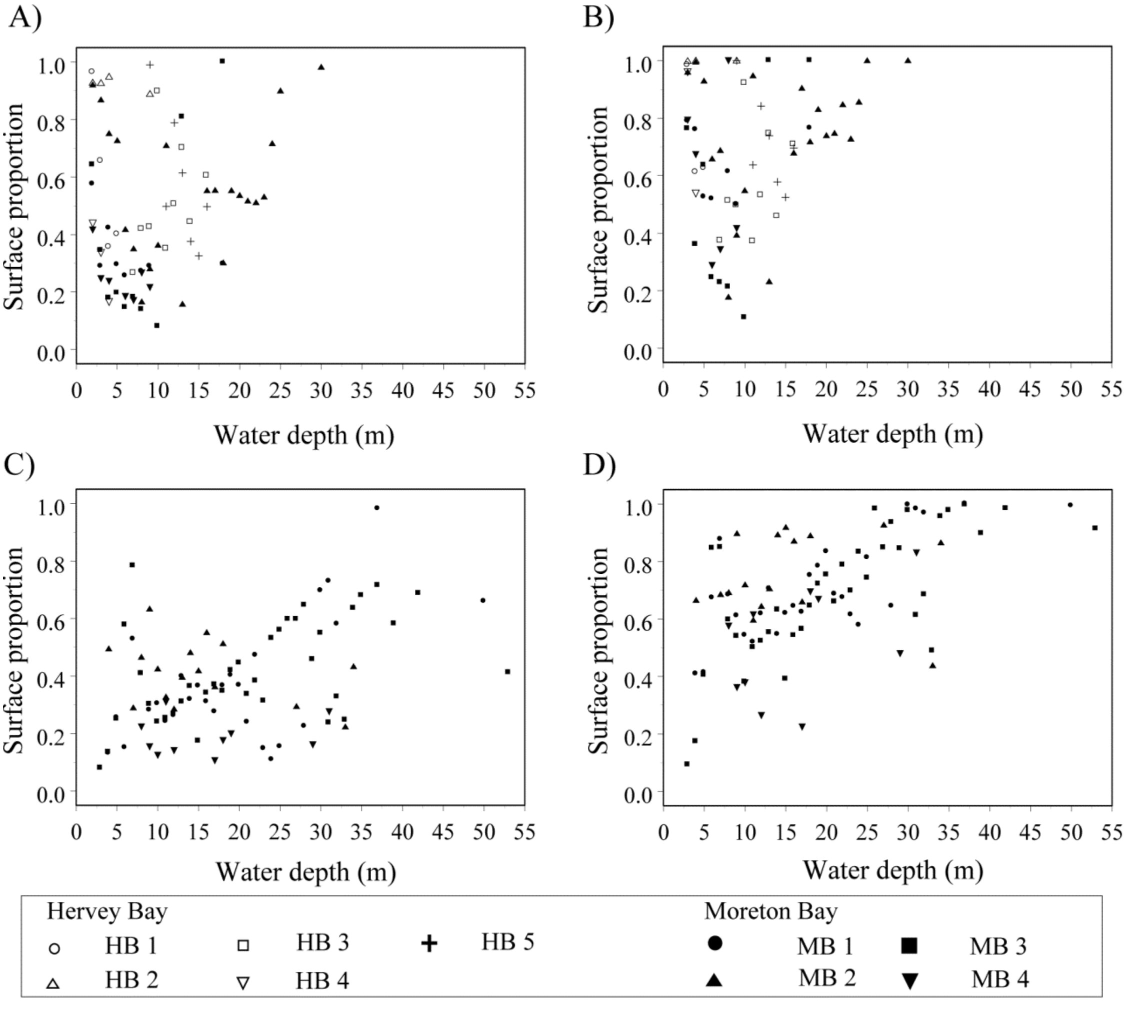
```
>surface proportion1.5 <- lmer(surface1.5 ~ water depth +  (1|animal) ,
family=binomial, data=surfaceA, weights=N/600, nAGQ = 100)
```

and

```
>surface proportion2.5 <- lmer(surface2.5 ~ water depth * habitat + (1|animal),
family=binomial, data=surfaceB, weights=N/600, nAGQ = 100)
```

The response variables are indicated as surface1.5 or surface2.5. The explanatory variables are water depth and habitat. The asterisk (*) represents the explanatory variables of a single effect from water depth and habitat and the interaction between the two. (1|animal) represents the animal treated as a random factor. Binomial link is specified using family, and weight is applied using N, which represents the number of sampling units. I treated 10 min as a sampling unit by dividing the number of depth records (N) by 600 (10 min as depth was recorded every 1 s). The nAGQ refers to the number of quadrature points and 100 represent Gaussian Hermit Quadrature approximation.

Appendix 5.2 Proportions of time dugongs spent in the detection zones over inshore waters (A: 0–1.5 m; B: 0–2.5 m) and in offshore waters (C: 0–1.5 m; D: 0–2.5 m). Each symbol represents individual animal.



Appendix 6.1 Estimates of dugong population abundance in A) Moreton Bay, B) Hervey Bay and C) Torres Strait using constant (Pollock *et al.* 2006) and depth-specific availability corrections.

Block	**Estimated dugong abundance (se)**	
	Constant corrections	**Depth-specific corrections**
A) Moreton Bay, November 2011		
Block 1	tfe	tfe
Block 2	tfe	tfe
Block 3	tfe	tfe
Block 4*	569 (87)	547 (81)
Block 5	tfe	tfe
Block 6	131 (65)	140 (65)
Total	*700 (109)*	*687 (104)*
B) Hervey Bay, November 2011		
Block 1	397 (152)	354 (139)
Block 2**	1363(533)	887 (407)
Block 3	148 (92)	98 (68)
Block 4	121 (114)	70 (74)
Total	*2029 (573)*	*1409 (442)*

*Three herds were censused (44, 117 and 170 dugongs, respectively)

**a herd of 25 dugongs was censused

***a herd of 20 dugongs was censused

'tfe' indicates too few sightings to estimate abundance; dugong sightings were <5.

Block	**Estimated dugong abundance (se)**	
	Constant corrections	**Depth-specific corrections**
C) Torres Strait, March 2011		
Block 0	578 (404)	702 (461)
Block 1A	467 (206)	566 (272)
Block 1B	1573 (775)	1789 (843)
Block 2A***	5234 (1514)	6950 (1711)
Block 2B	1117 (359)	1429 (419)
Block 3	2083 (862)	2831 (1043)
Block 4-5	297 (222)	371 (258)
Block 6	tfe	tfe
Block 7	tfe	tfe
Block 8	778 (386)	857 (375)
Block 9	497 (396)	662 (470)
Total	*12604 (2170)*	*16157 (2370)*

*Three herds were censused (44, 117 and 170 dugongs, respectively)

**a herd of 25 dugongs was censused

***a herd of 20 dugongs was censused

'tfe' indicates too few sightings to estimate abundance; dugong sightings were <5.